VI. CROONIAN LECTURE.—*The Evolution and Origin of the Amphibia.*

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The problem of the origin of the Amphibia is one which necessarily attracted the attention of zoologists during the period which immediately succeeded the publication of the "Origin of Species." Involving as it does the study of the most fundamental change in conditions of life which has occurred in the long history of the vertebrate animals, it still remains the most fascinating of all the problems of Phylogeny.

It is possible to view the problem as purely one of formal morphology, the establishment of a series of stages which show intermediates between typical fish structures and those of the homologous organs in Amphibia may be regarded as a solution.

But such studies, although they form a necessary foundation for further investigations, are now satisfying to few men: the centre of interest has passed from structure to function, and it is in the attempt to realise the conditions under which the transformation took place, and to understand the process by which the animal's mechanism was so profoundly modified whilst remaining as a working whole throughout, that the attraction of the problem lies.

During its passage from water to air the Amphibian ancestor had to replace a respiratory mechanism in which the gaseous interchange took place through gills by a lung, and for a long period had both organs functioning side by side. It had so to modify its fins and body as to be able to travel overland whilst retaining its power of swimming and feeding in water. The glandless and heavily-armoured skin of the early fish had to be so modified as to admit of exposure to air.

The sense organs had to be altered, and altered in such a manner as to be functional in both media. The olfactory organ, accustomed to the perception of the relatively

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great amounts of substances which can be conveyed by water, had to have its sensitiveness so increased as to recognize the much smaller quantities dispersed in the air, and the sense of hearing was either introduced *de novo* or gained a higher importance.

On the other hand, the lateral line system of neuromast organs, whose apparatus bulks so largely in the brain of a fish, became useless and was completely lost in fully terrestrial forms. These changes, and many more, involving as they do a reconstruction of most of the systems of organs of the body, had to be carried out in such a manner as to leave the animals not only capable of living but of competing with their neighbours, the fish.

Most of those who have attacked the problem have done so from the standpoint of modern fish and Amphibia, they have indeed been forced to do so, because only on living material is it possible to study the anatomy of the vascular system, of the brain and other organs, and only with recent material is the evidence of embryology available.

Most of the work has centred on the Dipnoi, fish so similar to the Urodeles that one of them was regarded by its first describer as an Amphibian. In their lungs and vascular system, in the skull, in the mode of development and characters of their larvæ and in their histology, these fish are indeed extraordinarily like the Urodela. But these resemblances are specifically to that order of Amphibia, they do not so clearly recall other and more primitive forms, and it is certain that the existing resemblances depend on the parallel evolution of not distantly allied stocks.

As the oldest Amphibia are found in rocks of Lower Carboniferous age, and belong to three sharply separated orders, it is certain that the actual origin of the group took place no later than Devonian times, and may have occurred in the Silurian, an epoch preceding the first appearance of the remains of bony fish.

Experience of the fundamental importance of palæontological evidence in the comparable problem of the origin of the mammalia, led me to study the Palæozoic Amphibia, and it is the results of these investigations which form the great bulk of this lecture.

Amongst the hundreds of Permian and Triassic Amphibia one group appears as a coherent whole, it is composed in the main of large animals with a characteristic dentition of labyrinthodont teeth, and with structural peculiarities in all parts of the skeleton which are common to a large number of animals occurring throughout this time. A review and analysis of the characters of these Labyrinthodonts enabled me to show, in a paper published in the 'Philosophical Transactions' in 1919, that they were indeed allied to one another, and that considered as a group they exhibited a series of changes in structure which proceeded in definite directions with time.

Of these changes the more important are :—

(1) That the early forms possess a hypoglossal foramen passing through the exoccipital, and that by a gradual shortening of the skull this opening moves further and further backward, until in the labyrinthodonts of the Upper Trias it no longer perforates the cranial wall, the hypoglossal nerve passing out behind the skull, as in most modern Amphibia.

(2) The skull and the anterior part of the body show a progressive flattening, reaching an extreme in such creatures as the Upper Triassic Metoposaurus, where the neck at the occiput is more than twice as wide as it is high.

(3) The brain case becomes progressively less well ossified, and the basioccipital, basisphenoid, and supra-occipital bones become reduced in thickness and finally disappear even as cartilages. The original tripartite condyle thus giving place to a pair of well-separated exoccipital condyles.

(4) The cavity in which lies the fore-brain is excavated in the upper part of a thick interorbital septum in all early forms. In later times it extends further downward, until finally it comes to rest on the dorsal surface of the parasphenoid; the originally tropibasic skull being thus converted into a platybasic cranium of modern Amphibian type.

(5) The interpterygoid variations steadily become larger, until they recall those of a frog. In association with this change the pterygoid, instead of articulating in part with a basipterygoid process of the basisphenoid, come to depend entirely on the parasphenoid for its support.

(6) The epipterygoid, which in the Lower Permian forms is a small bone resting on the pterygoid and basipterygoid process, and provided with a processus ascendens alone, gradually grows upward into an otic process which acquired an attachment to the pro-otic.

These changes and many more take place independently in a strictly parallel manner in many distinct phyla of Labyrinthodonts. In the few cases where we know approximately true phyletic lines, short though they be, it is clear that the changes progress regularly. An analysis of the whole fauna known from any one horizon shows that, although different phyla differ in the degree of advance of any character, they do not do so over a large range; and it is, in consequence, possible to make out the whole story by a consideration of all forms, whatever their exact mutual relationships.

The majority of the Lower Permian Labyrinthodonts were terrestrial animals; all those from the Upper Trias were aquatic—the majority of them, in all probability, incapable of progression on land. Consideration of the whole of the evidence, especially that which may be derived from the shoulder girdle, renders it certain that the Triassic amphibia were the descendants of terrestrial forms—that, in fact, we have in them an exact parallel to the living Perennibranchiate Urodela, now known to be only secondarily aquatic.

For the last seventy years it has been known that animals identical in the structure of the dermal roof of the skull and in their dentition with the Labyrinthodonts occurred in the Coal measures, and even in the Lower Carboniferous coal-bearing rocks of Scotland.

Despite the remarkable work of the amateur anatomists THOMAS ATTHEY and ALBANY HANCOCK carried out fifty years ago, these animals have remained practically unknown and their structure has been completely misunderstood. Largely from the material in the Newcastle Museum collected by THOMAS ATTHEY, I am now able to describe in detail the structure of every part of the skeleton in one form or another, and to restore the skeleton in three genera.

All the British Carboniferous Labyrinthodonts, some twenty in number, and, so far as can be determined from the very unsatisfactory remains which alone are known, all those from other parts of the world of pre-Stephanian age, belong to the hitherto practically unknown group of the Embolomeri. This group now proves to contain animals covering a wide range of adaptation : some of the genera contain primitively aquatic animals which show no signs of ever having possessed terrestrial ancestors ; others are clearly land-living, and a further large group is composed of Amphibia which have returned to life in the water. Despite these diverse habits, the fundamental morphology of the skeleton is strikingly uniform throughout the group.

That the Embolomeri are related to the Rachitomi, the Permian grade of the Labyrinthodonts, is made clear by the identical pattern of their skull roof and the similar range in head form. The remarkable and complex structure of the lower jaw is the same in both groups, and detailed resemblances between those parts of the skeleton which, in later Labyrinthodonts, do not exhibit evolutionary changes can be multiplied.

But far more impressive than these formal resemblances is the fact that in every respect their structure forms a logical starting point for the series of evolutionary changes which procure regularly with time in the Permian and Triassic Labyrinthodonts.

To use the technicality which is becoming universal amongst palæontologists, the evolutionary trends in accordance with which later Labyrinthodont evolution took place were already established in Carboniferous times.

The Carboniferous Labyrinthodonts of the grade Embolomeri have in common the following features :—

The skull is high.

The neural cranium is exceedingly well ossified, the basioccipital is a large bone with a nearly circular condyle, to which the small exoccipitals may or may not contribute. In all cases the latter bones articulate with the supraoccipital, and do not extend further forward than the vagal foramen.

The supraoccipital is a very large bone extending forward over the pro-otic.

The pro- and opisthotics are fused into a single bone which forms a powerful paroccipital process directed upwards and outward to support the tabular bone. There may or may not be a post temporal fossa.

The anterior part of the brain lies in an excavation in the dorsal part of a long interorbital septum, whose lower border is clasped by the parasphenoid.

The basisphenoid is a large fully ossified bone, whose lateral surfaces are produced into definite basipterygoid processes, ending in articular faces for the pterygoid and epipterygoid.

The dorsal surface of the head is covered with a continuous shield of dermal bones, so loosely articulated with the neural cranium, that the latter has often fallen out in the fossil skulls. The palate is entirely bony, the interpterygoid vacuities being mere slits.

The palatoquadrate bar is represented by two bones, the quadrate and the epipterygoid. The latter is a small bone whose lower end articulates by a synovial joint with the basipterygoid process, whilst the upright part is attached to the anterior border of the paraotic plate of the pterygoid and the dorsal margin produced into processes which separate the three divisions of the trigeminal nerve.

The pterygoid is a very extensive sheet of bone, supported on its admesial margin by a movable articulation with the basipterygoid process.

The anterior part, the palatal ramus, extends forward in symphysis with its fellow, so that the two form the middle of the palate. Its lateral border is attached to the prevomer, palatine and ectopterygoid. At its articulation with the basis cranii, this ramus swings round and passes into the quadrate ramus, a deep plate of bone standing nearly vertically in the skull a little lateral of the otic region. This para-otic plate has a vertical anterior margin the whole of which is in contact with the epipterygoid.

Posteriorly the ramus wraps round the quadrate, its posterior border being in contact with the squamosal and quadratojugal.

The lateral border of the palatal ramus of the pterygoid is attached by a deep overlap to the prevomer, palatine and transverse bones, whose outer surfaces are rigidly connected to the premaxillæ and maxillæ. The palatal nostrils are openings between the premaxillæ, maxillæ, prevomers and palatines, which in one series of forms are extremely small and laterally placed, whilst in another they are large and approach one another so closely as greatly to reduce the width of the prevomers.

The dentition consists of a single series of teeth occupying the whole of the palatal surfaces of the premaxillæ and maxillæ, and of a variable number of much larger tusks on all the bones of the palate except the pterygoids.

These teeth have a typical labyrinthine structure of extremely complex plicidentine at the base, which gives place to a more normal compact dentine toward the apex. They are attached to their supporting bones by fusion, and are shed by resorption of the bone. When so lost they are replaced by a new tooth, which has been developing in a neighbouring implacement. The whole dentition thus consists of a series of pairs of teeth which are functional alternately.

The lower jaw presents the following peculiarities. The articular and sur-angular are completely fused, and there is no trace of a retroarticular process. The prearticular is exceptionally long, extending forward in some forms very nearly to the symphysis. There are three coronoids wedged in between its upper margin, and the admesial surface of the dentary. These bones have a granulation of small teeth, but do not support large tusks. The upper part of the jaw is narrow, so that it may fit in between the maxillary and palatine teeth.

The vertebral column is throughout embolomerus, that is, it consists of a series of ring-shaped circum-chordal elements, two of which belong to each somite. Of these the anterior bears a facet for the capitulum of the rib, and in the caudal region gives origin to the hæmal arch. The other affords the main support to the neural arch.

With these exceptions they are nearly identical in structure, each consisting of a double cone of dense bone which surrounds the continuous notochord, and is itself surrounded by a ring of cancellous bone, with an external surface formed by a thin layer of compact bone.

The neural arch rests in the main on the posterior chordal element, bears a pair of powerful transverse processes in the presacral region, has well-developed zygapophyses and a high neural spine.

The presacral ribs are long, slender and curved, to pass round the nearly cylindrical trunk. They are double-headed throughout the precaudal series. In certain cases they bear uncinate processes.

The limb and limb girdles differ greatly in their structure in different members of the grade Embolomeri, and I prefer to deal with them and with the general body form and habits at a later stage of this lecture.

It is thus justifiable to say that, so far as concerns those structures which exhibit a steady evolution with time, the Lower Triassic Stereospondyls differ from the Lower Permian Rachitomi in the same way as the latter do from the Carboniferous Embolomeri. We are therefore justified in regarding the Embolomeri as the most primitive, as they are the oldest Labyrinthodonts.

The other orders of Palæozoic Amphibia are still very imperfectly known; but there is some evidence to show that the Lepospondyli and Phyllospondyli exhibit similar evolutionary trends to those which we have just established for the Labyrinthodontia; and that at any given period the members of these two orders are of more advanced structure than the Labyrinthodonts.

We can therefore accept the Embolomeri as the most primitive of all Amphibia, and those which must most nearly resemble the fish ancestors of that class.

The fact that the evolutionary trends which we have been considering pass onward unchanged from the Embolomeri, through the Rachitomi to the Stereospondyli, whilst the habits of the animals concerned change from a primarily aquatic through a terrestrial to a secondarily aquatic mode of life, suggests that they are not induced by any external environmental conditions but have their origin within the animal's body, and owe their constancy of direction to the mechanism which determines the characters of the adult being so constructed as to be capable of modification only in certain definite ways.

The interest of this conclusion is much enhanced by the occurrence of similar trends in other orders, even the Urodela, which differ in many respects from other Amphibia showing traces of their presence.

The extremely close resemblance between the Dipnoi and the Urodela, a resemblance covering the respiratory and circulating systems, the urogenital apparatus, the brain, the skull, the histology and the embryology throughout, indicates them as the first fishes to be considered in the search for Amphibian ancestors.

These resemblances are specifically between the Dipnoi and the Urodela, they appear most strikingly in a comparison of Lepidosiren with a perennibranchiate Urodele, and are not nearly so pronounced if Ceratodus be compared with a frog or a Cœcilian.

A comparison between the skeleton of a Dipneust and that of an Embolomer breaks down entirely, there are no significant resemblances at all; indeed the two differ very widely in most points. The explanation of this failure is obvious; we are comparing a truly primitive Amphibian with a modern fish, highly specialised and quite unlike its own Palæozoic ancestors.

The work of Prof. L. DOLLO and of Mr. E. L. GILL, and the present speaker, has made it certain that the most primitive known Dipnoan is the Middle Old Red Sandstone fish, *Dipterus valenciennesi*, and that this fish presents so many resemblances in structure to the contemporary Osteolepids as to show that the two groups arose from a common ancestor not much earlier in date.

It is from this hypothetical fish that I believe the Amphibia to have arisen. The evidence on which this view is founded is most conveniently presented by a comparison of the structures of the skeleton, of the body form and movements, and of the mode of life, in an Osteolepid and an Embolomerous amphibian. In order to secure the materials for such a comparison I have been forced to investigate the Osteolepid structure anew, and am able to add very many new and striking facts to our knowledge of the osteology of that group.

The Osteolepids resemble the Embolomeri in having a brain case which in all is well ossified, although in the Upper Devonian Eusthenopteron and the Carboniferous Megalichthys it is much less massive than in the Middle Devonian Osteolepis. This brain case is not divided into separate bones in any known specimens, but the different regions are easily recognised.

The basioccipital forms a large circular condyle deeply pitted or perforated by the notochord. The exoccipitals reach up to a well-developed supraoccipital, which in Osteolepis stretches forward over the whole of the hind brain, as it does in Embolomeri. The otic capsule forms a paroccipital process which supports the tabular, and may or may not be in contact with the skull roof for the whole of its length, precisely as in the Amphibia. As in them the anterior part of the brain lies in a cavity in the upper part of a thick interorbital septum whose lower edge is the parasphenoid.

