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The Skull of *Neoceratodus forsteri*: A Study in Phylogeny.

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INTRODUCTION AND ACKNOWLEDGMENT.

Recent work on the development of the Dipnoi, ganoids, and amphibians, and the increase of our knowledge of the constitution of the stegocephalian and cotylosaurian skulls, throw much light on the interpretation and significance of the structure of the adult skull of *Neoceratodus*. That this was so very soon became apparent to me whilst engaged upon a general survey of the skull of *Neoceratodus* in connection with a paper on the evolution of the Anamniota[1] and it was then decided to investigate the matter in more detail at a later date.

In the following pages I have recorded the observations made and the conclusions arrived at after comparing the various structures with those of the fishes and primitive tetrapods. This work has been made possible by the kindness of Dr. Thos. L. Bancroft, of Eidsvold, Queensland, who forwarded me three adult heads carefully preserved in alcohol; to him my thanks are tendered.

From one of these heads I have been fortunate in preparing a chondrocranium in a perfect state of preservation, denuded of every last scrap of tissue and of the investing bones, the latter being, of course, available for study as separate disarticulated bones. This was effected by over two years' careful maceration in alternating changes of calcium hypochlorite solution and water. Another of the skulls was dissected with a view to studying the relation of the nerves and more important blood vessels to the cranium. The third was divided along the sagittal plane; one-half was dissected to expose the bones in situ, the other was more rapidly macerated with a view to determining the extent and relations of the subnasal and labial cartilages. I failed to find the labial cartilages, and have reason to believe that the structures so named are fibro-cartilaginous, as are the subnarial cartilages, and, like them, devoid of serial homological significance.

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[1] Kesteven.—REC. AUSTR. MUS., xviii, 1931, pp. 167-200.

<div align="center">PART I.</div>

THE CHONDROCRANIUM AND ITS BEARING ON THE PROBLEM OF THE ORIGIN OF THE
TETRAPODS AND OF THE DIPNOI.

<div align="center">A. DESCRIPTION OF THE CHONDROCRANIUM.</div>

The general shape of the chondrocranium is well shown in Figures 1–4.

The cranial cavity is rather narrower than might be expected on viewing
the complete structure. Its widest part is in the region of the otocrane, about
half way between the pituitary fenestra and the posterior end of the specimen
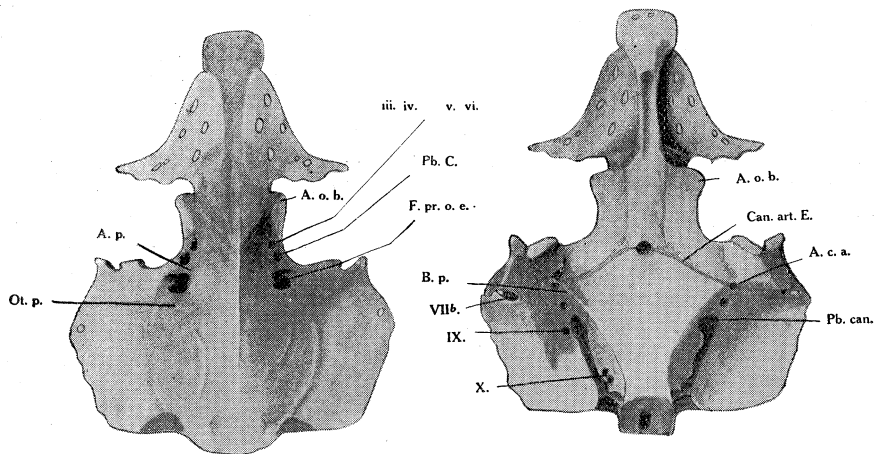

Fig. 1.—Dorsal aspect of the Chondrocranium of *Neoceratodus*.
Fig. 2.—Ventral aspect of the Chondrocranium of *Neoceratodus*.

figured. It is here a little less than one-half the width of the flattened area of
the basis cranii covered by the parasphenoid bone. It extends forward as far
as the antorbital buttress. The form and position of the otocrane and trigemino-
facial fossa are very similar to the piscine condition.

The great width of the posterior portion of the cranium is due to the very
solid and widely attached quadrates and the expansive arched sheet of cartilage
that, attached along the outer and upper edge of the quadrate and its otic root,
extends backward to roof over the gills, and is attached to the outer and upper
part of the otocrane and cranium behind it. The line of attachment to the
otocrane and cranium is tunnelled by a canal (sensory canal), which commences
in front at the foramen prooticum externum and opens behind above the foramen X.
This canal is plainly seen through the cartilage and is indicated in the drawing.

In front of the anterior root of the quadrate the cranium is markedly con-
stricted at the orbit; this is bounded anteriorly by an anorbital buttress, which
is stouter and more pronounced below, where it overlies the outer portion of the
palatine component of the pterygo-palatine bone.

In the region of the orbit the cranium is triangular in cross section, the base
of the triangle being the base of the cranium.

In front of the antorbital buttress the cranium becomes quadrilateral in cross
section and the cranial cavity gives place to the two olfactory passages, separated

by the mesethmoid cartilage. The roofing sheet of cartilage here is almost horizontal, and it extends further forward than the floor of the olfactory passages. Above the olfactory passages this ethmoidal roofing cartilage is obliquely truncated on each side, and is then continued forward much narrowed to just in front of the situation of the posterior boundary of the anterior narial apertures, when it is again expanded and then abruptly truncated. The nasal septum is deepest behind, between the openings of the olfactory passages, and gradually diminishes in depth as it passes forward, but presents a slight abrupt increase in depth immediately in front of the palatine symphysis. Anteriorly the cranium terminates in a horizontal prenarial spatulate sheet of cartilage with two small fenestræ near the margin, one on either side of the mid-line.

The tectum nasi is a very thin irregularly fenestrated sheet of cartilage, attached as shown to the lateral edge of the expanded upper edge of the nasal septum and to the obliquely truncated anterior margin of the mesethmoidal roofing cartilage. Its general shape is indicated in the drawing.

There is no trace of any solum nasi. At first it was thought that perhaps the arcuate subnarial cartilage lying behind and curving round the outer margin of the posterior narial aperture might represent a primitive solum nasi, but this is a fibro-cartilaginous structure and is attached, not to the chondrocranium, but to the fibrous mass that invests the ascending process of the palatine and descending process of the dermal ectethmoid. Both its structure and attachment would seem, then, to contra-indicate any such interpretation of the subnarial cartilage.

The three primitive roots of the quadrate are readily recognizable. The ascending process, or anterior root, lies in front of the large canal from the trigemino-facial fossa, and above that for the hyomandibular trunk of nerve VII.
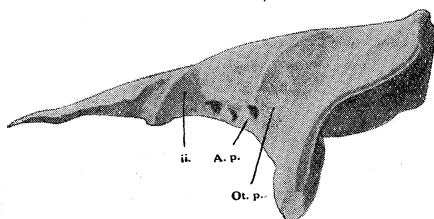

Fig. 3.—Lateral aspect of the Chondrocranium of *Neoceratodus*.

The otic process, posterior superior root, is placed above and behind the former of these two canals, and is separated from the basal process, posterior inferior root, below it by a large branch of the parabasal canal. The anterior portion of the parabasal canal, which transmits the ophthalmic artery, lies between the basal and ascending processes. Immediately in front and to the inner side of the anterior aperture of this last canal there is a flange of cartilage which connects the basal process with the mesethmoid region of the cranium below the exit of nerve V[1]. This little flange was regarded by Bridge[2] as "representing the palatopterygoid cartilage." This, however, it cannot be, as indicated by the development of the quadrate (*vide* Edgeworth[3] and Greil[4]).

[2] Bridge.—Trans. Zool. Soc., Lond., xiv, 1898, p. 352.
[3] Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.
[4] Greil.—*In* Semon's Zoolog. Forschungsr. Austr. Malay. Archipel., i, 6, 1908, pp. 661-934.

The whole of the area on the base of the cranium covered by the parasphenoid and pterygo-palatine bones is level, except for a shallow sulcus, slightly deeper in front, for the reception of the palatine symphysis.   Viewed from below the
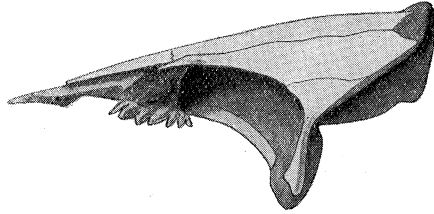

Fig. 4.—The same as Fig. 3, but with the major bones in place.

antorbital buttress stands out prominently where it lies above the palatine bone, and just in front of this the oblique inferior margin of the anterior aperture of the olfactory canal is visible.

Describing teleostean skulls, I have recognized occipital mesotic, preotic and prepituitary segments of the cranial floor.[5]   These same segments are recognizable in the floor of chondrocranium of *Neoceratodus*, but one notes at once the much greater extent of the prepituitary segment, correlated, of course, with the greater development of the prosencephalon.   As in the teleostean skull, the mesotic segment is largely wanting, owing to the encroachment of the cava sacculi.   Except for the greater extent of the preotic area, there is also a marked similarity in the side wall to that of the teleostean skull.   There is no outstanding ridge dividing the trigemino-facialis fossa from the lateral cranial fenestra, as these two are divided by bone in the bony crania, and the cranial temporal fossa has the outer wall nearer the mid-line than the outer wall of the ganglionic fossa, instead of further from it, as in the majority of the bony fishes.