The basisphenoid in both fish and Amphibia has definite basipterygoid processes with which the epipterygoids articulate.

But the Osteolepids differ from the Embolomeri and from all other vertebrates except their descendants, the Cœlacanths in the presence in their basis cranii of a long unossified tract, lying between the basioccipital and the basisphenoid and bounded laterally by the pro-otics.

There can be no doubt that this region of the basis cranii remains unossified to allow of a dorso ventral flexure of the skull, whose possibility is made clear by the presence of a hinge between the parietals and frontals on the dorsal surface. The whole arrangement is no doubt associated, as a similar mechanism is in Dinosaur skulls, with the possession of long jaws with powerful teeth.

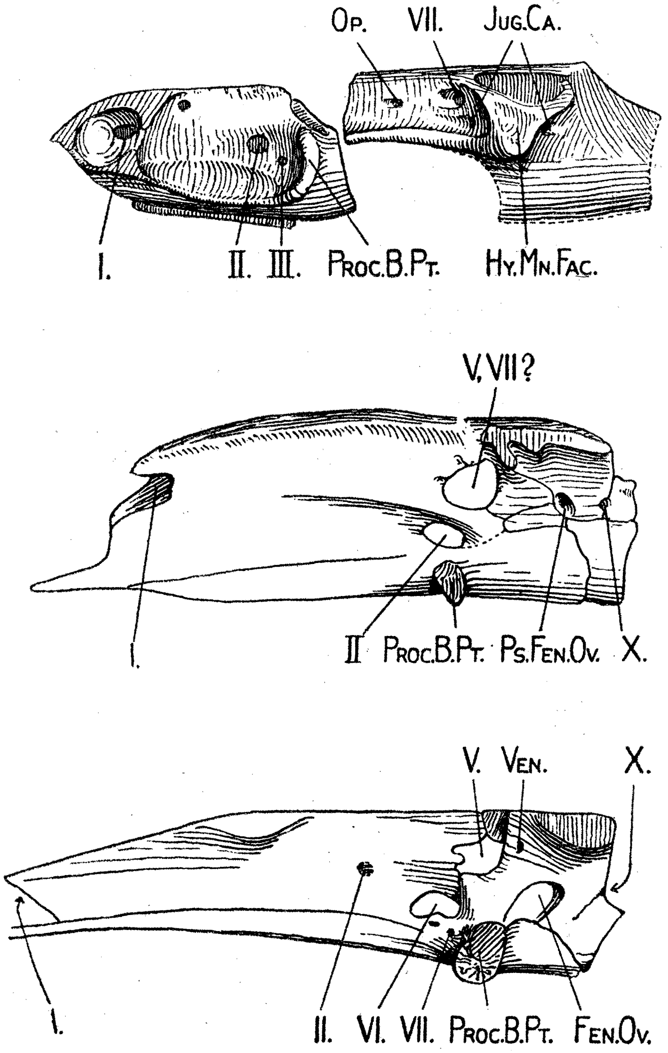

Fig. 1.*—Left lateral aspects of the brain cases of :—*Osteolepis macrolepidotus,* Middle Old Red Sandstone, Tynet Burn, Banffshire. × 3 approx. *Palæogyrinus decorus.* Middle Coal Measures, Fifeshire. *Eryops megacephalus.* Lower Permian, Texas.

The shield of dermal bones which cover the outer surface of the head in both Embolomeri and Osteolepids is composed in the main, of homologous bones. The lateral line canals enable us to recognise the tabular and post-parietals : the supra and inter-temporals and the ring of circumorbital bones, the post-frontal, post-orbital, jugal, lachrymal and pre-frontal.

The cheek, in the fish, is composed of a variable number of bones, five, three, two and one occurring in different genera. Of these, one is shown by its relation to the quadrate and maxilla to be the quadrato-jugal ; the squamosal, the only other bone in Amphibia being either an enlargement of one of the other bones or the product of their fusion.

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* A key to the reference letters will be found on page 257.

Certain of the Embolomeri (*Eogyrinus*) show an interesting intermediate condition in the fact that the upper edge of the squamosal in them merely articulates with and is attached by ligaments to the lower surface of the supra-temporal, whereas in Osteolepids these two bones are completely separated by the spiracular notch, and in later Amphibia they are rigidly connected by a digitated suture.

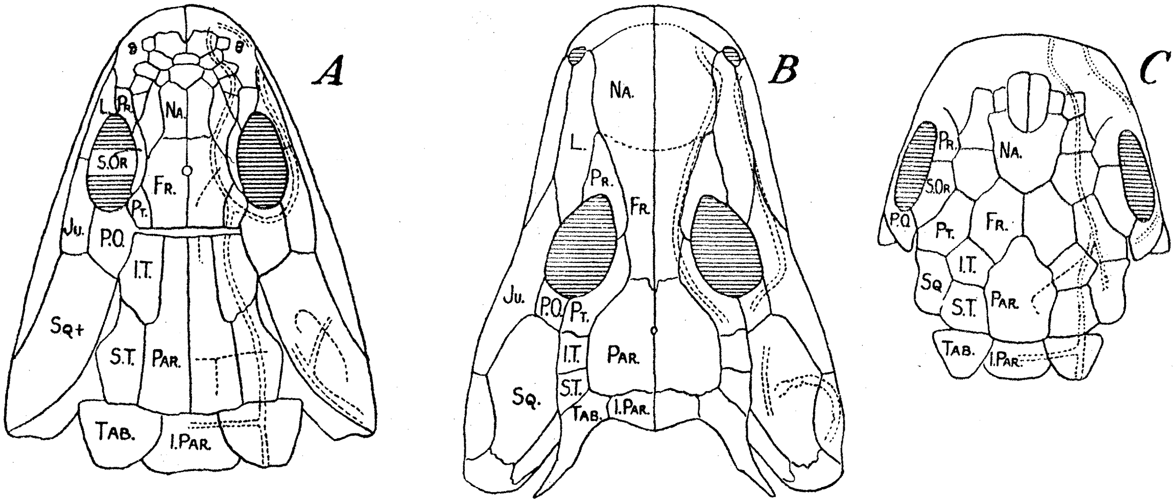

Fig. 2.—Dorsal views, reduced to the same size, of the skulls of :—A. *Osteolepis macrolepidotus*, Middle Old Red Sandstone, Tynet Burn, Banffshire. B. *Palæogyrinus decorus*, Middle Coal Measures, Fifeshire. C. *Dipterus valenciennessi*, Middle Old Red Sandstone, Achanarras, Caithness.

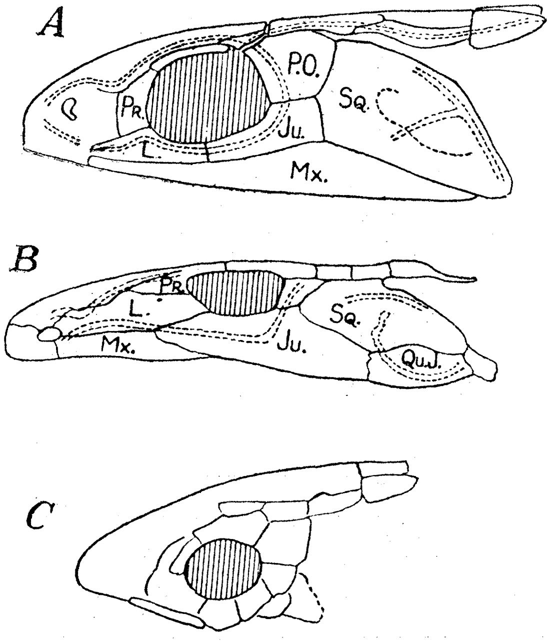

Fig. 3.—Left lateral views, reduced to the same size, of the skulls of :—A. *Osteolepis macrolepidotus*, Tynet Burn. B. *Palæogyrinus decorus*. C. *Dipterus valenciennessi*.

In both Osteolepids and Embolomeri the palate is bony, the interpterygoid vacuities being small.

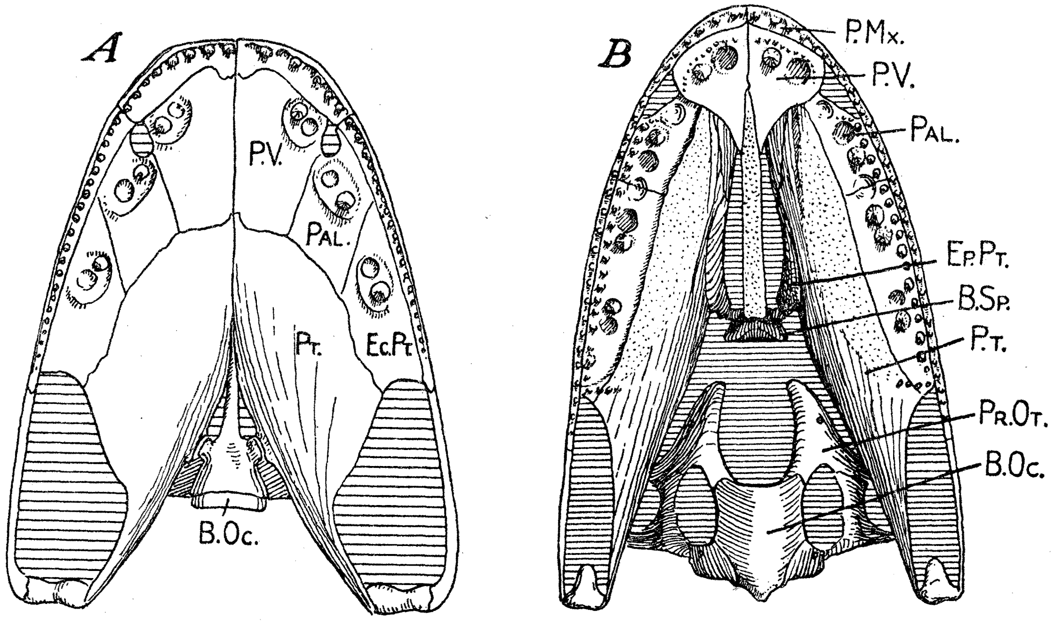

Fig. 4.—View of the palates, reduced to the same size of :—A. The Loxommid Amphibian, *Baphetes kirkbyi*, Middle Coal Measures, Fifeshire. B. The Osteolepid fish Eusthenopteron, Upper Old Red Sandstone, Scaumenac Bay, Canada.

In the Osteolepids, the palato-quadrate cartilage is represented in the adult by a continuous chain of bones, which begins posteriorly with the quadrate, and extends forward as a border to the upper and anterior edges of the para-otic plate and the inner margin of the palatal ramus of the pterygoid until the anterior bone rests on the ethmoidal region. One of these bones, which may collectively be called the suprapterygoids, is applied to the vertical anterior border of the para-otic plate of the pterygoid, separates the various branches of the Vth nerve and articulates with the basipterygoid process : it thus agrees perfectly with the epipterygoid of the Embolomeri.

The pterygoids, prevomers, palatines and ectopterygoids are identical in morphology in the Osteolepids and Embolomeri and the resemblance in such details as the distribution and mode of replacement of teeth is truly astonishing. The internal nostril found in all Osteolepids is identical in position, size and borders with that of certain Embolomeri.

The Osteolepid jaw is morphologically identical with that of the Embolomeri, but in the majority of cases, though not in Eusthenopteron or in the large Upper Devonian Polyplocodus, the coronoids bear large tusks, and are separated by foramina leading down into the jaw for the reception of the palatine teeth.

No such detailed comparison can be made between the Embolomeri and Dipterus because as an adaptation to a durophagous habit the skull and lower jaw of that fish present a reduction of the maxilla, and a consequent migration of the external nostril to the lower surface of the snout : a loss of the palatine and transverse bones ; the development of a pterygoidal tooth plate and a lengthy suture between the pterygoids and the parasphenoid, a shortening of the mouth, with an associated alteration in direction of the quadrate, and modification of the lower jaw, which are not and cannot be expected to be found in the rapacious Labyrinthodonts.

We have thus arrived at a formal solution of our problem, the Amphibia have arisen from an early and unknown group of bony fish, from which the Dipnoi and Osteolepids also sprang, which in the main features of its osteology resembled the latter group, differing only in the absence of certain specific adaptive characters.

But such a formal solution leaves untouched the main problem, the question of how the fundamental changes in mode of life occurred in such a manner that all the intermediate stages between fish and Tetrapod were capable of effective functioning. The most vital, and perhaps the most readily discussed, of these changes is that of the respiratory type.

In the Osteolepids, Dipnoi, and Amphibia there are three independent series of respiratory organs—the internal gills found in all fish, the lungs, and the external gills found in larvæ and in some adult Amphibia, and in the larvæ of Polypterus and two of the three living Dipnoi.

The Osteolepids possess a complete series of five pairs of branchial arches, implying the presence of a series of internal gills. In two Palæozoic Amphibia it has long been known that larvæ occurred which possessed a series of branchial arches represented in the fossils only by the gill rakers which covered their admesial surfaces. These arches approach the middle line, both dorsally and ventrally, and do not in the least recall the homologous structures in Urodela, which there give attachment to external gills. I am thus inclined to the view that they possessed functional internal gills.

In the Stereospondyli only one larva is known, the small Brachyopid described as *Brachyceps wilkinsoni*. In this specimen the branchial arches of opposite sides have very widely separated dorsal ends, continued by delicate extensions for a long distance. There can be no doubt that these structures formerly supported large external gills, which indeed persisted into the adult in the allied Dwinasaurus. It is thus natural to suppose that, as in the case of the Urodela, the external gill was originally a larval organ carried on to adult life during a secondarily aquatic stage.

The lungs of Lepidosiren and Protopterus, completely similar to those of the Amphibia in their blood supply, have always been regarded as the strongest evidence in favour of the close affinity of the two groups.

In Osteolepids we have no direct evidence of the condition of the lung, but in their descendants, the Cœlacanths, there is a large median air bladder, lying immediately below the vertebral column, which was, no doubt, inherited from them. In the fishes of the genus Osteolepis the ethmoidal region of the skull is occupied by a mass of finely cancellar bone in which lie a pair of small, laterally placed, nearly spherical cavities for the olfactory organs. These communicate with the exterior by anterior, and with the buccal cavity by posterior nares, exactly as in a Tetrapod. This arrangement, which is not paralleled in any other group of fish except imperfectly in the Dipnoi, presumably implies that Osteolepis habitually breathed air to reinforce the oxygen supply which it received through its gills.

The late JOSEPH BARRELL endeavoured to show that the habit of air breathing early arose in fish under circumstances in which they were intermittently exposed to conditions of poorly oxygenated water, and led to the introduction of a lung or air bladder as an essential feature of all bony vertebrates. By an application of his criteria of the conditions of sedimentation to published accounts of rocks of Old Red Sandstone age, Dr. BARRELL reached the conclusion, long upheld by Dr. J. W. EVANS, that such rocks are, in the main, the product of flood plain, river, and torrential deposition in countries with an arid climate and seasonal rainfall. Although some of the rocks—the Caithness flagstones, for example—in which the remains of Osteolepids are found must have been laid down in very extensive lakes, there can, I think, be no question that in the main Dr. EVANS'S and Dr. BARRELL'S conclusions are correct, and that Devonian times were characterised by a widespread occurrence of country with wide and superficial rivers traversing broad flood plains in arid or semi-arid countries. Under these geographical conditions the disconnected pools which represent the rivers during the greater part of the year are necessarily very poor in oxygen because they are rapidly filled with decomposing organic matter, which remains there until destroyed by bacterial action.