The resemblance to the teleostean arrangement extends to the otocrane.   The posterior ampullary recess, the meeting place of posterior and horizontal semi-circular canals, lies to the outer side of the fore end of the postotic portion.of the side wall of the cranium.   The anterior ampullary recess is confluent with a large fossa utriculi, which in turn is not separated from an arcuate fossa, there being none such formed.   In the teleostean skull, it will be remembered, the anterior semicircular canal, not enclosed in a bony canal, lies among the loose connective tissue mesial to and slightly behind the arcuate fossa, whilst the utriculus is packed in the same tissue behind and below it.   In *Neoceratodus* a large cavum utriculi is formed between the basal and otic roots of the quadrate, with the ascending root in front.   The anterior vertical semicircular canal tunnels the cartilage of the roof of this cave and opens into it against the anterior wall.   Immediately to the inner side of this opening is a ridge of cartilage which strongly recalls the anterior boundary of the arcuate fossa of the teleosts, and would seem to support a suggestion previously made, that the arcuate fossa, though not now accommodating the anterior vertical canal, was developed in relation to it (Kesteven, *loc. cit.*, p. 205).

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[5] Kesteven.—REC. AUSTR. MUS., xv, 1926, p. 203.

The two vertical semicircular canals lie just beneath the cartilage in the roof of the otocrane, and are visible through it. The horizontal canal lies at a lower level, lateral to the base of the triangle whose sides are the other two canals. By transmitted light this canal may be seen below and mesial to the sensory canal. The two vertical canals meet and open together in the roof of the otocrane in front of the posterior ampullary fossa.

The large cava sacculi lie mesial to the cava utriculi and at a lower level, encroaching on the cranial floor, just as so often occurs in the teleostean skull.

The Foramina and Canals in the Chondrocranium.

The large olfactory passages leave the fore end of the cranial cavity on either side of the vertical plate of the ethmoid cartilage, which, further forward, is uninterruptedly continuous with the nasal septum. This canal accommodates the olfactory lobes; its floor is slightly elevated above that of the fossa, whereon lie the lobes of the prosencephalon. At the anterior end of this fossa there is a little pit that apparently lodged a venous sinus of some size. I find that a groove leads from each of these little venous (?) fossæ mediad, to the posterior aperture of a canal which runs forward through the vertical plate of the ethmoid, and then divides into right and left branches, which open below the inner limit of the anterior margin of the floor of the olfactory passage. There are also two canals passing direct from the little fossa to this same anterior opening. This is the condition on the right side of the specimen; on the left the three canals have separate apertures close to one another along the margin.

The optic foramen lies at the angle between wall and floor of the prosencephalic fossa about the middle of the antero-posterior length thereof. A groove, which lodged the optic artery, leads back and mediad from this foramen to the internal aperture of the canal for the cerebral artery at the side of the pituitary fossa.

In the roof of the cranium directly above the optic foramen there is a fossa from which canals pass out right and left to open on the antorbital buttress just below where this merges into the horizontal roofing plate of the ethmoid cartilage.

The oculomotorius foramen is at the level of and just in front of the post-pituitary eminence.

I have been unable to detect any separate aperture for the exit of the fourth nerve.

A separate abducent canal is apparently present. In *Lepidosiren*, Bridge[6] describes the course of the superior palatine branch of the facial nerve, and on plate 28 in figure 6, he illustrates the inner aperture of the canal along which it passes, whilst in figure 3 he indicates the external aperture. Now in *Neoceratodus* I find the internal aperture of a canal (whose external aperture is placed just within the rim of the external foramen for the first branch of the fifth nerve) in just the position of the internal aperture of the canal for the palatine branch of the facial nerve illustrated by Bridge.

Notwithstanding the description of Bridge, I am of the opinion that we have here the abducent canal. To this conclusion I am forced by the facts that this canal reproduces with remarkable approximation the position of abducent the canal

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[6] Bridge.—Trans. Zool. Soc., xiv, 1898, p. 348.

not only in *Amia* (Allis[7]) and most teleosts (*cf. Scomber*, Allis[8]), but also in the reptiles (Kesteven[9]) and some amphibians, *e.g., Siren* (H. W. Norris[10]). In some elasmobranchs the nerve takes a similar course to the orbit (*cf. Squalus*, Norris and Hughes[11]). When to these facts is added that this canal opens, not upon the base of the cranium, but on to the orbit, it would appear only reasonable to regard it as the abducent canal.

The trigemino-facialis fossa presents three apertures in its outer wall. Of these the first two open externally, one in front of and the other behind the ascending process of the quadrate, and, exactly as in the Amphibia, the former transmits the first branch of the trigeminal nerve, and the latter (foramen prooticum internum) the second and third branch of this nerve as well as buccal and ophthalmic branches and lateralis branch of the facial nerve. The third canal passes out and backward between the otic and basal roots of the quadrate and transmits the truncus hyomandibularis of the facial nerve.

The glossopharyngeus foramen perforates the side wall of the cranium just below the posterior ampullary fossa and appears externally on the side of the cranium lateral to the anterior end of the parabasal sulcus.

The vagus foramen is situated somewhat higher and a little further back than the last. This canal divides very soon into two. One branch, doubtless carrying the lateral line components of the nerve, turns dorsad and communicates by a groove on the back of the cranium with the posterior aperture of the lateral line canal. The other and larger branch passes out and ventrad as well as backward, becoming wider as it extends; it has two apertures placed close together below the hinder end of the parabasal sulcus. Bridge[12] states that in *Lepidosiren* the anterior cardinal vein emerges from the cranial cavity through this foramen. I believe that in *Neoceratodus* the vein which he thus designates leaves the cavity through a canal placed below and behind the vagus canal.

Turning now to the outside of the cranium, the optic foramen is found just behind the antorbital buttress. At the back of the orbit, at the junction of inner and posterior walls, and just above that little flange of cartilage which Bridge regarded as representing the palato-pterygoid, there is the common orifice of the oculomotorius and canal for the first branch of the fifth nerve. Immediately outside this is the tiny orifice of the abducent canal, and below it the opening of a communication with the parabasal canal. Lateral to these again is that anterior aperture of the parabasal canal which has been described as transmitting the ophthalmic artery. Above this last is the large aperture of the canal for the main mass of the nerves originating in the trigemino-facial ganglion, foramen prooticum externum. The external aperture of the canal for the truncus hyomandibularis facialis is placed above the body of the quadrate.

The jugular vein* and posterior carotid artery have impressed their track along the underside of the cranium in the form of a deep sulcus, which is situated below the external apertures of the ninth and tenth nerves, and which is continued forward as a closed canal between the basal process and ascending

[7] Allis.—Journ. Morph., xii, 1897, p. 517.
[8] Allis.—Journ. Morph., xviii, 1903, p. 237.
[9] Kesteven.—Journ. Anat., lii, 1918, p. 458.
[10] Norris.—Journ. Morph., xxiv, 1913, p. 262.
[11] Norris and Hughes.—Journ. Comp. Neurol., xxxi, 1920, p. 313.
[12] Bridge.—Trans. Zool. Soc., xiv, 1898, p. 350.
* This is the "vena capitis" and "vena capitis lateralis" of Greil, Edgeworth, and Allis.

and otic processes of the quadrate; the resemblance which this canal and its contents bear to the conditions in the birds and reptiles leads one naturally to designate it parabasal canal (*vide* Kesteven[13]), and the sulcus may likewise be designated parabasal sulcus. The situation of the anterior opening of the canal has already been described. Besides the superior jugular vein, the sulcus and canal also carry the posterior carotid artery. Inside the canal the artery divides into its terminal cerebral and palatine arteries just as in the reptiles. The cerebral artery turns mediad through its own canal to enter the side wall of the pituitary fossa once more as in the reptiles, and, also with the same similitude, the palatine artery is continued forward immediately above the parasphenoid. There is, however, a larger terminal branch of the parabasal canal which runs straight forward to the anterior aperture already mentioned, and transmits a branch which may be termed the ophthalmic artery, and an equally large branch inclines dorsally to open into the foramen prooticum externum, transmitting orbital artery and vein. The anterior carotid is accommodated in a canal which runs parallel to, but below, that for the hyomandibular branch of the facial nerve. This canal communicates with the parabasal close to the departure of the canal for the cerebral artery, and there is probably an arterial anastomosis in this situation. Spencer's work[14] on the blood vessels of *Ceratodus* has been largely followed in this connection. Besides the larger branch above mentioned, there is a second much smaller communicating canal between the parabasal and the foramen prooticum externum. Just where the canal for the cerebral artery leaves that for the palatine there is a small communicating branch, which passes forward slightly laterad and dorsad to open just outside the common aperture of the canals for nerves III, IV, and V1, and just behind this a short passage connects with the canal for the truncus hyomandibularis nervi facialis directly above it. This last appears just within the nerve canal as viewed from within the cranial cavity, and it is *more* than probable that we have here the canal for the palatine branch of the facial nerve which Bridge describes; its cranial opening is placed just lateral to the internal foramen for the abducent nerve. It is particularly interesting to compare the situation and contents of the fore part of the parabasal canal with the same structures in the reptiles. In both cases the carotid artery is joined, just before it branches, by the palatine branch of the facial nerve, which tunnels the side wall of the cranium to reach it, and after giving off the cerebral artery the terminal (palatine) branch of the vessel continues forward accompanied by the nerve, imbedded in the basis cranii. In the case of *Neoceratodus* the hinder part of the parabasal canal carries also the external jugular vein or a tributary thereof; this leaves the artery where that makes a slight bend mediad before giving off the cerebral artery, and continues straight forward.

Though it has not been possible to trace the nerves in question, there seems little doubt that the lateral line sensory canal which tunnels the attachment of the suprabranchial cartilaginous roof, carries the ramus lateralis accessorius, and that the facialis fibres of the nerve enter the canal from the foramen prooticum externum, whilst the vagus components enter from the back of the canal along the groove above mentioned as leading from the dorsal branch of the vagus canal

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[13] Kesteven.—Journ. Proc. Roy. Soc. N.S.W., lix, 1925, pp. 108-123.
[14] Spencer.—Linnean Society of N. S. Wales, Macleay Memorial Volume, 1893, pp. 1-34.

to the hinder end of the sensory canal. There are a number of perforations in the roof of the sensory canal along its length. Bridge makes no mention of this canal in *Lepidosiren*, but the "schlafengrube" of Hyrtle is its posterior opening. The lateralis fibres of the vagus reach it through the perforation which leads from it to the under side of the cranium.

B. COMPARATIVE REVIEW AND PHYLOGENY.

The "elasmobranch" completeness of this chondrocranium would make the identification of certain areas and their comparison with the structures of other crania a difficult problem, were it not that in the other two recent Dipnoi the cranium is incomplete. Comparison of *Neoceratodus* with these enables us to arrive at a correct understanding of its parts. This understanding is further assisted by the consideration of the early stages in the development of all three chondrocrania.

Comparison of the cranium in its entirety can only be made with the chondrocrania of the Amphibia, although it presents resemblances in particular areas to those of the fishes and reptiles.

If the chondrocranium of *Lepidosiren* or *Protopterus* be compared with that of one of the urodeles (*e.g.*, *Triton*), it will be found that, part for part, there is a very close resemblance as far forward as the planum internasale, except for the large lateral cranial fenestra, the large cava sacculi, the absence of external apertures to the otocrane, and the separate exit of the ninth nerve. In these features the dipnoan crania resemble those of the fishes.

In the urodeles, as the planum internasale is approached, the trabecular crest is rapidly reduced in height, and from here forward the trabeculæ are flattened in the horizontal plane; beyond the "planum" they separate again and are continued forward, the trabecular cornua forming the outer angle of the front margin of the solum nasi. In the fishes also it would appear that always the trabecular cornua lie below the nasal sacs.

In early stages in the two Dipnoi, on the other hand, the trabecular crest continues undiminished in height for a little distance forward of the posterior margin of the planum internasale, and then gives off antorbital processes. The "planum" itself is tilted dorsad so that its anterior margin is actually higher than the dorsal margin of the trabecular crest. For a short interval it appears that the crests become separated and are then reunited *above* the nasal sacs; from the resulting median strip of cartilage the internasal septum hangs down. To either side of this cartilage the fenestrated tectum nasi is attached. Bridge[15] has identified two spurs at the anterior margin of this tectum as "trabecular cornua," and he compares them with the trabecular cornua of *Bufo* as described by Parker. But the trabecular cornua of the anurous amphibians, like those of the urodeles, lie below the nasal sacs, not above them.

The origin of the antorbital process from the trabecular crest in *Protopterus* was noted by Winslow[16] as a feature wherein it differed from all other forms studied by him.

In a number of the Urodela and Anura, if not in all, from the front margin of the planum internasale or mesethmoid plate there rise two cartilaginous plates,

[15] Bridge.—Trans. Zool. Soc., xiv, 1898, p. 340.
[16] Winslow.—Tuft's College Studies, 5, 1898, p. 192.

which may or may not extend forward along the inner margin of the trabeculæ in front of the "planum." These, with further growth, give rise to the tectum nasi and the upper part of the lateral wall. The prominent posterior part of this wall was termed the "lamina cribrosa" by Winslow (*loc. cit.*) and the "planum antorbitale" by Gaupp.[17]

On comparing these structures with those anterior to the ethmoid plate in *Lepidosiren* and *Protopterus*, one is compelled to conclude that they are homologous, and that the antorbital process of these forms is really a modified planum antorbitale.

Since there is no trace of any solum nasi in *Neoceratodus*, it appears that in the recent Dipnoi the whole of the structures developed in other vertebrata directly from the trabeculæ in front of the planum internasale below the nasal sacs are not represented.

There can be no doubt that, in all its parts, the quadrate of the Dipnoi is completely homologous with that of the Amphibia; to this conclusion we are forced by the relation of the three points of attachment to the areas of the cranium, and to the branches of the fifth and seventh nerves. The ascending process is attached to the trabecular portion of the cranium between the first branch of the fifth, and second and third branches, and the buccal and ophthalmic branches of the seventh. The otic process is attached to the otocrane laterally and anteriorly, behind the last nerves and above the hyomandibular branch of the seventh. The basal process is attached to the anterior end of the parachordal region of the skull basal plate, and is crossed superiorly by the last nerve mentioned.

With the single exception of *Ichthyophis* (Edgeworth[18]), these relations are maintained throughout the whole of the Amphibia and, if the epipterygoid of the reptile be the ascending process of the Amphibia, throughout the Reptilia as well. Relationships persistent through two whole classes must surely be of fundamental phylogenetic significance, and may confidently be made use of for the purposes of studying the autostylism of those few elasmobranchs and bony fishes which present the feature. The autostylism referred to is that of the hinder quadrate end of the subocular arch, not the anterior attachment to the planum ethmoidale, or a process thereof.

As far as I have been able to ascertain, autostylism among the bony fishes is confined to the Mormyridæ, but before proceeding to the examination of its form in these fish it were well to note and consider a statement by Edgeworth[19] that the Dipnoi are more primitive than the Amphibia in the more anterior attachment of the basal process of the quadrate.

This statement is fairly certainly based on the observation of Agar[20] that the basal process of *Protopterus* is attached to the trabecular, and his own many observations that in the Amphibia the attachment is to the basal plate or floor of the otic capsule.

Now Agar's identification of the trabecular, as distinct from the parachordal region of the chondrocranium, is clearly based upon the relation to the fore end

    [17] Gaupp.—*In* Hertwig's Handbuch der vergleichend. u. experim. Entwicklungslehre, iii, Jena, 1905.
    [18] Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.
    [19] Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264; *loc. cit.*, lx, 1926, pp. 298-308.
    [20] Agar.—Trans. Roy. Soc. Edinb., xlv, 1906, pp. 49-64.

of the notochord.   Such a standard of identification is, of course, not open to objection, but it is an arbitrary one.   Conclusions as to what is or is not primitive based on this standard are liable to lead us astray.   Thus the notochord in the Dipnoi does not extend so far forward as it does in the Amphibia, and much of the cranial axis that in the Amphibia is regarded as parachordal is in the Dipnoi regarded as trabecular; for example, the trigemino-facialis fossa situated well behind the pituitary region in the latter is deemed to be trabecular, as also is the region of the skull base behind the emergence of the roots of the fifth and seventh nerves, whilst the same regions are deemed to be parachordal in amphibians and all those vertebrates in which the notochord extends forward up to or beyond them.   There is another method of determining the trabecular and parachordal regions of the primordial skull rudiments, which regards the trabeculæ as lying on either side of the infundibulum.   If this standard of measurement be adopted (and it seems the more useful in view of the variable length of the notochord, and of the trabeculæ and parachordal rudiments), then we can find no differences in the points of attachment of the basal processes of the Dipnoi and Amphibia.

If we are to regard the basal processes of the Dipnoi as having attachment to the trabeculæ and therefore as being more primitive, then, since the identification of the trabeculæ is determined by the length of the notochord, it would seem that we must regard the short notochord as the more primitive, surely an untenable position.

Assheton[21] has described the development of the chondrocranium of *Gymnarchus niloticus*, one of the Mormyridæ.   He states that "the palato-pterygo-quadrate bar articulates, but is not fused with, the skull in the anterior part of the auditory capsule, just under the horizontal canal" (p. 406), and this is quoted by Edgeworth[22] as evidence that Teleostomi are descended from autostylic and monimostylic ancestors.   In the earlier part of the sentence quoted, Assheton describes the hyomandibular and palato-pterygo-quadrate as being no longer distinct, and his figures plainly show that it is the hyomandibular constituent of the composite bar that articulates as described.

Study of Assheton's description and drawings convinces that the autostylism of *Gymnarchus* presents no resemblance to that of the Dipnoi and Amphibia.   Neither ascending, basal, nor otic processes are developed.   Edgeworth's[23] description of the fate of the oto-quadrate cartilage in *Neoceratodus* might give rise to the belief that the hyomandibular may be regarded as being normally a contributor to the formation of the otic process, but as against this there is the mode of formation of the otic processes in the closely related *Lepidosiren* and *Protopterus* (Agar, *loc. cit.*).   Moreover, the oto-quadrate cartilage is said to gain attachment to the base of the chondrocranium, whereas the definitive otic process of *Neoceratodus* is separated from the base of the chondrocranium by an appreciable thickness of cartilage, the basal process.

Among the Elasmobranchii, only the Holocephali are autostylic and monimo-stylic.   The so-called otic process of *Heptanchus* and *Cestracion* articulates with a special postorbital process of the cranium and presents no relationships in common with the otic process of the quadrate of the Dipnoi and amphibians,

[21] Assheton.—*In* The Work of J. S. Budgett, pp. 293-421, 1907.
[22] Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.
[23] Edgeworth.—Quart. Journ. Micro. Sci., lxvii, 1923, pp. 325-368.

nor does the quadrate of these forms present anything homologous with the ascending and basal processes of those others.

Allis[24] writes: ". . . . the efferent mandibular artery of *Ceratodus* . . . . is shown, in Greil's figures of this fish, . . . running upward and forward posterior and then mesial to the entire quadrate. This relation of the artery to the otic process would seem to definitely establish that the otic process of the Notidanidæ is the homologue of the otic process of *Ceratodus*, as de Beer concludes, and that both these processes are the homologues of the metapterygoid processes of the Holostei and Teleostei."

The vessel referred to can only be the hyoid artery and anterior carotid of Spencer.[25]

Kellicott[26] has stated that ". . . . the Elasmobranch similarities (of the vascular system of *Neoceratodus*) seen in the arrangement and distribution of the carotid arteries and the connection between the anterior carotid artery and the vessels of the hyoid arch, ... all prove to be in the nature of parallelisms . . . ." when their development is worked out.

This being so, Allis is on very unsafe ground in attempting to defend any homology based on the relation of the vessels.