Thus, during Devonian times the conditions were such as to exaggerate the advantages of air as a respiratory medium. Under these circumstances the habit of taking air into the pharynx would be expected to arise, as it has done since in many siluroids, and even in roach and other British freshwater fish; and to a consistent addition to this habit it is natural to attribute the presence of a lung or an air bladder introduced to render air breathing more effective.

The original conclusion that the internal nostrils of Osteolepids imply an air-breathing habit is confirmed by the fact that whilst the Old Red Sandstone Cœlacanth Diplocercides possessed similar internal nostrils, the marine Triassic and Cretaceous Cœlacanths possess only an external nostril, usually divided into two as it is in Actinopterygii.

It is interesting to notice that the respiratory movements of Ceratodus are carried out by the same structures as those of Urodeles, and that they have an almost identical rhythm. In Ceratodus water is drawn into the buccal cavity through the mouth by lowering the basihyal, whilst the operculums are pressed inward so as to close the gill chamber. The mouth is then closed and the water expelled behind the operculum by raising the floor of the buccal cavity.

In the Urodela air is taken in through the nostrils by lowering the floor of the buccal cavity by means of the hyobranchial apparatus. This air is then forced down into the lungs by raising the basibranchials, the internal nostrils being closed by valves. Expiration takes place through the mouth.

These processes then differ only slightly, are carried out by the same muscles and, no doubt, controlled by the same nervous mechanism ; the transition from one type of respiration to the other can thus be carried out without any radical re-arrangements in the central nervous system.

We have still to account for the external gills. These structures occur in the larvæ of Lepidosiren and Protopterus, not in those of the certainly more primitive Ceratodus. The breeding habits in these fish appear to provide an explanation of this difference and to throw light on the original function of the external gills.

Lepidosiren and Protopterus lay a large number of heavy yolky eggs in a burrow in the ground under a very shallow sheet of water. In this burrow the male remains on guard for a considerable time. The eggs hatch and the young larvæ stop in the burrow until in Protopterus the internal gills become functional, the lung is fully formed, and the external gill begins to show reduction. In Lepidosiren the larvæ remain in the nest for a long time, perhaps till after the establishment of a functional lung, metamorphosis takes place, the external gills undergoing a very rapid reduction.

The function of the external gills thus appears to be to secure the necessary supply of oxygen to the developing larva in the dangerous period before the internal gills and lung become available. That the problem of aëration of a fairly large egg is difficult under the conditions in which Protopterus develops is vividly shown by the fact that two of the associated teleosts, Gymnarchus and Heterotus, develop a functional external gill by the great elongation of internal gill filaments.

Ceratodus does not make a nest but lays its eggs much as a newt does, scattered through and attached to the plants in fairly deep, permanent water. They thus develop under normal conditions in relatively well aërated water, and obtain a sufficient gaseous exchange through the skin and yolk sac until the lung and internal gills become functional.

Thus, it is natural to suppose that the external gills arose as a special accessory respiratory apparatus to carry the larva over the early stages of development. They must have arisen under the conditions which led to the production of a lung, and may have originated at the same time, either in the common ancestors of the Osteolepids, Dipnoi and Amphibia or separately in the latter two groups.

The fact that Polypterus, which has nothing whatever to do with the Osteolepids, differs from all other Actinopterygii in the possession of an external gill suggests that such a structure has indeed arisen several times.

The living aquatic Urodeles swim in a characteristic manner by lateral flexures of the whole body, each point along the axis exhibiting a regular rhythmical movement in a transverse plane, and each point being behind an anterior point in phase. The range of the excursion becomes greater as the posterior end is approached. The result is that a series of lateral waves appear at the head and pass backward over the body and tail. During this motion, when the animal is moving rapidly, the hands are pressed against the ventral and lateral surfaces of the body, and the hind legs are extended along the tail, with the soles of the feet inward.

This mode of swimming is identical with that which occurs in the fusiform Elasmobranchs, and in the Dipnoi and presumably in Polypterus; but it differs very markedly from that characteristic of the teleosts which occurs typically in a trout or goldfish. In these animals the chief swimming motion is restricted to the pedicel of the tail, and the dorsal and ventral muscles are usually out of phase, so that the caudal fin has a screw propeller action.

This difference in swimming habits is fundamental; it is associated with that process of loss of the epichordal lobe and gradual withdrawal of the muscular end of the body which is an essential part of the history of the Actinopterygii.

The Elasmobranchs differ from the Urodeles in that their paired fins are rigid structures, carried during swimming as projecting lateral keels used as stabilising planes and for bringing about changes of direction in a vertical direction. But Ceratodus and also Polypterus when swimming rapidly press their pectoral fins against the body exactly as do the Urodeles.

It is thus tempting to regard the mode of swimming used by all Urodeles as a direct inheritance from fish which had the type of locomotion possessed by the Dipnoi and Polypterus, but it has to be remembered that the evidence from many lines of investigation is conclusive in showing that the aquatic Urodeles are the descendants of terrestrial forms which have secondarily extended the length of the period of that life in water which is a necessary part of their larval existence.

There is, however, another feature of their locomotion which throws light on the whole problem. The Urodeles and the lizards, and quite certainly also all the early reptiles, walk on land in a manner which is an exact repetition of the swimming of a Urodele. In them the body is again thrown into lateral flexures, waves starting at the head and passing backward to the tail; the limb is always at its extreme anterior position when the glenoid cavity with which it articulates is facing anteriorly; that is, when it lies in the posterior half of a concave lateral surface. The relation of the phases of the fore and hind limbs of the same side depends on the length of the body.

It deserves to be noted that this motion by itself will enable the animal to walk without any independent movement of the limb apart from such motion in a vertical plane as is necessary to enable it to engage and to be lifted up from the ground, and to ensure that the friction between the foot and the ground be greater than that between the ground and the ventral surface of the animal.

The length of the stride can, however, be increased by a fore and aft movement of the leg at its articulation with the body, and the friction between the foot and the ground will be increased if the foot be enabled to remain in a fixed position on the ground by the provision of an elbow joint and flexible wrist capable of movement in a horizontal plane.

I have already shown that all tetrapods have passed through a stage represented by such Amphibia as Eryops, and such reptiles as Diadectes, in which the humerus is only capable of movement of translation in a horizontal plane, and the elbow joint exhibits considerable freedom of motion in both horizontal and vertical planes. This type of limb seems to me to be an actual illustration of the results of the conditions which I have just pointed out.

The persistence of this type of body movement through the terrestrial stage to the secondary aquatic life of Urodeles is evidence in support of the view that it was in the first instance a direct inheritance from fish ancestors. It is clear that such walking movements are merely those used by fish in swimming transferred to land, and that they are carried out by the same structures without any profound modification.

If now we turn to a consideration of the skeleton of Eogyrinus, the most primitive known amongst the Amphibia, we find an animal, with a comparatively small head, a long cylindrical trunk, and in all probability, if we use the structure of Pholidogaster as an indication, a very long and certainly flattened tail. The only limb bone known, a femur, is very short—perhaps half the length of that of a crocodile of similar size.

The remains of this animal, and indeed of all other Carboniferous Embolomeri, always occur in association with the much more abundant fragments of fish, and there can, I think, be no question that the animals lived habitually in the water, feeding on fishes and only passing over the land from one pool to another either to find deeper water or to escape the attacks of the large fish.

Eogyrinus has a shoulder girdle of unique structure. The primary girdle is represented by a single bone, the scapula, on each side. This bone bears a very indefinitely demarcated glenoid cavity, which faces directly outward, and has three processes radiating from the central mass; of these the dorsal is much the larger and bears, on the outer surface and toward the cranial margin, a depressed and roughened area for attachment to the cleithrum.

The two other extensions lie in the horizontal plane of the glenoid cavity and served purely as muscle origins. The small size of the bone and the character of the glenoid surface suggest that only very slight movement of the forearm at the shoulder joint was possible, and that the definite restriction of the humerus to motion along a single track, which is so marked a feature of the shoulders of Rachitomous Amphibia and early reptiles, had not yet been acquired. If this bone be compared with the scapula of an Osteolepid it will be found to differ in being somewhat larger and especially in the twisting round of the glenoid cavity on to the outer surface and the associated growth of a posterior process of the scapula behind it. By these changes the limb, instead of being directed backward nearly parallel to the body, acquires a normal position at right angles to the animal's principal plane and is firmly held in place by three sets of muscles.

The shoulder girdle of Eogyrinus is unique also in the character of its dermal elements. It retains the full series of four pairs of dermal bones found in primitive bony fish, and adds to them a median interclavicle, firmly attached to and indeed wedged in between the lower ends of the clavicles.

The most dorsal pair of elements, the post-temporals, are rigidly attached by obvious roughened and scarfed faces to the ends of the tabular horns. The supracleithra are small quadrangular elements and the cleithra and clavicles broad plates of bone distinguishable by little but their surface ornament from those of Osteolepid fish.

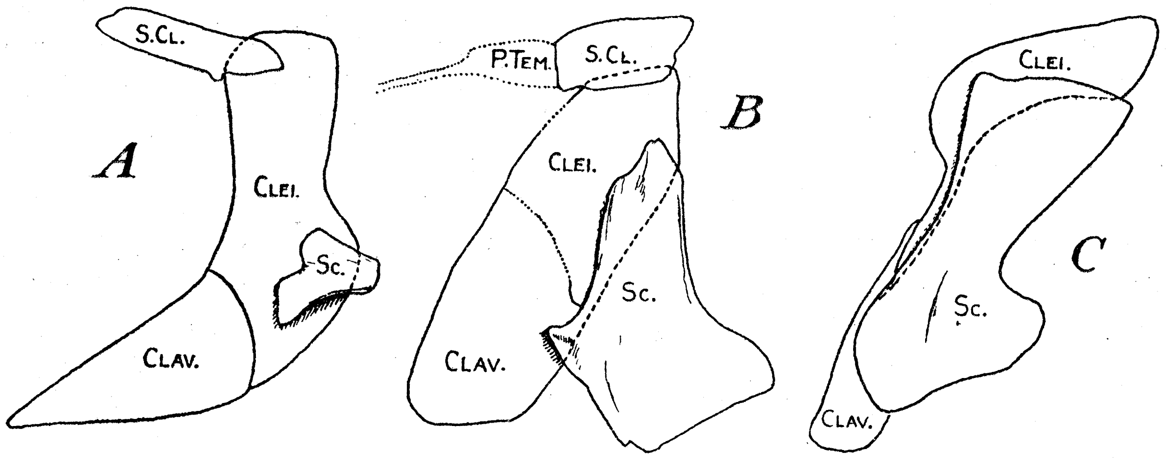

FIG. 5.—Drawings of the visceral surfaces of the right halves of the shoulder girdles, the interclavicles being omitted of:—A. The Osteolepid fish Eusthenopteron. B. The Embolomerous Amphibian Eogyrinus. C. The Rachitomous Amphibian Cacops.

The dermal shoulder girdle of Osteolepids is histologically identical with the scales which cover the body; it forms in them, as it does in Polypterus and Lepidosteus, a margin to the gill chamber, and no doubt arose merely to provide a firm starting point for the squamation and an attachment for the anterior end of the lateral muscles of the trunk left isolated by the great extension of the gill clefts, which is an essential part of the process of evolution of bony fish.

The association of these dermal bones with the shoulder girdle is hence in all probability accidental, the pelvis far removed from the gill region has no such structures.

The changes which are necessary to convert the fish-like shoulder girdle of Eogyrinus into that of later Amphibia are capable of a mechanical explanation, or rather they can be shown to fulfil mechanical needs.

The typical shoulder girdle of the terrestrial Labyrinthodonts is already fully developed in the Stephanian Embolomerous form Diplovertebron.

The changes which have occurred are that the scapula, at any rate in the better-known Rachitomi, has developed a screw-shaped glenoid cavity, involving the limitation of the movement of the humerus to a definite track, and that the dermal elements have become much modified. The connection with the skull is lost and the post-temporal and supracleithrum go with it; the ventral part of the cleithrum and the dorsal part of the clavicle which is articulated with it are reduced to slender rods, and have sunk down into the muscles losing their connection with the skin: whilst the remaining parts of these bones retain their original widths and superficial position. The interclavicle has grown much larger so as to afford a firmer attachment to the clavicles.

These changes appear to depend on alteration in the musculature. The posterior edges of the cleithrum and clavicle are cut away so as to free a larger area of the scapula for the attachment of scapulo-humeralis muscles.

The loss of the connection with the skull results in such freeing of the head as allows of lateral movement, a motion which becomes more and more restricted, and finally lost by the development of a pair of well-separated exoccipital condyles in later Labyrinthodonts.

This possible lateral motion of the head is most readily carried out by cranio-clavicular muscles, and the range of action of these muscles can only be increased by lengthening them, such lengthening is most conveniently done by cutting away the anterior borders of the clavicles and cleithra. Thus attached from both edges these then become converted into narrow rods.

This analysis presupposes that the shoulder girdle lies some way behind the skull. This is in fact the case in all Embolomeri, but in later Labyrinthodonts, and the early reptiles, the shoulder girdle moves up to the head, presumably to decrease the load carried by the fore limbs. Such situation must have entirely prevented lateral movements of the head.

Another change of importance found in the secondarily aquatic Labyrinthodonts is an immense widening of the lower ends of the clavicles, the mechanical meaning of this arrangement is obscure, but it is clearly a condition following on the terrestrial type just described. It occurs even in the Lower Carboniferous Pholidogaster and gives still further evidence of the great age of the Amphibia.

The structure of the pelvis of the Embolomeri is fish-like in one respect. In them the ilium shows no trace of rib attachment, and bears a long posterior process. The perfect sacrum of Eogyrinus shows that these ilia rested on long sacral ribs, exactly as does a scapula on those of the thorax, and was attached to these by muscles. There is less complete evidence of a similar structure even in the terrestrial Diplovertebron.

Thus, as in the case of the respiratory movements, locomotion in the most primitive Amphibia is carried on by a series of muscular movements carried out by the same structures and with the same rhythm as in the fish ancestors, the first tetrapods in fact swam upon land. But once the terrestrial habit was established, evolutionary changes take place in the limbs and limb girdles which, unlike those which we have already considered, have directly adaptive results, and alter their direction with modification of the habits of life.

On one other important element in the story of the conversion of a fish into a Tetrapod, some light is thrown by the structure of the Embolomeri.

In Osteolepis, the internal ear is known to have a very simple arrangement of semicircular canals, the vestibule opening into the cranial cavity by an aperture of considerable but not very large size. The cavity for the saccular part of the labyrinth is large and part of its outer wall appears to remain unossified. The hyomandibular articulates with the paroccipital process nearly in contact with the skull roof, and as in the majority of teleostomi is perforated by a canal for the passage of the hyomandibular trunk of the VII$^{\text{th}}$ nerve. The so-called jugular vein passes through a canal which perforates the paroccipital process.