In the Holocephali the whole length of the subocular arch is rigidly united to the cranial axis along the base thereof. The quadrato-meckelian joint is thrown very much further forward than in any of the other forms, and from the back of the quadrate a horizontal sheet of cartilage extends to behind the otocrane. This sheet becomes somewhat narrowed as it passes back, and opposite the foramen for nerves V and VII a triangular vertical sheet, the back wall of the orbit, rises from its upper surface. The base of this triangle is attached to the outer and anterior aspect of the otocrane. A search here for the homologues of the three processes of attachment of the dipnoan quadrate is vain; no part presents the relations to nerves and skull regions that any one of the three processes presents.

The autostylism of the Holocephali is in no way homologous with that of the Dipnoi and Amphibia, though it may be a primitive form of it.

In their autostylism and in the form of the nasal roof the chondrocrania of the Dipnoi are definitely amphibian in character. In the form of the otocrane, with its large cava sacculi, absence of external fenestræ and large internal lateral cranial fenestra, and in the possession of a separate foramen of exit for the ninth nerve, they are just as definitely piscine, whilst in the complete suppression of all but the quadrate portion of the subocular arch the Dipnoi resemble, but outstrip, the reptiles.

Among recent writers on the origin of the Tetrapoda there are two somewhat opposing views; on the one hand it is believed that the Dipnoi and Amphibia, along with other lower vertebrata, have been evolved from autostylic and monimostylic ancestors (Edgeworth[27]), and on the other that the Amphibia were derived from the crossopterygian fishes without the intervention of any dipnoan-like form (Watson,[28] Gregory[29]).

[24] Allis.—Journ. Anat., lxiii, 1929.
[25] Spencer.—Linnean Society of N. S. Wales, Macleay Memorial Volume, 1893, pp. 1-34.
[26] Kellicott.—Mem. New York Acad. Sci., ii, 4, 1905, pp. 135-249.
[27] Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.
[28] Watson.—Mem. Proc. Manch. Lit. Phil. Soc., lvii, 1, 1912.
[29] Gregory.—Ann. New York Acad. Sci., xxvi, 1915, pp. 317-383.

The variety of the autostylic monimostylic and semimonimostylic conditions, and the absence of homology in their various modes of attachment to the skulls which is manifested by the bony and cartilaginous fishes, appears to me as evidence that these are adaptive modifications, and that such resemblances as they happen to present are purely analogous. From this I would conclude that they are descended from streptostylic ancestors.

From the peculiar combination of piscine and amphibian characters in the dipnoan chondrocranium I would conclude that the Dipnoi probably approach closely to the form of the common ancestor of the two groups (Dipnoi and Amphibia). I have elsewhere shown[30] that there is a good deal of other evidence indicating their common origin.

PART II.

THE IDENTITY OF THE COVERING BONES AND THEIR BEARING ON THE ORIGIN OF THE TETRAPODS AND OF THE DIPNOI.

(Figures 5 and 6.)

A.—DESCRIPTION OF THE COVERING BONES.

The large parasphenoid needs no particular description. My specimens were all truncated in front of the posterior end of the bone, and my figure indicates the position of only so much as was preserved in the specimen illustrated (Fig. 5).
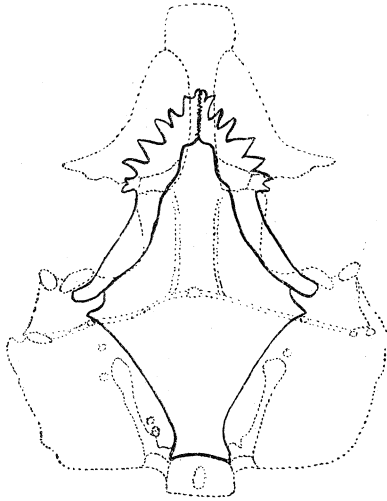

Fig. 5.—Slightly schematic presentation of the dorsal cranial and periotic bones of *Neoceratodus forsteri*.

The bones on the base of the skull on either side and in front of the para-sphenoid have been regarded as composite bones and designated pterygo-palatines, the designation conveying the generally accepted interpretation of their composition. With the designation and the interpretation it conveys it appears only reasonable

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[30] Kesteven.—REC. AUSTR. MUS., xviii, 1931, pp. 167-200.

to agree. We may recognize palatine and pterygoid portions of the bone and an ascending process of the former portion. The palatine is that portion of the bone on which the large composite tooth is set; the pterygoid portion lies behind it.

The palatine portion lies against the basis cranii beneath the olfactory passages and the antorbital buttress, with the cusps of the tooth standing out beyond the cartilaginous basis. The pterygoid presents a free semilunate area of its dorsal surface immediately behind the antorbital buttress; for the rest, the dorsal surface lies against (1) the outer edge of the under surface of the cranium at the site of the prosencephalic fossa, (2) the under surface of that little flange of cartilage which Bridge regarded as representing the pterygoid process, and (3) the inner aspect of the body of the quadrate. The two palatine portions meet in a median suture and that which is presumably the posterior margin of each palatine bone is in sutural contact with the corresponding half of the fore end of the para-sphenoid bone. The inner margin of the pterygoid portion on each side sutures with the outer margin of the fore end of the parasphenoid; the quadrate process makes no contact with any bone.

The ascending process of the palatine lies against the side wall of the cranium in front of the antorbital buttress and behind the anterior aperture of the olfactory passage. This process is attached to the outer edge of the palatine rather nearer to the front end than the middle of the length, by a small round pedicle, and expands as it rises. The front corner of its dorsal edge is definitely sutured to the posterior median dorsal covering bone by two or three little digita-tions. For the rest, except for the pedicle of attachment the process has an unfinished appearance and lies imbedded in a mass of fibrous tissue, wherein is also imbedded the descending process of the "ectethmoid," with which process it sutures.

The large size of this ascending process relative to its pedicle of attachment gives the impression that it has an origin independent of the palatine bone; if this be so it will have to be considered in reviewing the identification of the "ectethmoid."

The prevomers are but two small plates placed on the side of the inferior margin of the septum nasi a short distance in front of the palatine bones. The inferior surface of each is entirely covered by the elongated, slightly curved, cutting vomerine tooth. These bones make no contact with any other bone.

There is in *Neoceratodus* the same number of dorsal covering bones as in the other two Dipnoi, and in the following description the designations of Bridge[31] for the bones in *Lepidosiren* will be used, but in the comparative review of these bones another interpretation of their homologies is offered, based on a comparison with the covering bones of osteolepid fishes and primitive stegocephalians.

The dermal ethmoid lies in contact with the dorsal surface of the cranium above the olfactory passages. The posterior margin of the bone lies above the antorbital buttress, the anterior above the posterior margin of the anterior nares. It is sutured behind to the fronto-parietal and dermal ectethmoids.

The fronto-parietal is in contact with the flattened dorsal area of the cranium behind the antorbital buttresses, with the sagittal ridge which extends back from that area, and with the dorsum of the cranium behind and between the site of the posterior vertical semicircular canals. Its outer margin is overlapped by the

[31] Bridge.—Trans. Zool. Soc., xiv, 1898, pp. 325-376.

inner margin of the dermal ectethmoid. Between the site of the posterior semi-circular canals, and the flattened area in front of the antorbital buttress, the bone is separated from the cranial roof by the origin of the muscles of mastication, except for the very narrow strip in contact with the sagittal ridge. A little spur extends downward and out on either side just in front of the antorbital buttresses to make sutural contact with the ascending process of the palatine.

The dermal ectethmoid makes true sutural contact with the fronto-parietal for the anterior third of their contiguous margins, but overlaps that bone in a sutura notha for the remainder of the length. The descending antorbital process of the bone makes true sutural contact with the ascending process of the palatine and effects a synchondrotic union with the upper surface of the palatine itself just behind that process. The ascending process of the palatine and descending process of the dermal ectethmoid together constitute a nearly complete bony anterior wall to the orbit. Posteriorly the very thin, almost membranous, expansion of this bone is in contact with the dorsum of the cranium lateral to that posterior portion of the fronto-parietal which also is in contact with the cranium; for the rest, the dermal ectethmoid forms a partial roof for the orbit and a covering to the muscles of mastication lateral to the fronto-parietal and mesial to the
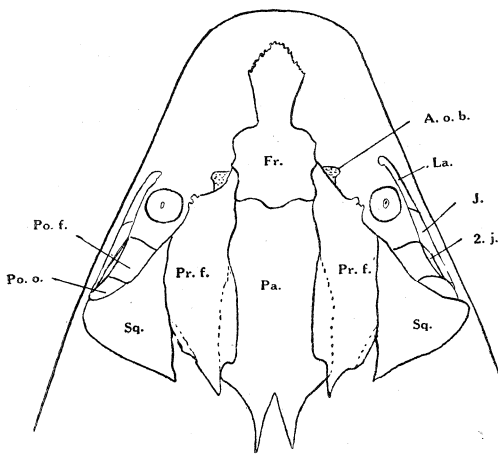

Fig. 6.—Outline of ventral aspect with bones in place.

squamosal bone. In front of the fronto-parietal, the dermal ectethmoid forms a sutura notha with the dermal ethmoid on each side near the posterior margin thereof.

The squamosal bone presents two portions for description. The dorsal squame, triangular in outline, lies in the same plane as the fronto-parietal and dermal ectethmoid, and completes the roof of the muscles of mastication. The descending process is a splint, which is expanded and hollowed out inferiorly to fit the quadrate cartilage just above the articular surface, and is continued up along the outer edge of that cartilage; bending backward it lies along the thickened outer edge of the cartilaginous suprabranchial roof for a short distance, then, lifting free of the cartilage, it joins the outer angle of the dorsal squame, thickening the outer margin of that squame for a short distance before it terminates. The suture

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between the dermal ectethmoid and the squamosal is a squamous suture, the dermal ectethmoid overlapping the more median bone. Günther[32] designated the descending process, os quadratum, and the squamous portion of the bone, tympanic lamina, and in his Figure 1, Plate xxxv, presents a very correct picture of all the bones which he shows in this side view of the complete skull.

No two writers have described the circum-orbital bones of *Neoceratodus* alike, and I find that the specimen I have dissected presents a condition quite different to any heretofore described.

Including the little bone which Huxley[33] described and indicated with the letter "E," there are in my specimen six of these bones (Fig. 8a). Commencing above behind the eye there are two attached respectively to the dermal ectethmoid and the squamous portion of the squamosal and to one another by their contiguous margins. These may be known for the present as the two superior postorbital bones. The inferior postorbital bone lies below these and is attached to the lower edge of both of them. Its hinder margin is just in front of the descending process of the squamosal, separated from and attached to it by connective tissue. The posterior subocular bone is attached to the lower edge of the inferior postorbital but extends forward beyond it under the eye. Its posterior margin is attached by fibrous tissue to the lower end of the descending process of the squamosal, and it extends from this point forward and inward (mediad), providing a weak bony margin to the hinder part of the upper jaw. Where this bone lies below the postorbital bones its upper edge is directly above the lower, but as it passes beneath the eye the upper edge is turned outward slightly, so that the bone comes to lie obliquely beneath the eye, forming an incomplete floor which slopes inward and downward. The anterior subocular bone is attached to the fore end of the last bone. Their margins of attachment are parallel, but this bone rapidly bends into the vertical. Its anterior end is attached to the antorbital buttress by a mass of strong fibrous tissue.

The sixth periotic bone lies over the descending process of the squamosal with its anterior margin attached to the posterior margin of the inferior postorbital bone. All of these bones, except the hinder of the two superior postorbitals, lie more deeply than the larger covering bones, separated from the deep layer of the skin by an appreciable thickness of tough fibrous tissue, by which they are bound together.

The operculum is firmly bound to the postero-lateral margin of the squamous portion and descending process of the squamosal bone, and has the sub-operculum bound to its lower margin.

All six periotic bones lie deeper than the sensory canals, which, in this region, appear to have imperfectly ossified walls, for the knife commonly "grits" when cutting through them. This leads to the belief that none of the bones I have just described corresponds with any of the three, four, or five subocular bones previously described (except Huxley's bone "E"), all of which are said to have been tunneled by sensory canals. All are quite strong squames of bone, and I am at a loss to understand how it comes about that they could have been missed by previous workers; this made me hesitate in coming to the above belief, but quite definitely they are none of them tunneled by sensory canals.

[32] Günther.—Roy. Soc. Lond. Phil. Trans., clxi, 1871, pp. 511-571.
[33] Huxley.—Proc. Zool. Soc. Lond., 1876, p. 37, fig. 7.

B.—COMPARATIVE REVIEW AND PHYLOGENY.

1. The Bones of the Palate.

The posterior portion of the pterygo-palatine bone of *Lepidosiren* is undoubtedly the pterygoid bone.

The pterygoid bone of the Dipnoi is developed as a covering bone on the base of the cranium, and in the recent forms shares in the formation of the cranial wall and floor, though not appearing internally.

The pterygoid bone of the recent Amphibia is developed as a splint on the pterygoid portion of the primitive subocular arch.

Both are ectochondral membrane bones, but there the resemblance ceases, and I am utterly unable to persuade myself that it is reasonable to regard as homologous bones developed in relation to such fundamentally different structures.

On the other hand it seems obvious that the pterygoid bones of the Dipnoi, embolomerous Amphibia and cotylosaurian reptiles are homologous.

Since the Dipnoi have both pterygoid and parasphenoid well developed it may appear that I have been in error in deriving the reptilian pterygoid from the parasphenoid bone. This question is returned to on a later page.

Watson's[34] proposal to arrange the palates of *Loxomma, Eryops, Rhinesuchus, Capitosaurus* and *Cyclotosaurus* in series and derive the pterygoids of the capitosaurian palates, and through them those of the Branchiosauria and Batrachia Salientia from the first of the series, is certainly enticing, but it is convincing only if one completely neglects the genetic relationships italicized above.

The form which the pterygoids present in the Dipnoi is the only form which is present in the most primitive amphibians and reptiles, and in all of them it is applied to the basis cranii, taking more or less share in the formation of the floor and side walls of the cavum cerebri.

Without exception the pterygoid of the recent Amphibia is developed in relation to the pterygoid process of the quadrate.

Comparing the palates of the capitosaurian amphibians with those of the Urodeles, impressing *Batrachosuchus* to complete the set, one finds a series which connects by easy gradations the palates of *Eryops* as the one extreme and *Branchiosaurus* or *Rana* as the other. There will be found in this series of palates no such marked break as is present between the embolomerous palate and that of *Eryops*.

On the other hand it is possible to arrange a series of palates commencing with the Dipnoi, and passing through the embolomerous, *Loxomma,* type to *Seymouria* and the chelonians, and thence to all or any of the recent or fossil reptilian types, and again the series will present no discontinuity. There is no need to depart from the chronological order in arranging these series.

On comparing the palate of *Batrachosuchus* with that of the Urodeles, *e.g., Sieboldia* or *Menopoma,* one finds so complete a resemblance between the pterygoids of the two forms that one must conclude that they had a like genesis; that is to say, both were developed in relation to the pterygoid portion of the subocular arch. Now we may pass to the other rachitomous and stereospondylous amphibian palates, and, step by step, from palate to palate, assure ourselves that the pterygoids in all had a like genesis. In all these cases the pterygoid articulates with the

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[34] Watson.—Journ. Anat., liii, 1919, pp. 239-240.

edge of the covering bones of the basis cranii, at the side thereof. The bone is also applied to the underside of the quadrate and the base of the otocrane where the quadrate roots find attachment, but in no case is the bone applied to the base of the cranium itself.

Returning again to the Dipnoi, we have the evidence of embryology that there can have been no relation to the subocular arch in the genesis of the pterygoid. Unless the published descriptions and drawings of the embolomerous palates are misleading, the pterygoids are, as in the Dipnoi, applied to the basis cranii; there is, therefore, reason to suppose that they were genetically related thereto as covering bones.

There is conclusive evidence in the development of the pterygoids of the Urodeles that the relation to the side of the basis cranii is secondary. It will be remembered that the bone first appears in relation to the pterygoid process, that it grows backward, acquiring relationship to the quadrate and still later to the base of the otocrane and sphenethmoid region of the cranial axis. In the anurous Batrachia there is never any relation to the basis cranii; on the other hand the relation to the quadrate is apparent relatively earlier than in the Urodeles.

In passing, it is of interest to note, though a basipterygoid process has been described in *Eryops* and some other rachitomous amphibians, this is only a local broadening of the basisphenoid behind the prootic fissure, and therefore well behind the pituitary fossa. From this it follows that the so-called basipterygoid process is not homologous with that of the reptiles, which is situated in front of the incisura prootica and almost under the pituitary fossa.

From the foregoing facts it is to be concluded that the pterygoid of the Amphibia generally is not homologous with that of the reptiles, birds, and mammals, nor with that of the primitive embolomerous Amphibia.

A difficulty which stands in the way of the acceptance of this idea is presented in the question—if the pterygoid of the embolomerous Amphibia is not represented by the similarly named bone in the rest of the Amphibia, what represents it in the palate of these creatures? Apparently there is no trace of it, but why?

The answer to this question may perhaps be introduced by another—What has become of the parasphenoid in the higher tetrapods? The bone is well developed in the fishes, Dipnoi and most Amphibia; how comes it, then, that there is no trace of it, except perhaps a persistent anterior piece, the vomer, in all the other forms?

It would seem that in the Dipnoi we are presented with a condition near the dawn of the pterygoid of the higher tetrapods, and that in the Embolomeri and Cotylosauria we see a further stage in its evolution. The variety of palates of the branchiosaurian type already known from the Lower Permian and Upper Carboniferous must surely indicate that the group had its origin at an earlier time, so that, although the only amphibian type as yet known from the Lower Carboniferous is the embolomerous, there is every reason to believe that the other type must have been contemporaneous with it.

The Embolomeri present in the skull so many reptilian features that there can be no doubt that they are representatives of the group which stood in the direct line of the descent of the reptiles.

Since there is strong evidence that the typical amphibian as well as the "reptilian" amphibian palate existed side by side in Lower Carboniferous times, we must hark back for the ancestors of both.

That early common ancestor doubtless had a complete subocular arch, palato-pterygo-quadrate; for we find evanescent traces of it in the life history of the Dipnoi, and the more or less complete arch in the Amphibia, excluding, probably, the Embolomeri. One visualizes this ancestor as having been dipnoan-like in being monimostylic and autostylic, and in the possession of three basal covering bones (the parasphenoid and paired pterygoids); amphibian-like in the possession of a complete subocular arch with investing bones; fish-like in the possession of reduced (?) hyomandibular and opercular elements.

From this group there resulted, on the one hand the rapidly evolving stock from which there was derived the Dipnoi, Embolomeri, and the reptiles, and on the other hand the more static branch which, retaining the complete subocular arch, yielded only the rest of the Amphibia.

It is probable that the primitive ectochondral covering of the basis cranii was a single continuous plate of bone as in the fishes and the great majority of the amphibians, the parasphenoid bone. If in the Dipnoi in place of three bones there were but one, developed from three centres which fused, there is no doubt that we should all agree in designating the bone parasphenoid, but the three centres do not fuse and we find parasphenoid and paired pterygoids. In the Embolomeri and primitive reptiles we see the central portion of the parasphenoid more and more reduced, till, as pointed out by Broom, it is reduced to the vomer of the higher reptiles and the mammals.

Whilst it is possible that the pterygoid bones of the Dipnoi arose as new structures, and not from the fragmentation of the parasphenoid, it is quite obvious that they have no relation to a cartilaginous pterygoid process, for none such is developed in the Dipnoi. It follows that the bone cannot be homologous with the pterygoid bone of the majority of the Amphibia. On the other hand it is homologous with the pterygoid bones of the Embolomeri and the reptiles and the mammals.