The region where a fenestra ovalis would be expected is only known in two Embolomeri, and in each case there is complete evidence to show that no such opening occurs. The pro- and opisthotics bear a deep pit on their suture in the proper position, but this is closed by a thick floor of bone. In one Embolomerus form a stapes is shown in position, it is a short curved rod of bone, more than a centimetre wide and 5 mm. thick, which stretches from the otic capsule upward and outward until it ends in the otic notch, flush with the general outer surface of the head. Its presence shows that a tympanic membrane had already been developed, and that the sense of hearing was already in existence. But this stapes lies at right angles to the direction of the hyomandibular of fish, and articulates much lower down on the otic capsule.

There is, however, in all the members of that group of Embolomeri which includes Loxomma, a curious pit on the quadrate, so placed that it faces toward the otic capsule which must have housed some structure. This can only have been a cartilaginous process from the stapes, representing the lower part of the hyomandibular.

The living reptiles exhibit a curious four-rayed columellar apparatus, one leg passing inward to the fenestra, the opposite one to the tympanic membrane, a third goes downward to the hyoid, and the fourth is attached to the end of the paroccipital process—that is, it occupies the position held by the head of the hyomandibular in Osteolepis. I believe the process to have been present in Embolomeri, and that both it and the foot plate of the stapes represent the original head of the hyomandibular divided into two by an enlargement and migration upward of the hyomandibular foramen, the inner of the limbs so formed migrating downwards over the jugular canal to its final position.

The fact that a tympanic membrane connected to the otic region by a stapes can be formed before the formation of a fenestra ovalis is an astonishing one, perhaps most readily understood if it originally took place in water, where the amount of energy which can be conveyed by sound waves of reasonable amplitude is greater than in air.

We have thus seen that in some cases, at any rate, the mode by which the changes necessary to convert a fish into Amphibian took place was such as to demand little modification of function of any part of the animal, and to avoid the necessity of any sudden reconstruction of the nervous mechanism which controlled its activities.

Furthermore, the transformation as a whole is built up by the modification of many sets of organs, and we have seen reason to believe that these changes took place independently over a long period of time. Some, such as the introduction of a lung in fish ; others only after the animals had definitely become Tetrapods.

In this long-drawn out metamorphosis the origin of the Amphibia resembles that of the Mammalia, but it seems to differ greatly from that of Reptilia, a group whose earliest members differ only in very slight particulars from those Embolomeri which we have seen to be the most primitive of all known Amphibia.

Thus a study of fossil history enables us to obtain a clearer conception not only of the nature of the morphological changes involved in the origin of the Amphibia, but also of the conditions under which and modes in which these changes occurred, and at the same time it adds another to the many cases known to palæontologists of an evolution proceeding steadily in definite directions with time, and contrasts it with another type of evolutionary change with an obvious adaptive significance.

The arguments of the foregoing Lecture rests on the structures of the Embolomerous Amphibia and of the Osteolepid fish. Of the former group practically no information is to be found in print. The only important papers—those by T. ATTHEY, A. HANCOCK and D. EMBELTON—were published nearly fifty years ago, and, though of considerable accuracy, and distinguished by very remarkable morphological insight, they have never been correctly interpreted by any subsequent writers, and in any case are not concerned with those structures which we now know to be of the greatest importance.

I therefore give accounts of the structure of the skull in three genera, an account of the post-cranial skeleton with a restoration of the animal in one of them, and a very brief account of the skeleton in the little Stephanian Diplovertebron. I then give an account of the structure of the Osteolepid skull and lower jaw founded on the genera Megalichthys, Eusthenopteron and Osteolepis. Finally, I refer to one or two problems on which this material throws light, but which do not formally form part of a study of the Origin of the Amphibia.

Orthosaurus pachycephalus, BARKAS, 1873.

= *Loxomma Allmanni*, HANCOCK and ATTHEY, 1870, 1871, 1872; EMBELTON and ATTHEY, 1877; L. C. MIALL, 1874; *non* HUXLEY, 1862.
= *Megacephalus macromma*, BARKAS, 1873.
= *Pteroplax cornuta*, HANCOCK and ATTHEY, 1868, *in errore.*
= ? *Rhizodus lancifer*, NEWBERRY, 1856.
= ? *Pteroplax brevicornis*, THOMSON and YOUNG, 1871.
= ? *Leptophractus lineolatus*, COPE, 1877.

The commonest Embolomerous Amphibian in the British coal measures is that which is usually but incorrectly determined as *Loxomma Allmanni*, HUXLEY. Comparison of the figures of the present paper with that of the type specimen will show that although allied, the two forms are different. The earliest certain name for the animal is *Orthosaurus pachycephalus*, BARKAS.

Orthosaurus is represented by a complete uncrushed skull filled with ironstone, from Coalbrookdale, No. R. 555, in the British Museum, by two incomplete skulls from the New Main Seam of Newsham, Northumberland, and four more from Staffordshire, in the same Museum, and by two complete, six incomplete skulls and a large number of isolated skull bones from Newsham, and an incomplete skull from the Parrot coal of Pirnie Colliery, Fifeshire, in the Hancock Museum, Newcastle-on-Tyne. There are one complete and nine incomplete rami of the lower jaw from Newsham, in the Newcastle Museum, and other fragments from various localities in the British Museum.

It is remarkable that except for a single intercentrum speared by a palatal tooth of the Newcastle skull D.M.S.W.2,* no bones of the trunk have ever been found definitely associated with remains of Orthosaurus ; it is thus impossible to determine which of the great numbers of isolated vertebræ and ribs of Embolomeri in Newcastle belong to it. As the skulls are much the commonest at Newsham, it is probable that the majority of the loose bones are really Orthosaurus.

No isolated neural cranium of Orthosaurus is known, and the dorso-ventrally crushed examples remaining *in situ* in the many skulls afford little information about its structure.

The isolated basioccipital D.M.S.W.9, is a small bone, somewhat conical in shape, the base forming the larger part of the deeply concave single occipital condyle ; the rounded ventral surface is largely ridged for the attachment of the hinder end of the parasphenoid, laterally the suture between the two bones passes over a pair of low, rounded eminences, the first trace of tubera basisphenoidales for the attachment of the recti capitis muscles.

The exoccipital is distorted in all the known specimens, but it has been crushed in so many different ways that the main outlines of its structure are clear. The lower end (D.M.S.W. 2 and 5) articulates with the upper surface of the basioccipital, the inner margin meeting or very nearly meeting its fellow of the opposite side so as to exclude the basioccipital from the brain cavity. The articular face for the basioccipital is continuous with another which forms the upper part of the single nearly circular occipital condyle, which is thus structurally triple as is that of a turtle.

Above its base the exoccipital rises as a massive column (D.M.S.W.2.), whose inner surface forms the side wall of the brain case, whose caudal surface bears an articular face carried on a low projection, and whose outer face is freely exposed. This column has a suture with the supraoccipital above, and is fused with the paroccipital in front. The upper ends of what appear to be the exoccipitals reach up to the roof of the skull on the outer side of the supraoccipital, the three bones forming a joint surface facing backward and upward and terminating below and behind in an abrupt margin, below which the hinder surface of the exoccipital begins. (D.M.S.W.3, 5, 7.) The lower part of the exoccipital is perforated by a small foramen agreeing exactly with the hypoglossal foramen of a reptile. (D.M.S.W.2.)

The supraoccipital is a small bone wedged in between the par- and exoccipitals and the

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* Number D.M.S.W. 1, etc., were given by me to the specimens in the Hancock Museum, Newcastle-on-Tyne, for convenience of reference.

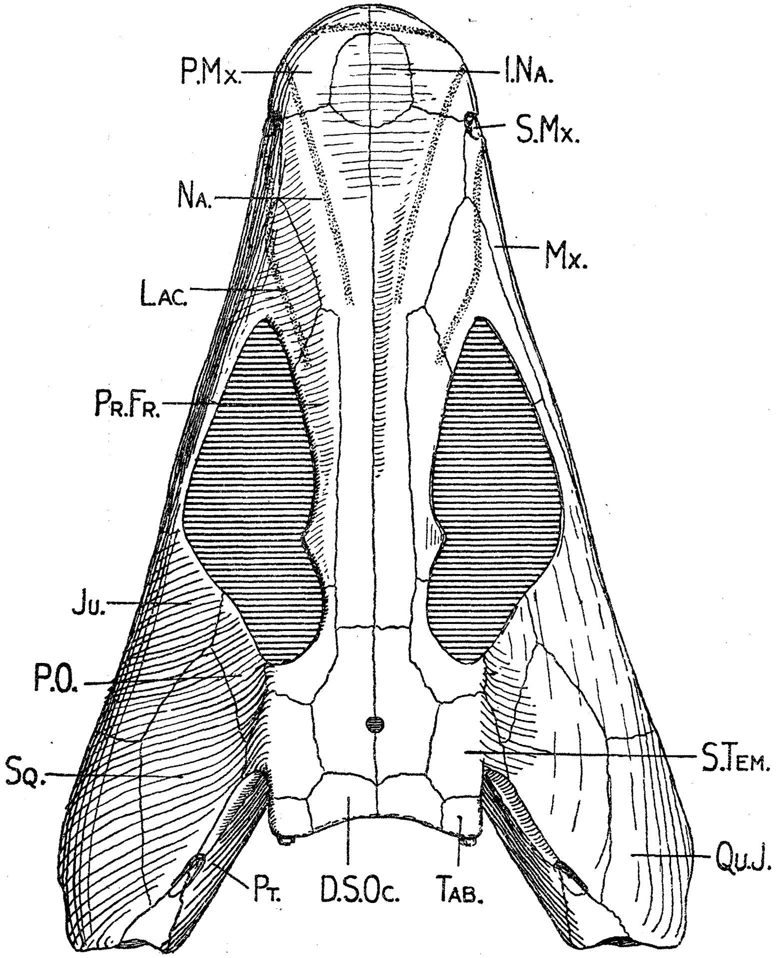

Fig. 6.—*Orthosaurus pachycephalus*, Barkas. Dorsal aspect of the **skull** × 4/9. Outline from B.M.N.H., No. 555, from Coalbrookdale; **all details** from the Newcastle skulls Nos. D.M.S.W. 1, 2, 4, from **the Low** Main Seam, Newsham.

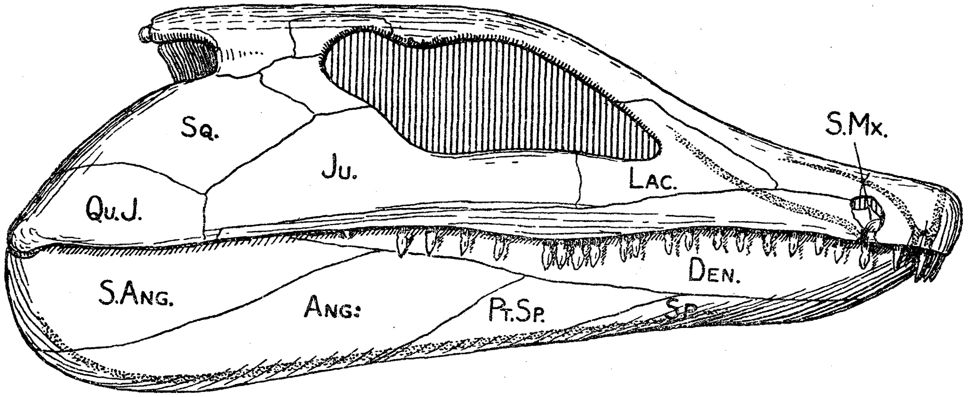

Fig. 7.—Right lateral aspect of the skull and lower jaw, × 4/9, from the same material as fig. 6.

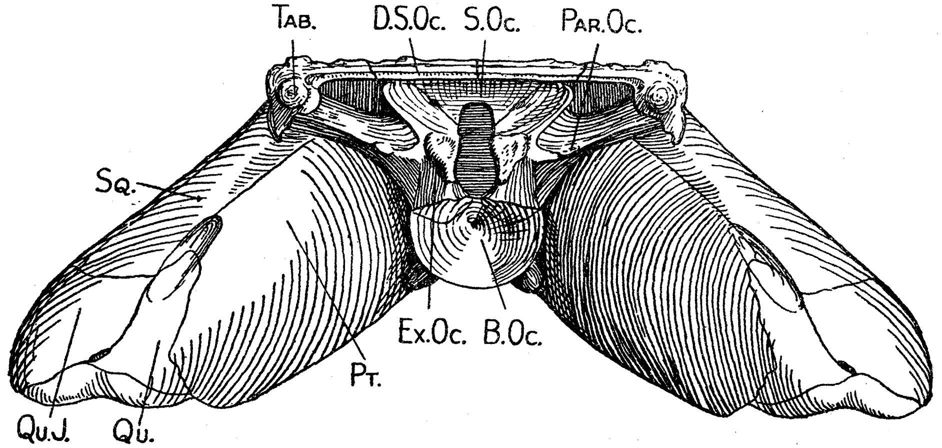

Fig. 8.—*Orthosaurus pachycephalus*. Reconstruction of the occipital aspect of the skull, from the same material as fig. 6 × $\frac{2}{3}$.

skull roof. It forms the summit of the foramen magnum. A small foramen enters the suture between the ex- and supraoccipital.

The paroccipital process is very much crushed in all the specimens available. In D.M.S.W.7 it has slipped backward so that nearly a centimetre of its dorsal surface is exposed behind the roof of the skull. This specimen, especially when considered in connection with D.M.S.W.5 and 3, shows conclusively that there was a post-temporal fenestra of considerable width and depth. D.M.S.W. 15, an isolated tabular, shows the grooving of the lower surface for the articulation of the outer end of the paroccipital process, and D.M.S.W.16 shows that the outer end of this process was of very considerable antero-posterior length. The hinder border of the paroccipital process at about the middle of its length, bears a short process, presumably a muscle attachment. D.M.S.W.16 shows that the outer surface of the lower part of the paroccipital process is pitted as is that of Eogyrinus, but the region where the fenestra ovalis is to be expected is not exposed in any specimen.

The basisphenoid and indistinguishable parasphenoid are well exposed from below in most of the skulls. The rounded lower surface of that part which covers the basioccipital gradually narrows as it is traced forward, until it suddenly gives rise to the short well-formed basipterygoid processes which project downward and a little outward. The anterior and lateral surface of each process forms an articular face which is obscurely divided into two—an upper for the base of the epipterygoid, and a lower for the pterygoid itself. The admedian surface of each basipterygoid process is impressed by a groove, which descends from the side of the basis cranii, coils round the process and finally plunges into a foramen in the lower surface of the basisphenoid in advance of the process; these grooves and foramina are obviously for the internal carotids, which had a normal reptilian course.

Further forward the parasphenoid continues as a sheath to the lower margin of the well ossified inter-orbital septum.

The structure of the roof of the skull was well described by EMBELTON and ATTHEY (1877), and is obvious from figs. 1 and 2 of this paper. Only two additions need be made to ATTHEY'S description. The skulls D.M.S.W. 1 and 2 show definite internasal ossicles, small paired bones lying in the sutures between the premaxillæ and nasals; their presence is confirmed by the shape of the hinder margin of isolated premaxillæ.