Watson[35] has stated: "The vast majority of these amphibia, including the latest and most typically amphibian, retain a typical ectopterygoid, so that it is quite impossible for this bone to be the homologue of the amphibian pterygoid." Separated from its context this becomes ambiguous. The contention was that I had been wrong in arguing that the reptilian ectopterygoid is the homologue of the amphibian pterygoid, because quite a number of stegocephalians possess an ectopterygoid.

The contention fails unless it be proven that the amphibian os transversum is homologous with the reptilian bone of the same name. It appears never to have been noticed that among the recent Amphibia two bones, clearly not homologous, have been designated "palatine." Of the two bones that which has been so designated in the Urodeles appears to be the homologue of the palatine of the Stegocephalia. The palatine of the Branchiosauria and anurous Amphibia, on the other hand, situated as it is behind the internal nares, is the homologue of the os transversum of the Stegocephalia and the caecilians. There can be no doubt that it is homologous with the "palatine" of *Ichthyophis*, and this form stands as definitely intermediate between the Anura and the Stegocephalia.

Ichthyophis is also of interest as presenting the reduced amphibian pterygoid in the form and situation of the reptilian os transversum.

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[35] Watson.—Journ. Anat., liii, 1919, pp. 239-240.

2. The dorsal covering bones and the periotic scutes.
(Figures 6 and 8a.)

Omitting for the present the series of periocular bones, there is in *Neoceratodus* the same number of bones as in the other two recent Dipnoi, and, as their relations are in most respects very similar, it was taken that they might be regarded as homologous throughout. The application of the same names to the bones in all three, of course, involves the acceptance of this idea, but a statement by Bridge seems to indicate the need of a re-examination of the position, at least in respect of certain of the dorsal covering bones. The statement is as follows: "If the 'scleroparietal' (dermal ectethmoid) of *Ceratodus* is a 'tendon-bone,' it probably has no counterpart in any fossil Dipnoid; and as the fronto-parietal of *Protopterus* and *Lepidosiren* is situated internal to the jaw muscles, which could scarcely have been the case with any of the cranial plates of *Dipterus* and its allies, the same conclusion may be suggested with regard to this bone" (Bridge[36]). Now, if the latter part of this statement holds true, then also we cannot regard as homologous the fronto-parietals and squamosals of *Neoceratodus* and the other two recent Dipnoids, because in the former they are situated external to the muscles and in the latter they are covered by the same muscles.

A comparison of the fronto-parietal and squamosal of *Neoceratodus* with those of *Lepidosiren* reveals at once that in certain parts of the bones there is complete similitude. The descending process of the squamosal of *Neoceratodus* corresponds absolutely with that portion of the bone in *Lepidosiren* which is applied to the quadrate cartilage. Again, in both the fore end of the fronto-parietal is applied to the dorsal surface of the ethmoid roofing cartilage, and sutures with the hind end of the dermal ethmoid.

An almost parallel condition is presented by the parietal and squamosal bones in certain of the chelonians. In *Chelonia* the parietal bone contributes to the formation of the cranial wall, and also develops a large temporal flange which contributes largely to the roof of the temporal fossa. In *Chelodina* the cranio-mural portion of the bone is more extensive, and there is no temporal roofing plate. In *Chelonia* the squamosal bone is applied to the upper surface of the quadrate and here contributes to the wall of the tympanic cavity; it further expands upward and medially to contribute to the side wall of the temporal fossa. In *Chelodina* the temporal roofing plate is not developed. The examples chosen are not unique, but are exemplary of whole groups throughout which the bones are very correctly regarded as entirely homologous.

Though the parallel is not absolute it is sufficiently close to justify us in regarding the two bones as homologous in the three recent Dipnoi.

Like that of *Ceratodus*, the dermal ectethmoid of *Lepidosiren* is articulated or sutured to the ascending process of the palatine bone, and forms the dorsal margin of the orbit, lying beneath the skin. There can be no reason to doubt that we have the same bone to deal with in both cases.

Since we may rest assured that all the bones in the three recent Dipnoi are homologous, either of the two forms which most of these bones present may be used for purposes of comparison with other animals.

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[36] Bridge.—Trans. Zool. Soc., xiv, 1898, p. 367.

The terms dermal ethmoid, dermal ectethmoid, and fronto-parietal convey no ideas of serial homology. They are, therefore, unsatisfactory designations unless it can be shown definitely that they are not serially homologous with any bones in the fishes or amphibians.

It is quite clear that the recent Dipnoi present a skull pattern dorsally that had no representation among the early fossil forms. The outstanding modification that is observed is the reduction in the number of plates. Now, whilst it would be foolish to attempt to derive the dorsal skull pattern of the fishes or Amphibia from that of the recent Dipnoi, it is not unreasonable to assume that the same force which brought about the reduction in the number of plates and increase in size of the remainder, acted on the Dipnoi in the same manner as it acted on the fishes or amphibians. If from a comparative review we conclude that the dorsal covering bones of the Dipnoi are similar to those of primitive fish or amphibian, then we may regard the bones as homologous.

In the first place it is desirable to assure ourselves that the squamosal is correctly named.

Thyng[37] studied the development of the squamosal bone in the mammals and Urodeles, and then carefully compared his findings with the conditions in the adult crania of the stegocephalians and primitive reptiles. He concluded that the squamosal bone is essentially a bone developed in close association with the quadrate, and that it overlies the otic capsule. The relation which it commonly acquires with the parietal is to be regarded as secondary to these other features. Among the dorsal skull patterns which he illustrates is that of the Rachitome *Chelidosaurus*. Gregory[38] reduces Embleton and Atthey's illustration of the dorsum of the embolomerous *Loxomma* to simple lines, and letters the bones. These two temnospondyline skulls are remarkably similar, and Gregory's identification of the squamosal is the same as Thyng's. He also adopts Thyng's designation "supratemporal" for the bone between the squamosal and the parietal. Watson[39] states that in *Loxomma* the pterygoid ". . . . unites with the squamosal *to form a floor to the otic cavity. . . .*" This is quite incomprehensible; such a condition would be absolutely unique, and it is probable that the bone which the pterygoid meets in this situation is a prootic ossification.

Thyng's definition of the squamosal bone may be accepted. We find that the squamosal of *Lepidosiren* complies with this definition in its relation to the quadrate and to the otic capsule, and it is impossible to regard the squamosal of *Neoceratodus* as other than homologous with that of *Lepidosiren*. There can be no doubt that the squamosal of the Dipnoi is completely homologous with the similarly named bone in the temnospondyline amphibians.

The dermal ethmoid is certainly placed too far back to permit of its being regarded as representing the nasal bones of either the crossopterygian fishes or the temnospondyline Amphibia. On the other hand, there can be no valid objection to regarding it as representing the fused frontals. Similarly, it is reasonable to regard the so-called fronto-parietal as representing the fused parietals.

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[37] Thyng.—Tuft's College Studies, ii, 1906, pp. 35-73.
[38] Gregory.—Bull. Amer. Mus. Nat. Hist., xlii, 1920, pp. 95-283.
[39] Watson.—Mem. Proc. Manch. Lit. Phil. Soc., lvii, 1, 1912, p. 3.

In passing, it may be observed that the so-called pineal foramen of some of the osteolepid fishes is certainly placed a long way too far forward for it to have been a pineal foramen in the reptilian sense. May it have been a dorsal narial aperture comparable to that of the cyclostomata?

Bridge in his discussion of the identification of the dermal ectethmoid has fairly convincingly proven the correctness of his views, but his name for the bone is merely a synonym for prefrontal, that being the accepted designation today for every bone he compares it with.

The interpretation of certain of the periotic bones is made obvious by Gregory's[40] work on the evolution of the lachrymal bone. The lachrymal and jugal bones (la and j, fig. 1) are recognizable at sight, whilst that which I described as the inferior postorbital may confidently be identified as the quadrato-jugal. Of the two superior postorbitals, it may be that the anterior is the postfrontal forced down in front of the postorbital by the remarkable posterior expansion of the prefrontal.

The little broken squame behind the quadrato-jugal and postorbital may be a reduced interoperculum, though its position external to the squamosal is against this interpretation.

3. The Evolution of the Squamosal Bone.

(Figures 7 and 8.)

So far in the attempt to identify the bones of the dipnoan skull I have, as it were, looked forward, but if there be truth in the suggestion that these interesting forms approach closely to the common ancestor of themselves and the Amphibia, it should be possible to recognize some of these bones, probably in more primitive form, in more or fewer of the palæozoic fishes.

The ctenodont Dipnoi are found together with osteolepid crossopterygians in the Lower Old Red Sandstone of Scotland; both the Dipnoi and crossopterygians were, therefore, well established at that time. Any common ancestor must be sought in Silurian formations. The only ostracoderms that might have been considered in this connection are the Arthrodira, and they, apparently, are of no greater antiquity than the Dipnoi themselves. Among the elasmobranchs the Acanthodei alone present any features which entitle them to be regarded as possibly resembling the ancestors of the bony fishes, Dipnoi, and Amphibia, and it is particularly interesting to note that in the ichthyodorulite, *Onchus*, there is strong evidence that the group existed in Silurian times. This, of course, is also indicated by the fact that several genera from both the acanthodian families flourished in Lower Devonian times.

Even so, if it be regarded as proven that some such type as *Mesacanthus* stands close to the stem of all the higher vertebrates, we still cannot trace directly backwards the evolution of the cranial bones, for the record is far too incomplete.

Any attempt to homologize the cranial elements of the fishes, dipnoans, and amphibians can only be made under the assumption already made use of, that, having evolved from a common ancestor, the same inherited potential produced the same cranial elements in all.