In D.M.S.W. 2 there are septomaxillæ on both sides; they are small, entirely superficial bones with the usual pitted and grooved external surface. They rest on that part of the upper margin of the maxilla which forms part of the nostril, and they largely fill that opening. The dorsal margin bears a small point at about the middle of its length. The attachment to the maxilla is an extremely loose one, and it is probable that the bones really acted as valves, closing the nostrils when the animal was submerged.

One other curious feature of the skull roof deserves notice: in D.M.S.W. 2 there are a pair of small perforations in the suture between the premaxillæ and the nasals

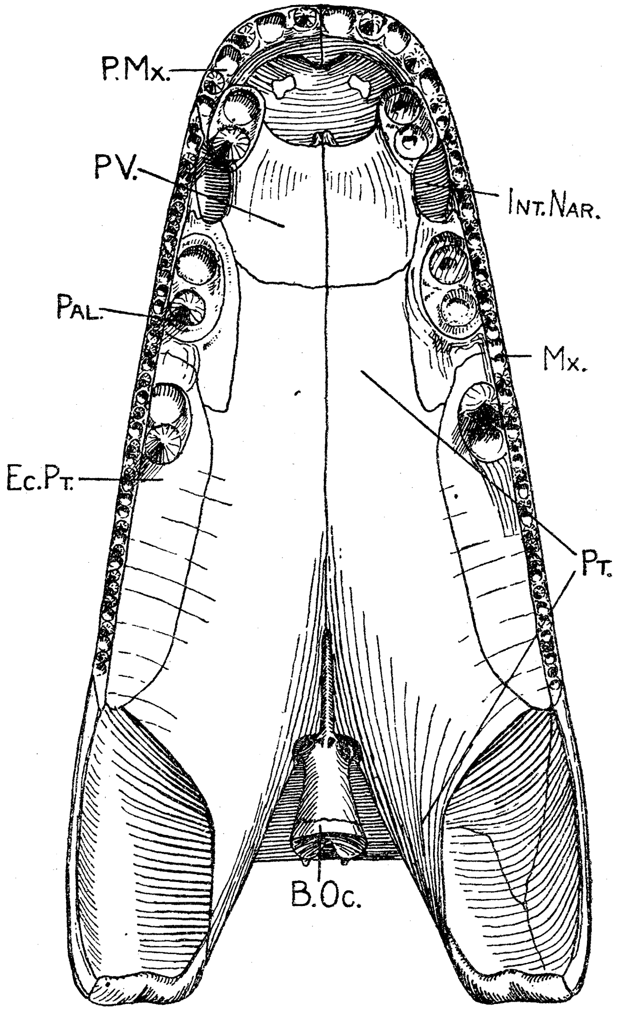

Fig. 9.—*Orthosaurus pachycephalus.* Palate × $\frac{1}{3}$. From the Newcastle skull D.M.S.W. 2, which is a very large individual with a skull with nearly parallel lateral sides.

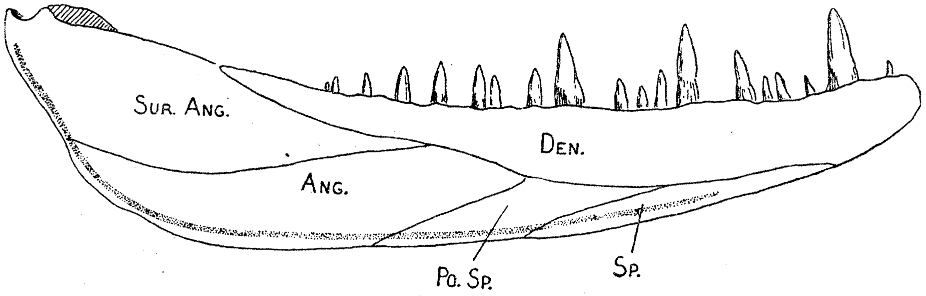

Fig. 10.—*Orthosaurus pachycephalus.* Right ramus of the lower jaw, outer aspect × $\frac{1}{3}$. From the whole Newcastle material.

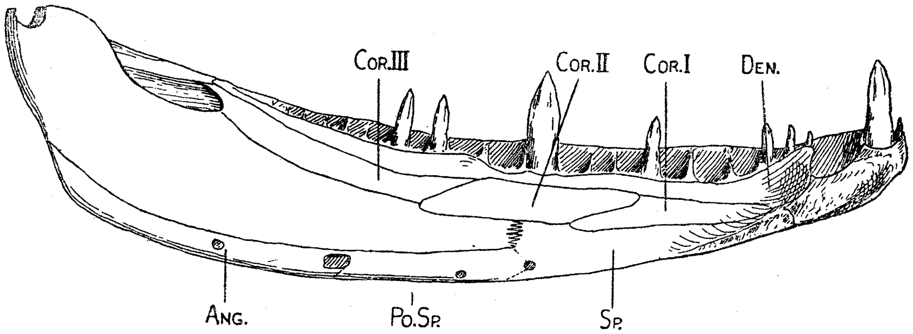

Fig. 11.—*Orthosaurus pachycephalus.* Left ramus of the lower jaw inner surface × $\frac{1}{3}$. From the whole Newcastle material.

which served, as do similar openings in Mastodonsaurus, to receive the tips of the enlarged teeth of the anterior end of the lower jaw; they are not present in the smaller skull D.M.S.W. 1.

My former short description of the palate requires certain small corrections and extension. The large series of skulls available shows that the proportions are very variable. My 1912 figure represents a very broad skull; fig. 4 of this paper an unusually narrow and very large skull, which may be specifically distinct.

The palate as a whole appears to have been nearly flat, and is supported by bone throughout the whole of its extent, with the exception of very small nares, anterior palatal vacuity, interpterygoid vacuities and sub-temporal fossæ.

The pterygoid is a very large bone formed by an enormous palatal ramus which articulates with its fellow in a very long median suture, and has the whole of its lateral margin in contact with the other bones of the palate. The palatal ramus passes directly by an upturning of its admesial edge into the quadrate ramus, which rises nearly vertically towards the skull roof. The upper and hinder border of this part of the bone overlaps the inner and hinder surfaces of the well-ossified quadrate, and has a long suture with the subotic border of the squamosal. At the point where these three bones meet there is a peculiar sharply defined pit on the upper surface which, in the uncrushed skull, must have faced toward the otic region.

The prevomers (D.M.S.W. 13 is an isolated example) have a long median suture with each other. Their anterior border is thickened and forms the hinder margin of the relatively large anterior palatal vacuity, which exists to receive the points of the large anterior teeth on the mandible. The lateral border of each is in contact with the premaxilla and maxilla by a thick sutural surface in front, whilst in the middle of its length it forms the inner border of the naris and posteriorly has a suture with the palatine. Just within its contact with the maxilla in front of the nostril the prevomer usually bears a single large tusk, with a pit for the replacing tooth alongside it; exceptionally either two teeth or none may be present, according to the stage of tooth replacement.

Further examination of the material shows that my former account of the palatine and transverse bones was incorrect in one respect. The palatine is a small rhomboidal bone which forms the hinder border of the naris, and then extends backward between the prevomer and pterygoid on one side and the maxilla on the other, until it terminates at a suture with the transverse bone. The palatal surface bears a large oval depressed area surrounded by a low, ill-defined ridge. In this area are situated two pits for the tusk and its replacing tooth; these pits are visible even when a tooth is present, and vary in structure according to the condition of the tooth, whether it is functional, has just been shed, or is in process of growth.

The transverse bone lies immediately behind the palatine and has a very similar structure, bearing a similar depressed area and tooth pits toward its anterior end. In my former description, on the evidence of an isolated specimen of the two bones conjoined (D.M.S.W. 8), I regarded the two sets of teeth as both belonging to the palatine, and the transverse as toothless. The present reading depends on two isolated palatines (D.M.S.W. 9 and 12) and on a visible suture between the two sets of teeth in D.M.S.W. 1 and 2. There is, however, a very remarkable possibility presented by D.M.S.W. 8, where the hinder end of the posterior tooth-bearing bone appears to be natural, and by D.M.S.W. 3 : this is that the second tooth-bearing bone is really short, a suture separating the bone described above as transverse into two, an anterior tooth-bearing and a posterior toothless (the transverse of my 1912 description). Though the evidence is not good enough to be certain of the presence of a hitherto unknown bone in a Tetrapod skull, nevertheless the possibility is sufficiently great to be worthy of consideration in all discussion of the homologues of fish and Tetrapod palatal elements.

Lower Jaw.—It is now apparent that my former description of the lower jaw of " Loxomma " was very incomplete, though I believe that most of my determinations of sutures were accurate.

As shown by the uncrushed skull in the British Museum, the ramus of the lower jaw was thick from side to side, the meckelian cavity being very roomy and the bones thin. All the bones unite by deep overlaps, the sutures on the lingual surface running longitudinally. The well-preserved rami are all crushed quite flat, the two surfaces being brought into contact ; during this distortion the bones of the inner surface slid over each other so that their apparent widths vary very greatly in different specimens ; furthermore, no complete and well-preserved ramus is known. The determination of the real structure is thus very difficult ; figs. 5 and 6 represent the jaw as crushed flat, the widths of all the bones being an average of many specimens. The main outlines of the structure are, however, quite certain.

The material in the Hancock Museum is as follows :—

D.M.S.W. 26, a complete right ramus, outer surface, sutures not visible.

D.M.S.W. 19, left ramus of the same individual as 26, broken off through the hinder end of the dentary ; sutures between dentary, splenial and post-splenial well shown on the outer surface, between pre-articular and splenial and these two elements and the two anterior coronoids on the inner side.

D.M.S.W. 21, left dentary and splenial, isolated but imperfect anteriorly.

D.M.S.W. 24, anterior part of right dentary, splenial and anterior coronoid, inner surface exposed.

D.M.S.W. 17, right dentary with the two anterior coronoids in position, inner surface.

D.M.S.W. 23, middle part of right ramus, both surfaces exposed, shows sutures between dentary, sur-angular, angular, post-splenial, pre-articular and posterior coronoid.

D.M.S.W. 20, middle part of left ramus, both surfaces exposed, shows sutures between dentary, sur-angular, angular, post-splenial, and pre-articular.

D.M.S.W. 22, hinder part of left ramus, both surfaces exposed, shows sutures between dentary, sur-angular, angular and pre-articular.

D.M.S.W. 4, impression of the upper surface of the hinder part of an uncrushed jaw.

Collation of the details of the foregoing specimens will show that the important and difficult sutures of the inner surface have all been confirmed in the most satisfactory manner by disarticulated specimens; the structure of the jaw as represented in figs. 5 and 6, is thus certain except for those possible errors of proportion which have been explained above.

The articular is a small but very powerful bone; its upper surface being entirely formed by the very deep hemicylindrical articular face, which makes a very accurate fit with the quadrate. The caudal surface descends immediately from the posterior margin of the articular area, there being no trace whatsoever of any post-articular part of the jaw. The lateral surfaces are entirely covered by the pre-articular and sur-angular, which not improbably meet in suture behind it.

The sur-angular lies entirely on the outer surface, with its lower border in contact with the angular.

The angular is in the main a bone of the outer surface, but in the flattened rami it appears on the inner surface as a narrow strip along the lower margin of the jaw; this inner flange in life probably lay on the broad, rounded lower surface and may have been invisible in lingual view; it is pierced by one or more foramina leading to the cavity of the jaw.

The post-splenial (= pre-angular) was not recognised by me in 1912. No specimen available shows both sutures bounding it, and it is only by making very careful drawings, reduced to the same size, from all the specimens and then superimposing them that it is possible to be certain of its presence. It is a small bone lying between the splenial and the angular, and agreeing with the latter in lying almost entirely on the outer surface but having a minute internal flange in the crushed jaws.

The splenial is a remarkable bone, which at first sight lies entirely on the outer surface, its lower margin being turned in so as to form a shelf between the two rami anteriorly. Specimens D.M.S.W. 19 and 24 show, however, that the bone really has an internal flange, small compared with the size of the jaw, but larger than that of the post-splenial; the upper edge of this flange is shown to articulate with the two anterior coronoids, and its posterior end to be attached by suture to a bone which can only be the pre-articular.

The anterior coronoid is a small slip of bone lying between the dentary and the splenial and extending far forward into the symphysial region.

The middle coronoid is similar to the first, but lies on the inner surface of the dentary, articulating with the splenial and pre-articular below.

The hinder coronoid is only shown in D.M.S.W. 23, where its anterior end is broken away, and crushing of the jaw makes it appear as if it ended in a point, the pre-articular meeting the dentary in front of it; further development of this specimen shows that at the anterior end the bone is still quite broad. The actual contact of this and the middle coronoid is shown in no existing specimen.

The dentary is a large and very powerful bone, overlapping all the other bones of the outer side of the jaw. It has a powerful but very irregular symphysial face, the two bones having been separated by a mass of ligaments. The upper edge of the bone is entirely occupied by a single row of tooth implantations; these are formed by a deep wall of bone on the labial side, whose inner surface ends at a shelf running inwards nearly horizontally, the individual teeth are separated by ridges on the wall and shelf.

The most anterior tooth is very small; the second and third, which replace one another and are functional alternately, are very large, biting into the anterior palatal vacuity. Behind these tusks is a series of four or five small teeth, the dentary in this region being narrowed from side to side so as to fit in between the pre-maxillary and maxillary teeth and the great pre-vomerine tusk; behind this region, a functional diastema, the teeth again become large and continue to the hinder end of the dentary.

The lower jaw teeth are throughout much larger than the maxillary teeth but are of the same type, having a laterally compressed, lancet-shaped crown, with sharp anterior and posterior edges, supported by a nearly circular and somewhat bulbous base which is fused to the tooth-bearing bone. All the teeth are shed and replaced alternately, two neighbouring teeth being functional together only for a short time; this rule is by no means always followed, but is obviously the normal arrangement.

The marginal teeth of the upper jaw bite entirely outside the mandible.

A single embolomerous intercentrum presenting no distinctive characters, associated with D.M.S.W. 2, is the only bone of the post-cranial skeleton which can be definitely referred to Orthosaurus.

Palæogyrinus decorus, gen. et sp. nov.

Type and only known material, a skull from the Parrot coal, Pirnie colliery, Fifeshire, J. W. Kirkby collection, Hancock Museum, Newcastle. The type skull is preserved in a cannel coal and is to some extent disarticulated. The parts preserved are :—

The neural cranium, lacking the left exoccipital: the actual bone is preserved and has been exposed from both sides. The right side appears to be practically undistorted, but has the surface damaged. The left side has been slightly distorted, but its surface is well preserved. The mould of the right face of the preotic region is well preserved. The anterior end is well preserved as bone.

The left exoccipital, preserved as impression.

The tabulars, dermo-supra-occipitals, parietals, right supratemporal, intertemporals, frontals, nasals, postfrontals, lachrymals, and left maxilla, are articulated and represented by remarkably sharp impressions of both surfaces, squeezes from which give the whole structure with perfect clearness.

Right maxilla, only partly exposed, but represented by impressions of both surfaces.

Left jugal, represented by bone on one slab and by a sharp impression of its outer surface on the other.

Left squamosal, quadratojugal and quadrate, very nearly in natural relation to one another, represented by sharp impressions of both surfaces.

Posterior end of the right jugal in impression.

Right lachrymal, in impression of both surfaces.

Right pterygoid with the epipterygoid in natural articulation, palatal part imperfect, impression of both surfaces.

This skull is of great importance because it is the only one known amongst the Embolomeri in which an uncrushed, or at most slightly laterally-compressed brain case, is associated with a pterygoid which is not vertically crushed, although a little flattened. By making squeezes from the impressions in dental wax and then bending them until they fit it is possible to restore the natural shape of the skull with only a very small element of doubt. Figs. 13–16 are made from camera lucida drawings of such a reconstruction.

Except for the major part of the lower surface and anterior end, which are concealed by other bones, the basioccipital is well exposed and perfectly preserved. The posterior end forms a single deeply concave condyle, agreeing exactly with the end of an embolomerous centrum in structure. The lower surface of the bone is cylindrical, its hinder border forming the margin of the condyle. The upper surface posteriorly bears two facettes for the exoccipitals, which do not meet, so that the bone forms the middle part of the floor of the posterior part of the brain cavity. The bone is shown to run forward and to articulate with the basisphenoid.

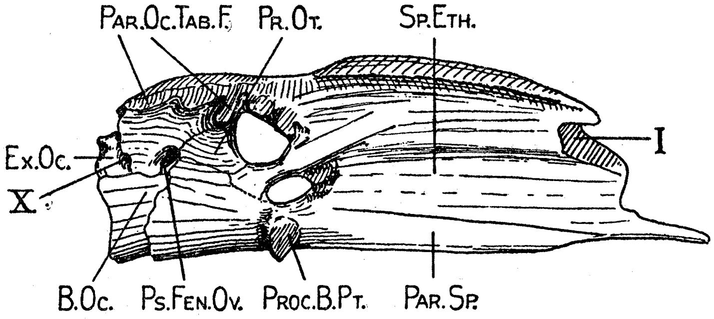

Fig. 12.—*Palæogyrinus decorus*, gen. et sp. nov. Neural cranium from the right side × $\frac{2}{3}$. Type specimen Hancock Museum, Newcastle, from the Parrot coal, Pirnie Colliery, Fifeshire.

The basi- and parasphenoids are fused, but can be distinguished by slight differences in texture. The parasphenoid covers the greater part of the lower surface of the basioccipital, overlapping the sides of that bone nearly to its articulation with the otic bones. In front of the otic region the joint bone bears a pair of well-formed basipterygoid processes which project laterally and somewhat downwards. The lower surface of each process at its root has a groove passing from the posterior round on to the anterior surface; this housed the internal carotid artery. The outer end of the process bears an articular face looking forward and outward, which surface is rather obscurely divided into an upper part directed a little dorsally, for the epipterygoid, and a lower for the pterygoid.

In front of the basipterygoid process the parasphenoid forms a dorsally channelled bone sheathing the lower edge of the " ethmoid."

The exoccipital rests on the upper surface of the basioccipital, the lower part of its posterior surface forming the upper part of the condyle and continuing the concave conical surface formed by the basioccipital. Above this base the bone rises as a massive column to articulate with the supraoccipital and paroccipital part of the skull. Its inner surface forms the side wall of the brain case, and is not apparently perforated by any foramen for the XIIth nerve, although the absence of this perforation cannot be affirmed with certainty. The posterior surface bears a peculiar little tubercle projecting backward in the plane of the outer surface, a little distance above the condyle. The outer surface is crossed by a horizontal groove which ends anteriorly at the foramen for the Xth nerve between the exoccipital and paroccipital.

The supraoccipital, paroccipital and pro-otic form a mass in which only a doubtful suture separating the pro-otic can be distinguished.

Except for the pineal foramen, the brain case has a continuous roof of cartilage bone. The upper surface of this roof is an accurate mould of the under surface of the dermal skull roof, there being no trace of any post-temporal fossæ. From the level of the foramen magnum as far forward as the pro-otic notch, the brain case is wide dorsally, its upper surface being abruptly truncated by flat lateral surfaces which are themselves supported by special processes from the tabulars and supratemporals.

The lateral surface of the otic region rises smoothly from that of the basioccipital; just above its suture with that bone at a point about one centimetre in front of the vagal foramen, it is abruptly excavated by a deep pit, whose bottom is shown to be closed by bone on both sides of the specimen. From this pit the apparent suture which bounds the pro-otic arises ; in other words, the pit lies on the suture between the pro-otic and paroccipital, the basioccipital forming part of its lower wall. It thus occupies the position of the fenestra ovalis, but differs from that opening in all other known Tetrapods in being a mere depression and not an opening into the cavity for the inner ear. On the right side the inner surface of the otic mass has been cleared over the region of the inner end of this pit and confirms the absence of a foramen. I propose to call this pit the pseudo-fenestra ovalis. Above it, the lateral surface of the otic mass flares outward, being drawn up into ridges which are truncated by a lateral articular surface, which, in life, was in contact with a special process from the skull roof.

The lateral surface of the pro-otic terminates in front in a smooth rounded notch, which forms the hinder margin of a large foramen completed by the " ethmoid."

The ethmoid is a large and very complex bone. Its anterior part is essentially an interorbital septum, whose thin lower edge is received in the groove in the upper surface of the parasphenoid : dorsally, this bone thickens and is tunnelled longitudinally by a pair of long narrow canals for the olfactory nerves; above these, the bone becomes massive and articulates with the roof of the skull. Posteriorly, the two canals for the olfactory nerves join and the roof must be pierced by a pineal foramen, but the crushing to which the specimen has been subjected prevents any account of this region. Still further caudally, the ethmoid is continued backward by a single process, whose dorsal surface is in contact with the roof of the skull, to articulate with the anterior end of the roof of the neural cranium in the otic region. At about the middle of its height, the posterior border of the ethmoid is produced backward in a pair of processes, which meet the basis cranii above the hinder end of the basipterygoid processes, and separate the large foramen in advance of the pro-otic, through which the V^th^ nerve issued, from another smaller foramen, through which the internal carotids appear to have entered the pituitary fossa and the optic and eye-muscle nerves must have left the cranium.

This account of the neural cranium should be compared with that of the same region in Eogyrinus on p. 223.

The general structure of the roof of the skull will be obvious from figs. 13 and 14. The sutures separating the bones of the table are all certain, that between the supratemporal and intertemporal, which is not well shown on the right side, being confirmed by the loss of the supratemporal on the left side.

The under surface of the dermo-supra-occipitals and of the posterior part of the parietals is moulded on the top of the neural cranium. The tabular articulates by interdigitating sutures with the supratemporal, parietal and derm-occipital, its lateral and hinder borders being free. At its inner end the bone is thickened, bearing three deep transverse ridges, whose abruptly-truncated inner ends abut on the otic region of the neural cranium. The tabular is prolonged posteriorly into a powerful horn, whose lower and inner surface bears a facet which is ridged and appears to be an articular face.

The whole of the lateral margin of the supratemporal and the hinder part of that of the intertemporal are free, the lower surface of these bones just within the margin having a broad sunken area with which the upper edge of the squamosal articulated, but to which it was not attached by suture. The lateral border of the postfrontal, on the other hand, is attached by suture to the postorbital, the outer surface of the two bones being continuous.

That part of the upper edge of the squamosal which articulates with the supratemporal is thickened and concave, so that there was during life a considerable mass of ligament present between the two bones. The common occurrence of isolated tables in Embolomerous Amphibia shows that the squamosal was readily detached by maceration after death. Caudal of its articulation with the roof of the skull, the upper border of the squamosal is suddenly depressed so as to form the anterior end and the whole lower border of the otic notch. The squamosal terminates behind by overlapping the dorsal surface of the quadrate, has a long suture with the quadratojugal, overlaps the hinder end of the jugal, and is in front itself overlapped by the postorbital.

The suture separating the prefrontal from the lachrymal is distinct on the left side of the skull, that between the lachrymal and nasal clear, but the separation of the lachrymal from the maxilla is not visible for its caudal half; the isolated bone of the right side shows, however, that it cannot be misplaced in the figure by more than a millimetre or two. There is thus no doubt that in this form, as in most early reptiles, the lachrymal

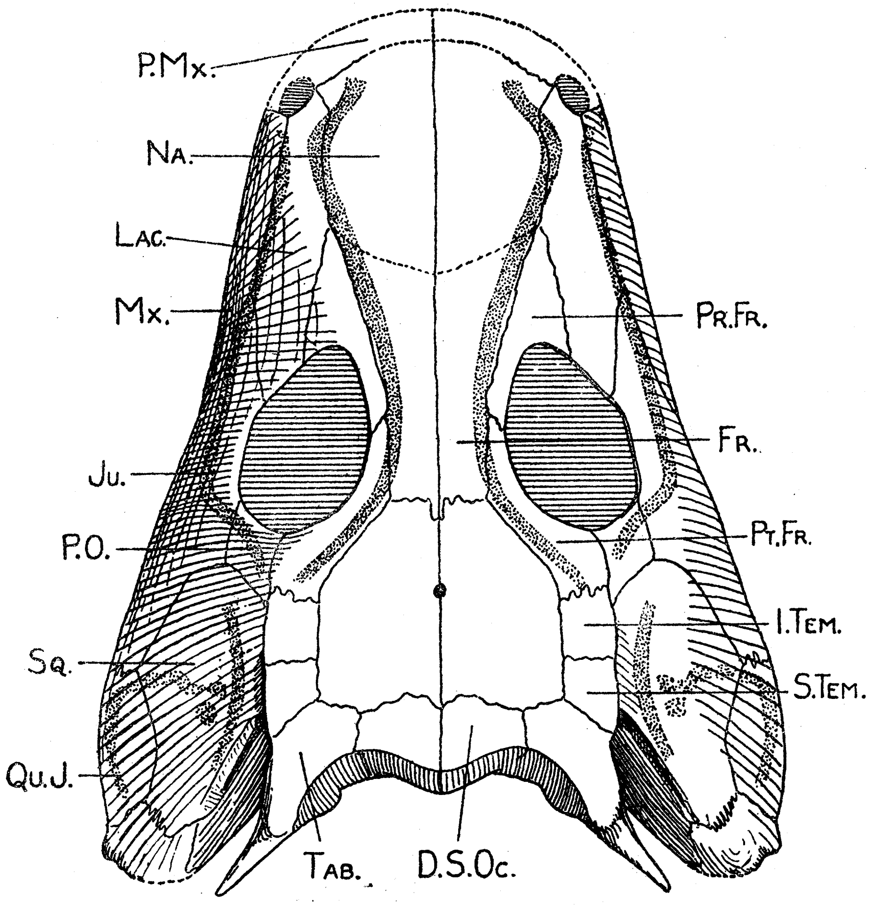

FIG. 13.—*Palæogyrinus decorus.* The dorsal aspect of the skull × $\frac{2}{3}$ from the type skull.

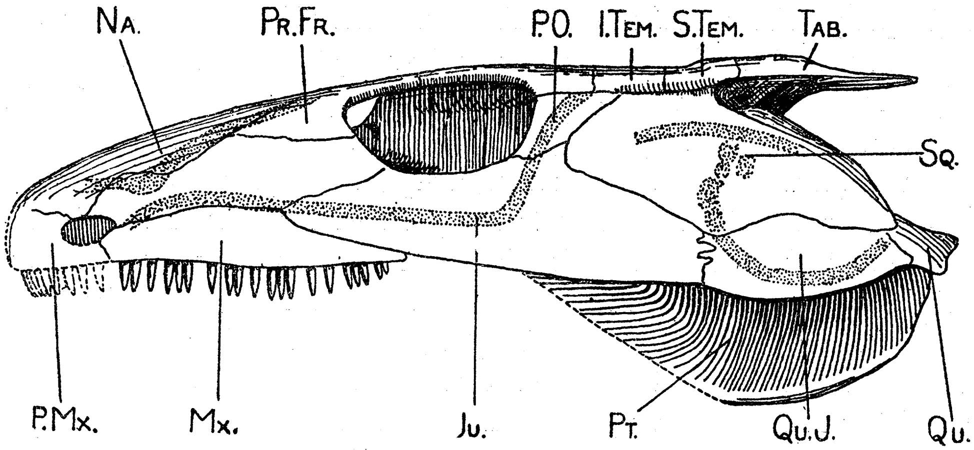

FIG. 14.—*Palæogyrinus decorus.* Left lateral aspect of the skull × $\frac{2}{3}$. From the type specimen.

extends from the orbit to the nostril, whose position is fixed from the preservation of the upper margin of that on the left.

The grooves for lateral line sense organs are shown with great clearness in this skull. They have their normal course, but certain of them, the occipital cross-commissure, and the posterior parts of the supraorbital canals, are missing. Below the maxillary canal the lachrymal is a thick bone and includes in its substance an actual canal lying below the groove and connected with it by small irregularly distributed foramina. This canal may have housed the actual sense organs as it does in fish, but it is equally probable that it only contained the nerve, the end organs lying freely exposed in the groove.

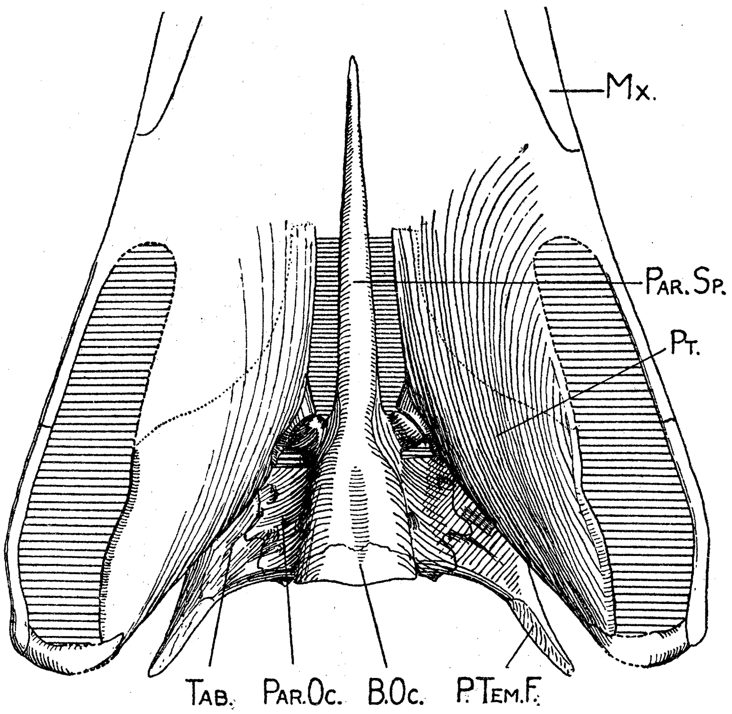

Fig. 15.—*Palæogyrinus decorus.* Palate × $\frac{2}{3}$. From the type specimen.

The right pterygoid is represented by the impression of both surfaces of the quadrate ramus, the articulation with the basis cranii and part of the palatal ramus; the epipterygoid is attached to it in natural position. As preserved, the quadrate ramus is slightly flattened, but the imperfect palatal part curves round in nearly its natural position. The quadrate ramus is extremely deep; its upper margin agrees exactly in length and curvature with that edge of the squamosal which lies below the otic notch, and was in life attached by suture to it. Below this attachment the bone forms a nearly flat, vertical plate to the level of the ventral surface of the basioccipital, the hinder end being applied to the inner surface of the quadrate. This upper part of the quadrate ramus has a thickened anterior margin which descends to the root of the articular process, and to which the epipterygoid is rigidly attached. This para-otic part of the quadrate ramus is continued downwards by a shell of bone, which covers the inner surface of the masticatory muscles and whose lower edge forms the inner margin of the infratemporal fossa. The lower part of the quadrate ramus gradually bends round as it is traced forward until it lies horizontally and passes insensibly into the palatal ramus. Much of the surface of the palatal and quadrate rami is covered with a granulation of small, sharp pointed teeth.