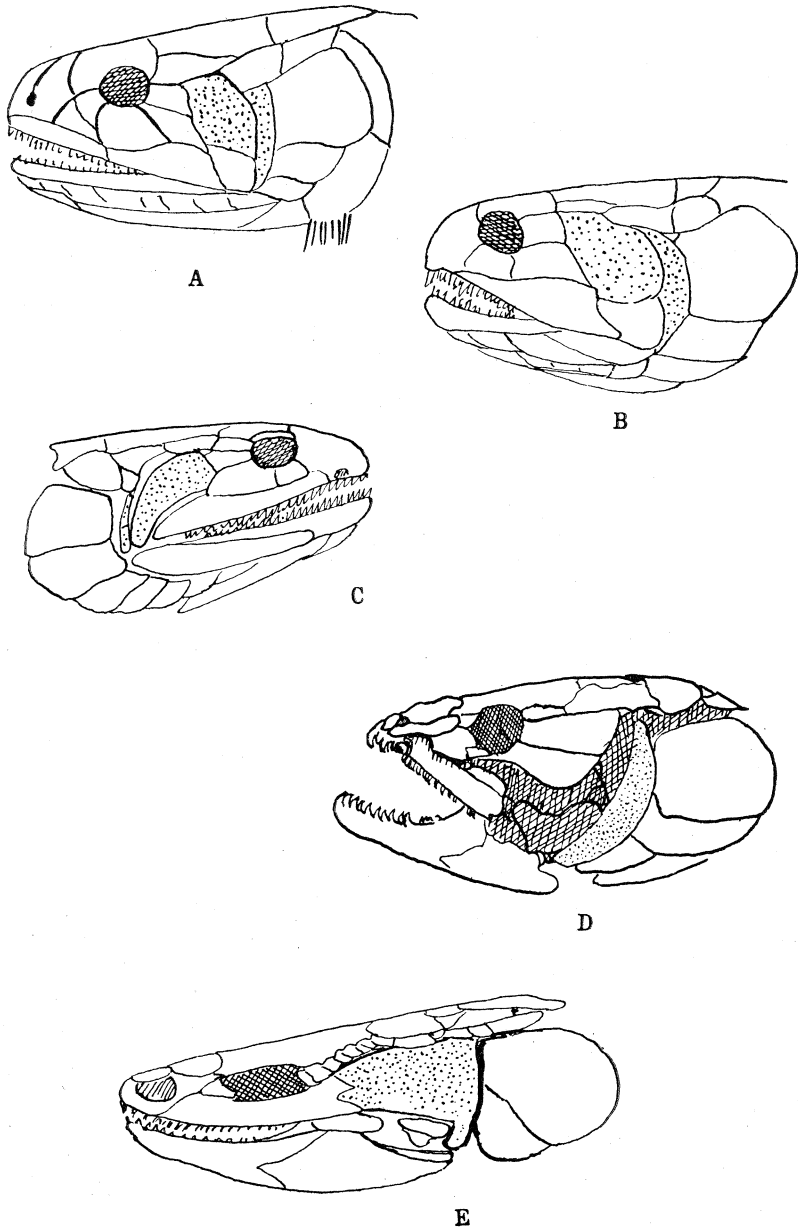[40] Gregory.—Bull. Amer. Mus. Nat. Hist., xlii, 1920, pp. 95-283.

Fig. 7.—The bones which are to be regarded as homologous with the tetrapod squamosal have been stippled. A, *Megalichthys* (after Wellburn from Gregory); B, *Rhizidopsis* (after Traquair from Zittel); C, *Osteolepis macrolepidotus* (from Gregory); D, *Amia* (from Allis); E, *Polypterus* (from Allis).

I have elsewhere offered[41] a mechanical explanation for the similarity in the fragmentation of the cranial wall, whilst Gregory[42] has offered a mechanical explanation for the fragmentation of the skull roof.

The importance of Gregory's postulate was realized by Adams,[43] who pointed out that it works out well in the case of *Polypterus*. It appears to me that the *potent mechanical factor in the evolution of the squamosal bones and in determining their position on the dorsum of the skull has been the assumption of monimostylic autostylism.* In all the freely streptostylic forms the great mass of the fibres of the adductor mandibulæ arose from the pterygo-quadrate and its hyomandibular suspensorium. With the reduction in the range of the streptostylism more and more of these fibres became transferred to the cranium itself. Not only was this so, but, as the hyomandibular and quadrate became successively shortened, their dermal covering bones also became approximated to the cranium, and ultimately became welded thereto.. It may be further postulated that such of these bones as already carried fibres of origin of the adductor muscle would increase in size, and that any two or three contiguous bones which gave rise to fibres of the same portion of the muscle would tend to become welded together.

It appears to me that along these lines the evolution of the squamosal bone can be clearly traced, and that very definitely an intermediate stage in its evolution has been preserved to us in *Polypterus*.

A general survey gives the impression that the teleosts have perpetuated and perfected the hyostylic streptostylism of the elasmobranchs. The ganoids, definite stages in this perfecting process, show also, in varying degrees, a tendency to throw off the hereditary streptostylic influence. This revolt is least manifest in the chondrosteous ganoids, which I have elsewhere shown to be more elasmobranch than teleost in character (Kesteven[44]). It is most marked in the Crossopterygii, and appears to a very slight extent in the Holostei.

The Crossopterygii are, of course, all streptostylic and hyostylic, but the firm union of the palato-pterygoid with the cranium anteriorly, and with the parasphenoid posteriorly, the development of true maxillæ and premaxillæ, the large size of the dermal plates in front of the hyomandibular bone, and their firm union with that element on the one hand and with the dermal covering plates of the cranium on the other, are all features which appear to indicate the attempted adoption of monimostylism.

Gregory[45] suggested that the preoperculum of the fish gave rise to the squamosal. It is more probable that it was that bone in fusion with one or more of the cheek plates behind the postorbitals that gave rise to the squamosal.

Before proceeding further it may be well to note that the possession of a true squamosal along with operculum and suboperculum by *Neoceratodus*, clearly indicates that the opercular bones took no part in the formation of the squamosal.

The identification of the preoperculum in the rhipidistian skulls is somewhat confused by Gregory's treatment of the question. As already stated, he expressed the opinion that the squamosal was derived from the preoperculum, and yet he identifies that which is assuredly a cheek plate as the squamosal of *Osteolepis microlepidotus* (*loc. cit.*, fig. 2). He does the like in his study on the evolution

[41] Kesteven.—Journ. Anat., lxi, 1926, pp. 121 and 129.
[42] Gregory.—Ann. New York Acad. Sci., xxvi, 1915, p. 327.
[43] Adams.—Ann. New York Acad. Sci., xxviii, 1919, pp. 51-166.
[44] Kesteven.—REC. AUSTR. MUS., xviii, 1931, pp. 167-200.
[45] Gregory.—Ann. New York Acad. Sci., xxvi, 1915, p. 337.

of the lachrymal bone in the case of *Osteolepis macrolepidotus*,[46] whilst his treat-ment of *Polypterus* and *Lepidosteus* and his failure to recognize the preoperculum of *Amia* as the squamosal, give the impression that either he has consistently mistaken the cheek plate for the preoperculum, or that in the later work he deemed the squamosal to have been derived from a cheek plate. Gregory (*loc. cit.*) has made the further error of identifying as the interoperculum a plate situated above and in front of the suboperculum in *Osteolepis microlepidotus*. *Amia* is in certain respects so essentially similar to the rhipidistean fishes that in those respects we may unhesitatingly use it as a standard for the identification of the affected cranial elements.

The position of the interoperculum in all these forms is determined by such a standard of identification as being behind, below, and internal to the sub-operculum and behind the preoperculum. This being so, the interoperculum can hardly have been retained and evolved into the quadrato-jugal, and this will become more obvious as we proceed.

Comparison of *Amia* (Fig. 7D) with *Megalichthys* (Fig. 7A) and *Rhizedopsis* (Fig. 7B) at once enables us to determine the preoperculum in the ancient forms. The resemblance is such that it were unreasonable to doubt that it is in these forms, as in the recent ganoids, closely adherent to a hyomandibular above and to the quadrate below.

It follows, since the interoperculum lies behind and internal to the pre-operculum, which in turn is bound to the quadrate, that, in the ganoids, the interoperculum is represented by one of the plates which has been designated lateral gular, or it is not present at all.

In *Osteolepis macrolepidotus* the preoperculum is apparently exposed behind the largest cheek plate which I have stippled in Fig. 7C.

In *O. microlepidotus* it is apparently quite covered by the large cheek plates; it will be remembered that in *Amia* the bone is very nearly covered by the muscle fibres that arise from it.

In the eight little drawings (Figs. 7 and 8) on pages 257 and 260 I have stippled those bones which, in fish skulls, it appears may be regarded as homologous with the squamosal, and stippled the squamosal bone itself in the last three of the series.

Consideration of the bones in question justifies the following conclusions. The squamosal bone of the Dipnoi and tetrapods is homologous with the pre-operculum of the ganoids in fusion with one of the large temporal cheek plates. This bone, the squamosal, will have been bound to the quadrate in its original preopercular part, and will have been kept so bound, and, in addition, have become equally bound down to the otocrane and side wall of the cranium itself by the need of a fixed point for the muscles which arose from its lateral surface. And this is how it comes about that the primitive relation of the preoperculum to the quadrate has persisted even to the embryonic stage of the mammalian squamosal bone. The second, cheek plate, component of the primitive squamosal was extra muscular; we see the two components fused in *Polypterus*; this is the portion that reappears as a covering for the muscles of mastication in *Neoceratodus*, the stegocephalians, cotylosaurs, etc.; in short, the squamosal of the temporal roof wherever it be found.

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[46] Gregory.—Bull. Amer. Mus. Nat. Hist., xlii, 1920, fig. 1.