The articular face for the basis cranii is carried on a short, thick pedicel, whose root rises from the inner edge of the palatal ramus where the anterior margin of the para-otic part of the quadrate ramus meets it. When restored to their natural shape and position in the skull, the pterygoids include a small interpterygoid vacuity, and form very deep flanges against the inner surfaces of the lower jaw from the palate to the quadrate, the basis cranii lying at the bottom of a deep groove when the skull is viewed from below.

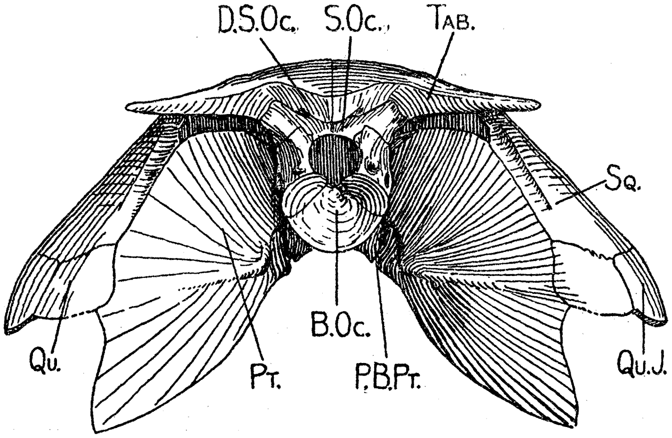

Fig. 16.—*Palæogyrinus decorus.* Occiput × $\frac{2}{3}$. Reconstructed from the type.

The most remarkable feature of the whole arrangement is the extraordinary narrowness of the infratemporal fossæ and the complete concealment of the masticatory muscles by the pterygoid, when the lower jaw is in place.

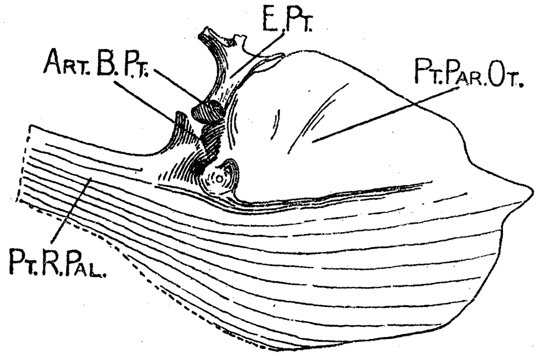

Fig. 17.—*Palæogyrinus decorus.* Right pterygoid and epipterygoid × $\frac{2}{3}$. Direct camera lucida drawing of an impression from the type specimen.

The epipterygoid is a small bone rigidly fixed to the anterior border of the para-otic part of the pterygoid. It terminates at the level of the top of the articular face of the pterygoid in a facet which articulated with the upper part of the basipterygoid process. The upper edge of the bone is much extended antero-posteriorly and is cut out by two well-defined notches separated by a special upstanding process. These notches are presumably for the maxillary and mandibular divisions of the fifth nerve; in life they lay on the level of the pro-otic notch, about 1 cm. lateral to the brain case.

So far as it is displayed, the maxillary dentition consists of a uniform series of small, close-set, sharp-pointed teeth with smooth crowns of nearly circular section.

Eogyrinus Attheyi, gen. et sp. nov.

= *Anthracosaurus Russelli*, HANCOCK and ATTHEY, 1869, 1870, 1871. ATTHEY, 1877: *non*, HUXLEY, 1863.
= *Pteroplax cornutus*, HANCOCK and ATTHEY, 1869, *in errore*.
= ? *Loxomma Allmanni*, EMBELTON, 1889, *in errore*.
= ? *Macrosaurus polyspondylus*, BARKAS, 1873.
= ? *Streptodontosaurus armatus*, BARKAS, 1873.
= ? *Leptognathus elongatus*, BARKAS, 1873.
= "*Pteroplax*," WATSON, 1912.

The large Amphibian described by ATTHEY as *Anthracosaurus Russelli*, HUX., is readily seen by comparison of HUXLEY'S and ATTHEY'S figures not to belong to that genus.

It is represented by splendid material in Newcastle, the more important specimens being:—

D.M.S.W. 27, the skull, figured by ATTHEY, with the two rami of the mandible and (28) a series of about twelve imperfect vertebræ, several ribs, scutes and a femur, and (29) three imperfect vertebræ, a rib and a scute, all belonging to the same individual.

D.M.S.W. 30 an isolated and incomplete brain-case.

D.M.S.W. 31, a fragment of a skull.

D.M.S.W. 32, a slab containing two characteristic scutes, several imperfect vertebræ, and several ribs, one being a sacral rib.

D.M.S.W. 33, the great vertebral column described by BARKAS as *Macrosaurus polyspondylus*, and by EMBELTON as *Loxomma Allmanni*. This specimen is not quite certainly determinable but the first sacral rib agrees well with that in D.M.S.W. 32.

D.M.S.W. 34. The complete pectoral girdle with the interclavicle nearly concealed, contained in two slabs of shale, which just touch. Described by HANCOCK and ATTHEY as *Pteroplax cornutus*, and later referred by them to the present species. They did not recognise that the two slabs were part of the same specimen and did not in the least understand its true structure.

D.M.S.W. 35, an isolated table of a skull used by HANCOCK and ATTHEY as one of the types of *Pteroplax cornutus*, and figured by ATTHEY, 1878, Pl. XVI, fig. 1.

Neural Cranium.—The basioccipital is only known by the section exposed at the hinder end of D.M.S.W. 27. It must have had a single concave condyle like that of all other Embolomeri and been largely concealed by other bones.

The right exoccipital of D.M.S.W. 30 is present, perfect except for slight crushing of its upper end. The base of the bone has an articular facet, whose shape is such that the bone can have formed no part of the occipital condyle, and must have left a wide strip of the upper surface of the basioccipital uncovered so as to form the lower part of the foramen magnum and of the brain cavity. The exoccipital forms a short column rising vertically to articulate with the paroccipital, and forming the side of the hinder part of the brain case. It is apparently not pierced by a hypoglossal foramen, although a deep notch on the outer surface may really mark the outer opening of such a canal now closed up by crushing.

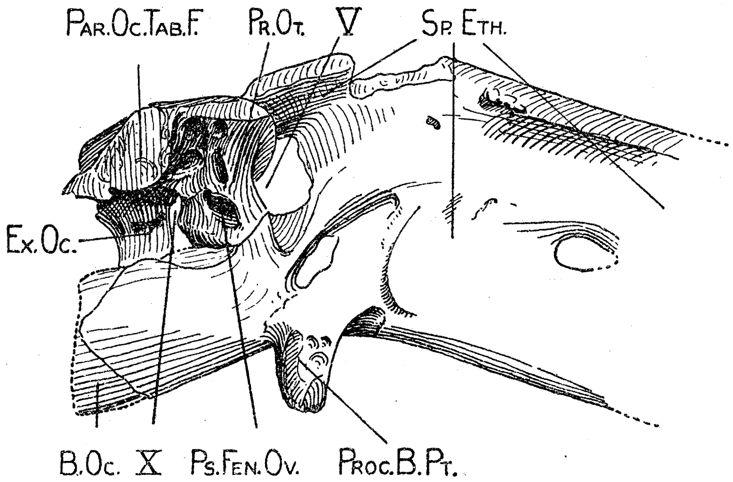

Fig. 18.—*Eogyrinus Attheyi.* Right side of the neural cranium ×$\frac{2}{3}$. From Newcastle Museum specimen No. D.M.S.W. 30, direct camera lucida drawing with the otic mass rotated into its natural position.

The paroccipital and pro-otic of the right side are present, very well preserved and exposed from all sides. The two bones are completely fused. They lie in their natural position, except that they have been twisted round so that the paroccipital process now lies nearly parallel to the long axis of the skull. The fused bones articulate by a narrow base with the basisphenoid above the basipterygoid process, and show an articular face which must in life have articulated with the anterior end of the basioccipital, that bone having been lost in the present specimen. Ventrally the joint bone narrows, its anterior border forming a smoothly rounded surface over which the fifth nerve passed out, and its hinder margin forming the anterior wall of the vagal foramen, a narrow slit in front of the exoccipital. Dorsally they widen and their outer surface passes outward as the lower surface of the paroccipital process until it is suddenly truncated by a vertical face for articulation with a special process of the tabular. The whole outer surface of the joint bone is covered by a series of deep steep-walled pits, the lowest and largest of which lies in the position that the fenestra ovalis should occupy. This pit, however, has a solid bony floor, and does not perforate the bone; it agrees exactly with the pseudo-fenestra ovalis described above in Palæogyrinus, p. 217. All the pits on the outer surface of the otic region are clearly of the same character. The dorsal surface of the joint bone presents a large articular face, which in life was in contact with the under-surface of the roof of the skull.

Slight crushing has twisted the paroccipital process so that its caudal surface now lies almost in the same plane as the inner surface of the otic bones; the true hinder margin of this surface is, however, made very obvious by a strong ridge and a little strip of hinder surface which has not been displaced and still occupies its natural position.

On the inner surface, the lower end of the joint bone shows a large articular area for the basis cranii. Immediately above this is a deep groove, obscurely divided into two, which covered the sacculus and utriculus. Arising from the anterior and upper end of this groove are two others at right angles to each other; one of these, for the posterior vertical semicircular canal, passes upward and backward until it is truncated by the surface to which the supraoccipital was attached; the other runs forward until it is suddenly deepened and then terminates at the anterior end of the bone.

The posterior part of the angle where the inner surface cuts the dorsal surface, is chamfered off by a face for attachment of the supraoccipital.

The interpretation of the grooves on the inner surface of the otic bones is very difficult; they are obviously associated with the semicircular canals, and the certain absence of any foramina tunnelling the bones shows that they must represent impressions of the outer surface of the labyrinth, that organ lying entirely within the bony cranial cavity, not separated from the brain by any bone. The conditions must, in fact, have been as in certain bony fish, and as in the rachitomous amphibian Trimerorachis. The basisphenoid and parasphenoid are indistinguishably fused. Posteriorly, the joint bone forms a thin film covering the ventral and lateral surfaces of the basioccipital; but leaving the dorsal part of the lateral surface of that bone exposed. In the pro-otic region the bone is more solid in structure, the lower end of the pro-otic articulating with a facet carried on the end of a projection from the upper edge of the bone. Ventral to this facet, the basisphenoid forms part of the border of the large opening through which the V^th^ nerve leaves the cranial cavity. Below this opening the basisphenoid is continued forward by a process which meets the back of the ethmoid and was in life separated from its fellow by a space through which the infundibulum and the optic and eye-muscle nerves passed downwards. This process forms the upper border of another opening whose lower border is formed by the parasphenoid, and which is closed in front by the ethmoid; through this opening the II$^{\text{nd}}$, III$^{\text{rd}}$, IV$^{\text{th}}$, VI$^{\text{th}}$ and ? VII$^{\text{th}}$ nerves left the cranial cavity and the internal carotid artery entered it.

In front of this opening the parasphenoid extends forward as a sheath to the lower edge of the ethmoid.

Only the hinder end of the ethmoid is preserved. It is a large well ossified bone, articulating with the table of the skull above. The hinder end of its upper surface is either split or perforated by a foramen for the pineal gland. The upper part of the bone is hollow and surrounds the olfactory lobes; this cavity contracts as it is traced forward and then splits into two very slender canals in which the olfactory nerves run forward. Below this cavity the bone forms an interorbital septum, which is perforated by a foramen, presumably for an interorbital vein, some five centimetres in front of the hinder end. The roof of the skull is best represented by D.M.S.W. 35, an isolated table whose determination is perhaps not quite certain. The ventral surface of this specimen is beautifully preserved although the other side is so much eroded that the sculpture is completely destroyed; the general structure will be obvious from fig. 14 and ATTHEY, 1878, Pl. XVI.

The whole of the ventral surface of the dermo-supraoccipital is roughened for contact with the supraoccipital. The tabular articulates by interdigitated suture with the dermo-supraoccipital, parietal and supratemporal. Its lower surface is very complex; on the admesial side it forms an articular face which stands almost vertical and articulates with the end of the paroccipital process and with the outer margin of the pro-otic further forward. Laterally to this articular face the lower surface of the

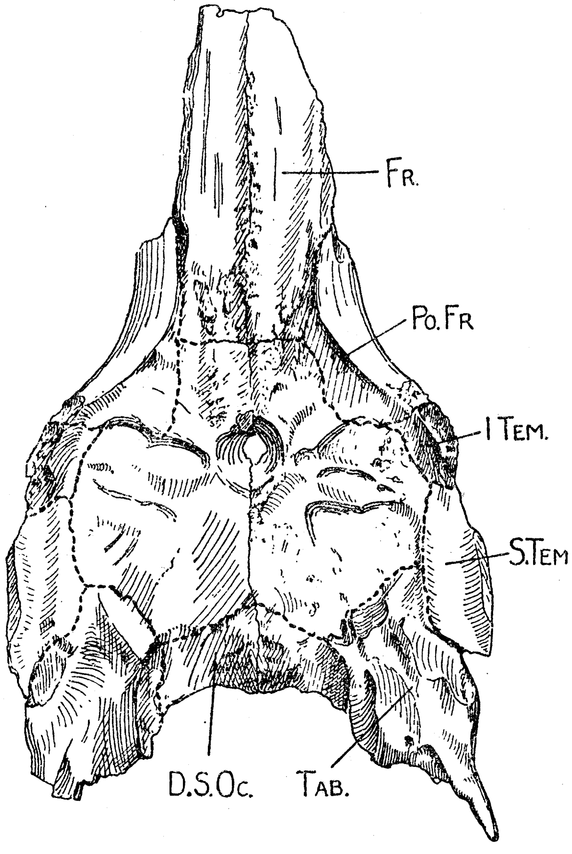

FIG. 19.—*Eogyrinus Attheyi*. The table of a skull viewed from the ventral side × $\frac{2}{3}$. Newcastle Museum, No. D.M.S.W. 35. The reference line S. Tem. ends in the middle of the wide, smooth groove of the supratemporal, with which the upper border of the squamosal formerly articulated.

tabular is free, the hinder part of the lateral border overhanging the otic notch. The anterior part of this border has an articular face for the squamosal. The posterolateral corner of the tabular is produced into a short and very slender horn.

The supratemporal articulates with the lateral border of the parietal, filling up the space between the intertemporal and the tabular. Its ventral surface bears a shallow groove which ends posteriorly in that articular face on the tabular which received the squamosal, that bone not being rigidly attached by suture to any bone of the table. Laterally to the squamosal groove the supratemporal bears a narrow articular face which can only be for the postorbital.

The postfrontal is rigidly attached by suture to the parietal, frontal and intertemporal, its lateral margin behind the orbit being thickened and deeply pitted for the attachment of the postorbital. The intertemporal bears a large, much pitted face by which it was attached to the postorbital.