Returning again to Watson's description of the quadrate and squamosal bones in *Loxomma* already quoted, I have carefully made wax models from his drawings and find that, if his description and illustrations be correct, then in this form the squamosal bone is placed between the quadrate and the cranium, and is the
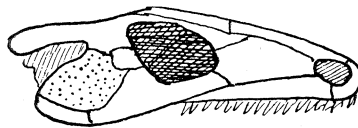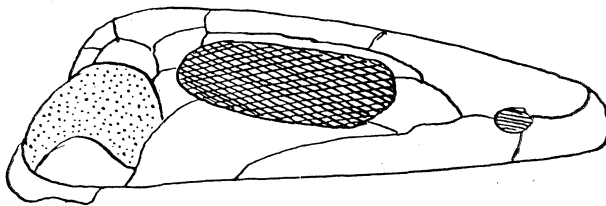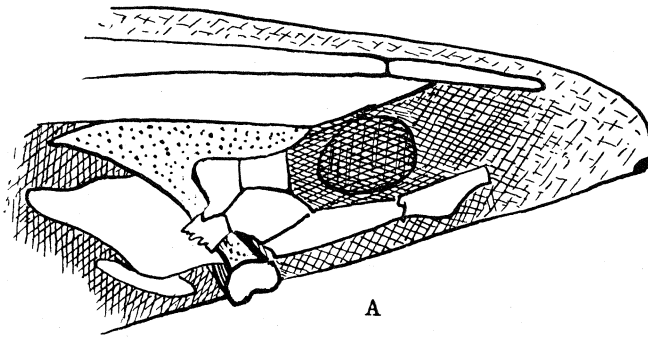

Fig. 8.—A, *Neoceratodus*; B, *Loxomma* (a reconstruction based on the figures of Embleton and Atthey) ; C, *Seymouria* (from Gregory). The squamosal bone has been stippled in the three drawings.

only means whereby the former is attached to the latter.   Such a condition is quite without parallel, and, moreover, it imposes a tremendous disability upon, and an extraordinary origin and direction for, the adductor mandibulæ muscles. The disability is that they are constrained to pull forward and up, so that they pull against the capsule of the articulation.   The extraordinary origin is that they arise from the *under* surfaces of the quadrate and squamosal bones; the dorsal and lateral surfaces of the quadrate are, according to his description, entirely covered by the subdermal squamosal and quadrato-jugal bones.

Whilst Gregory was in error in his identification of the interoperculum in the rhipidistian fishes, it is probable that he was correct in his indication of the bone from which the quadrato-jugal of the tetrapods has been evolved.   If the crossopterygian fishes present us with the homologue of the bone at all, it must have been the lower of the two cheek plates, as he indicates.

Reviewing, now, the structure of the skull of the Dipnoi, the comparisons that have been made, and the homologies that have been established, it becomes apparent that they support an opinion previously expressed.   The Dipnoi are primitive amphibians (Kesteven[47]).

They are also modified fish, but they have, as it were, progressed so far along the evolutionary road that led to the Amphibia that they are nearer the end of that road than they are to its beginning.

If the last two paragraphs be statements of fact, then the Dipnoi must approach more nearly to the structure of the common ancestor of all the amphibians than does any other known form; later it may be found that there is preserved to us among the known fossils a survivor from the same group as the common ancestor.

4. The Crossopterygian ancestry of the Tetrapoda.

It is believed by other workers that the tetrapoda were derived from the crossopterygian fishes.   It is proposed to examine the evidence on which this theory rests, in so far as that is derived from cranial structures.

Gregory[48] appears to have offered the most extended defence of the thesis. On page 337 of his work he itemizes nine changes whereby the "primitive stegocephalian skull has been derived from the rhipidistian."

A critical reading of his nine "advances" reveals the fact that they are for the most part concise descriptions of the observable differences, and where they are not so, then they are but recapitulations of his conclusions on the homology of the various bones.   Whilst we can agree with him in his decisions as to most of the homologies, it has to be pointed out that this is not evidence that the amphibian skull has been derived from the crossopterygian, but rather that both have inherited these similar elements in modified form from a common ancestor. One may point to the occipital bones of the mammals as being completely homologous with those of the birds, but this is not evidence that the former is derived from the latter.

Watson[49] has compared the bones on the base of the skull of *Megalichthys* with those of *Loxomma*, and his remarks are largely reprinted by Gregory in the paper

[47] Kesteven.—REC. AUSTR. MUS., xviii, 1931, pp. 167-200.
[48] Gregory.—Ann. New York Acad. Sci., xxvi, 1915, pp. 317-383.
[49] Watson.—Mem. Proc. Manch. Lit. Phil. Soc., lvii, 1, 1912.

above quoted. It is apparent that in some respects Watson has misinterpreted the palate of *Loxomma*, and that the comparisons with *Megalichthys* are loosely made.

The "curious type of tooth change" which is said to be "very characteristic of the Stegocephalia, and unknown elsewhere except in the Crossopterygian fish" and which he deems to be "a strong additional reason for regarding the Tetrapoda as derived from this group of fish," is by no means confined to the crossopterygian fishes. It is present in both agamid and varanid lizards and in the Boidæ among the ophidians. Among fish not crossopterygian this form of tooth change is found not only in *Lepidosteus*, as Watson states, but also in *Amia*, and is so frequent of occurrence among the Teleostei that one is almost tempted to describe it as the common tooth change among the bony fishes. Teeth are epidermal structures, and the form of replacement under discussion reproduces fairly faithfully, but on a bony basis, the mode of replacement which characterizes the whole of the Elasmobranchii. In short, this is a primitive mode of tooth replacement, and is due to the fact that the tooth buds have not been split off from the deeper layer of the dermis and submerged or grown down among the subcutaneous tissues.

On the other hand, the more advanced mode of development within a bony socket may not be relied upon very much as indicating any more than an advanced method of tooth replacement, for I find in my collection of teleostean heads that quite closely allied forms may exhibit the two modes of replacement.

Following a well-founded statement that the evidence points to the separation of the reptilian stock early in the history of the Stegocephalia, Watson proceeds: ". . . comparison [of *Loxomma* and *Pteroplax* skull] with *Megalichthys* shows an equally marked resemblance to the Crossopterygian fish."

"The basisphenoid of *Megalichthys* has sometimes carotid foramina just as in *Loxomma*." This, too, is merely a primitive feature, and, moreover, one which has been shown to have persisted in almost every one of the Gnathostomata, with the exception of those bony fishes which have a well developed myodome. Whether the canal actually perforates the fused basisphenoid and parasphenoid on the base of the cranium, as in *Loxomma* and *Megallichthys*, or whether it finds its way through at the outer edge of the latter bone where that sutures with the prootic, depends upon the width of the parasphenoid, and is entirely without significance. In some siluroids and apodes the canal perforates the fused bones, in others it passes in at the suture.

In the Elasmobranchii the canal perforates the cartilaginous basis cranii in a precisely similar position. *Doubtless the constancy of the Gnathostomata in this respect is traceable to the elasmobranch ancestor, and results from the mode of origin of the eye and the relation of its stem, the optic nerve, to the vascular hypophysis cerebri. The prime importance of these organs may well be supposed to have maintained a static condition in their vascularization.*

It is more than probable that the "basipterygoid process" of *Megalichthys* is parasphenoidal and not basisphenoidal as it is in the Embolomeri. That the . . . "long parasphenoid [of *Megalichthys*] extends forward to the premaxillæ as it *may* do in *Pteroplax*," is only a possible point of resemblance.

"The pre-vomer [of *Megalichthys*] is identical with that of Loxomma in the majority of its attachments . . . It meets its fellow of the opposite side, and *forms the front of the posterior naris* . . ." On the palate of a ganoid!

This passage was quoted by Gregory[50] as, indeed, were my other quotations from Watson here anent, and it is surprising that so keen a student of comparative craniology should have failed to observe the paradox.

If *Megalichthys* has the posterior naris bounded in front by pre-vomers at all, then that posterior naris must be in the roof of the mouth, and *Megalichthys* differs fundamentally from every other teleostome.

The palato-pterygoid of *Megalichthys* may resemble the palatine and pterygoid of *Pteroplax*, but such resemblance must be purely superficial. Any one of the Mormyridæ would present an even closer resemblance in the relation of the bones, for in these teleostean fishes the medial borders of all the median bones developed on the palato-pterygoid arch are actually fused to the lateral margin of the parasphenoid; but here, as in *Megalichthys*, all those bones are genetically related to the cartilaginous arch, so that their relation to the basis cranii is secondary and fundamentally different to that of the palatine and pterygoid of *Pteroplax*.

In conclusion, it may be stated that such resemblances as are demonstrable between the Crossopterygii and the Stegocephali are of two kinds; firstly, parallelisms, which are devoid of phylogenetic significance, and secondly, true homologies. All these latter are more satisfactorily accounted for by the assumption that both groups have derived them from a common ancestor than by the assumption that the tetrapods are derived directly from the Crossopterygii. The geological record of the antiquity of the two groups supports this view.

The conclusions I arrived at in a recent paper on the evolution of the Anamniota, and the genealogical diagram I then published, are supported by the present communication.

LIST OF ABBREVIATIONS USED ON THE FIGURES.

A.c.a.—External aperture of canal for the anterior carotid artery.
A.o.b.—Antorbital buttress.
A.p.—Ascending process of the quadrate.
B.p.—Basal process of the quadrate.
Can. art. c.—Canal for the cerebral artery.
F. pr. ot. e.—Foramen prooticum externum.
Fr.—Frontal.
J.—Jugal.
La.—Lachrymal.
Pa.—Parietal.
Pb. can.—Parabasal canal.
Pb. can. a.—Anterior aperture of the parabasal canal.
Po.f.—Postfrontal.
Po.o.—Postorbital.
Pr.f.—Prefrontal.
Q.j.—Quadrato-jugal.
Sq.—Squamosal.
II.—External aperture of optic nerve canal.
III, IV, V, VI.—Common aperture of canals for third, fourth, (?) and first branch of fifth, and sixth nerves.
VII.—External aperture of canal for the hyomandibular branch of seventh nerve.
IX and X.—External apertures of the canals for the ninth and tenth nerves.

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[50] Gregory.—Ann. New York Acad. Sci., xxvi, 1915, p. 332.

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