The structure of the table in D.M.S.W. 27 is not determinable, nor are the sutures on the rest of this skull readily determinable. ATTHEY'S account and figure, 1878, seem to give an accurate picture of the structure of the skull apart from the table, the sutures represented being to a large extent confirmed by isolated bones. The palate agrees in its general structure with those of Palæogyrinus and Orthosaurus: that is, the very large pterygoids are supported by freely movable articulation with the basipterygoid processes and cover the whole central area of the palate with the exception of a very small interpterygoid vacuity.

The palatine is the bone which in 1912 I believed to be the prevomer, because I then interpreted a deep pit lying close against the maxilla as the posterior naris. Re-examination of the material, and especially examination of much other material of allied animals, has shown that this depression must have some other function, and that the pair of very large anteriorly situated foramina formerly regarded by me as anterior palatal vacuities are the true posterior nares. It has also become obvious that the broad bar separating these openings is formed by the prevomers, which are devoid of teeth. The prevomer and palatine of my former description become respectively the palatine and transverse bones. They are remarkable in that the whole of their buccal surface is covered with an ornament of pits and grooves identical with that of the outer surface of the skull.

Lower Jaw.—The specimen D.M.S.W. 27 retains both rami of the lower jaw, the right being perfectly exposed from within and the left showing part of the lingual and the whole of the outer surface. Two fragments of the hinder end of the ramus give evidence about the articular and the sutures between other bones.

In the light of the structure of the lower jaw of *Orthosaurus*, now known from very adequate material, it is possible to make out the structure of the lower jaw of Eogyrinus with considerable assurance, especially as many of the displacements due to overlap of bones, which make the interpretation of the Orthosaurus jaw so difficult, do not occur in Eogyrinus.

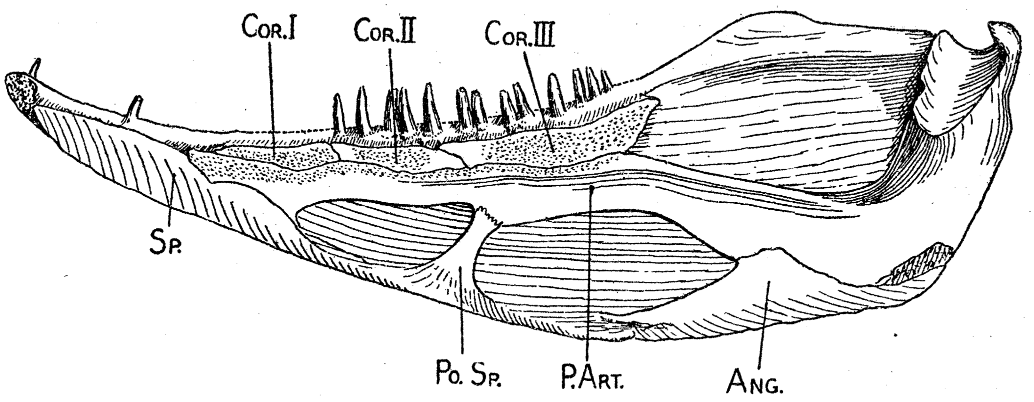

Fig. 20.—*Eogyrinus Attheyi.* Right ramus of the lower jaw, inner surface $\times \frac{1}{3}$. Newcastle Museum, Type specimen, No. D.M.S.W. 27.

The lower jaw of Eogyrinus is remarkable for the extreme depth of the posterior and the slenderness of the anterior parts. On the outer surface the sutures are only recognisable with difficulty. The dentary is shown to be a shallow bone forming a strip along the oral border of the jaw and entirely restricted to the labial side ; it overlaps all the bones which lie ventral and caudal to it.

The splenial, postsplenial, angular and sur-angular form a series, each overlapping the bone which lies behind it. The sur-angular seems to be entirely restricted to the outer surface of the jaw, being fused with the articular and presumably meeting the pre-articular in suture behind that bone. The other three bones are channel-shaped, forming the lower border of the jaw and appearing on its inner surface. The articular is an extremely powerful bone which resisted the crushing which has flattened all the other bones of the jaw. The condylar surface is concave, very deep, and produced into special upstanding processes posteriorly and internally and anteriorly and externally. It presents no trace of any postarticular projection, the hinder surface descending from the lip of the condyle to pass smoothly into the lower surface of the jaw. On the inner surface the bone is largely covered by the pre-articular.

The pre-articular is a very long bone, which runs forward from the articular very nearly to the front of the ramus. Posteriorly it has a suture with the inner flange of the angular, but is then separated from that bone and from the posterior part of the postsplenial by the enormous posterior mandibular vacuity. It then articulates by a suture with that slender process of the post-splenial which separates the two internal mandibular vacuities and continues forward, its lower margin forming the upper border of the anterior vacuity, until its anterior end is overlapped by the inner flange of the splenial.

Posteriorly the upper border of the pre-articular is thickened by a ridge on its lingual surface, and forms the inner border of the supra-mekelian fossa, in front of which it is in sutural connection with the three coronoids. The upper part of the bone below the coronoids bears a shagreen of small, sharp-pointed teeth.

The three coronoids form a narrow strip of rather massive bone wedged in between the dentary and the pre-articular. Each has its buccal surface covered with fine granular teeth, the regions where the individual bones are united by suture being free from this shagreen.

The dentition presents no feature of any special interest; the marginal teeth in both jaws are simple, conical and bluntly pointed; their bases are fluted and flare out to the attachment to the supporting bone. They are shed approximately alternately.

The grooves for the lateral line system have a similar distribution to those of Orthosaurus, there being a pair of grooves running from the interorbital surface directly forward to the hinder end of the nostril, another pair running along the maxilla, lachrymal, jugal and quadratojugal nearly parallel to the lower border of the side of the skull, and a transverse groove crossing from nostril to nostril on the premaxillæ.

The lower jaw supports the usual groove running parallel to its lower margin from the extreme anterior end to a spot little below the condyle, and has, in addition, a branch from this groove which originates at or about the suture between the angular and the sur-angular, and runs upward and forward on the latter bone to the caudal end of the dentary. These grooves were well figured by ATTHEY.

Vertebral Column and Ribs.—Specimen D.M.S.W. 27 has associated with it and belonging to the same individual a number of vertebræ and ribs. In most cases the neural arches have become separated from the centra, but a well-preserved example, D.M.S.W. 29, in which these elements had remained together was figured by ATTHEY in direct anterior view; this specimen is a last dorsal or anterior sacral.

The long series of dorsal vertebræ in D.M.S.W. 28 shows in natural order centra and intercentra alternately, exposed chiefly from the dorsal aspect. This specimen shows that the column was typically embolomerous, the centra (= pleurocentra) being complete biconcave discs perforated for the notochord and bearing large facets for the neural arch with the impression of the spinal cord between them.

The intercentra are complete discs with a central notochordal perforation; the central area of their ends is concave, but this is surrounded by a convex annular area extending half way to the centre. The cylindrical lower and lateral surface terminates in sharp, well-defined borders, which meet dorsally, so that in lateral view an intercentrum in its natural position between two centra often appears not to be a complete ring. The lateral surface of the intercentrum in the dorsal region bears a pit for the head of the rib. The dorsal surface has a pair of facets which articulate with the anterior part of the lower end of the neural arch.

The dorsal neural arch has a pair of facets for articulation with the centrum and intercentrum, these lie essentially on the lower surfaces of the transverse processes, which in the dorsal region project strongly, standing out beyond the sides of the centra; their distal ends bear facets for the articulation of the tubercles of the ribs. Definite pedicels can scarcely be said to exist, the neural canal being extremely small and lying between the inner ends of the transverse processes. The pre- and post-zygapophyses are powerful, their articular faces having the normal direction and being inclined at about 45° to the horizontal. The neural spine is of considerable height, laterally compressed and long; it rises from the roots of the zygapophyses. The whole neural arch is in fact strikingly like that of the first dorsal vertebra of *Plesiosaurus dolichodeirus.*

The sacral vertebra preserved in D.M.S.W. 29 differs from a dorsal in that the head of the rib has an articulation on the centrum as well as on the intercentrum.

The isolated and perhaps really indeterminable vertebral column D.M.S.W. 33, agrees exactly, so far as it can be compared, with the scattered elements belonging to the individual whose skull is D.M.S.W. 27, and its first sacral rib agrees closely with an example associated with characteristic scutes on D.M.S.W. 32. I therefore use it here because it is certain that whether or not it actually belongs to Eogyrinus it does agree with that animal in the important morphological features it shows and in size. The specimen was described and figured by EMBELTON, 1889, whose account, for its time an excellent one, is inaccurate and incomplete in one or two respects.

There is a continuous series of twenty-six presacral vertebræ preserved. These are all very much alike and agree exactly with the dorsals described above. The last is succeeded by the three sacral vertebræ, all in natural articulation with the dorsals and caudals. These elements differ from the dorsals in that the facet for the tuber-

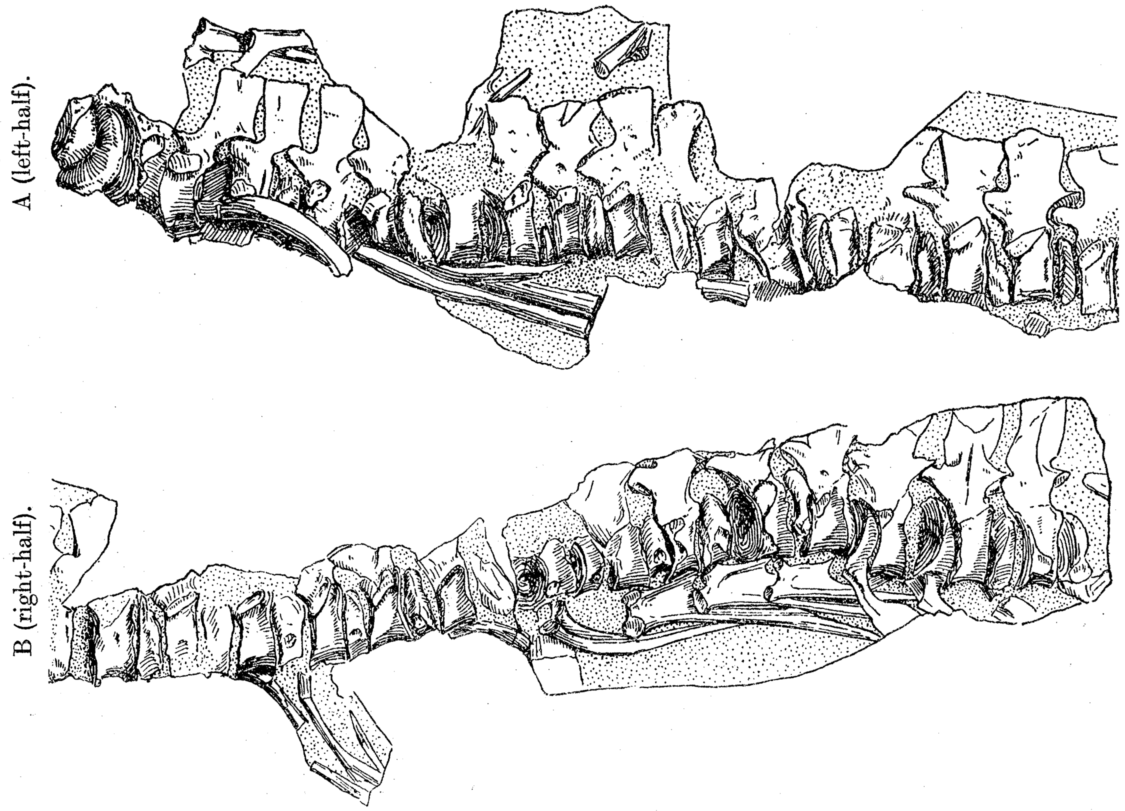

FIG. 21.—*Eogyrinus Attheyi* (?) Connected series of dorsal, sacral and caudal vertebræ, left side × 2/9. Newcastle Museum, No. D.M.S.W. 29.

culum of the rib is not carried out on a definite transverse process, but lies in the plane of the lateral surface of the centrum and is perhaps partly borne by that bone ; this facet lies well forward on the centrum and does not extend across the entire width of the lateral surface as in a dorsal. The facet for the head of the rib is shared by the centrum and intercentrum.

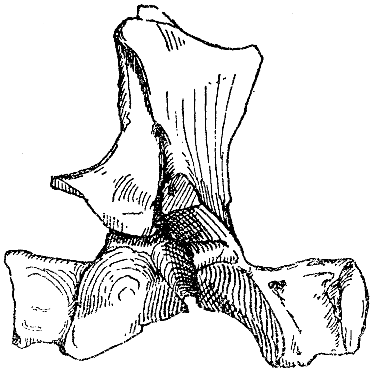

FIG. 22.—*Eogyrinus Attheyi* (?) Dorsal neural arch, caudal aspect × $\frac{2}{3}$. Isolated individual in Newcastle.

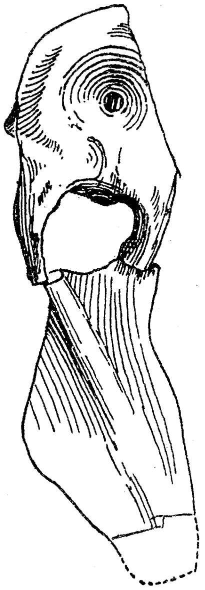

FIG. 23.—*Eogyrinus Attheyi*. Caudal intercentrum, caudal aspect, the hæmal arch broken off and turned round so as to appear largely in side view, × $\frac{2}{3}$. Newcastle Museum, No. D.M.S.W. 39.

The zygapophyses of the sacral vertebræ are placed rather more dorsally on the neural arch than those of dorsal vertebræ. The vertebra immediately succeeding the last sacral has a single rib facet borne on the centrum ; the intercentrum, though not well preserved, shows no trace of a pit for the head of the rib ; and the anterior edge of the centrum is also free from rib articulation. The next, second, caudal vertebra has an intercentrum whose lateral surface is wedge-shaped although the bone is shown to be a complete ring. This intercentrum is continuous with a large hæmal arch, which arises from its ventral surface as two slender roots, which pass downward and fuse, the lower single part of the arch is expanded antero-posteriorly and, though incomplete, shown to be of considerable length. An isolated intercentrum, D.M.S.W. 39, agrees exactly with that described above and gives a complete hæmal arch. The centrum of this vertebra bears a single facet for a single-headed rib. The neural arch is tall, lacks all trace of transverse process or rib facet, and has the zygapophyses placed high up.

The third caudal differs from the second in that it shows no rib facet at all. The fourth differs from the third in having a rib facet very low down on the centrum, not in series with those on the anterior caudals.

The connected series of vertebræ stops at this point, but there is a detached series of four caudals belonging to the same individual which appears to belong considerably further down the tail. The intercentra of these elements, although complete discs, have an almost lozenge-shaped lateral surface, the centra being widened both dorsally and ventrally; each intercentrum bears a hæmal arch, broken off short in the specimen. There is no trace of a rib facet on any element of the vertebræ.

A considerable number of dorsal ribs belonging to the individual whose skull is D.M.S.W. 27 are preserved in the collection. They are double-headed, the capitulum and tuberculum being well separated. The body of the rib is slender, nearly circular in section, but with a shallow groove down the posterior surface; the distal end is a little thickened and was continued by cartilage.

D.M.S.W. 32 has a series of ribs associated with characteristic scutes and thus undoubtedly belongs to Eogyrinus: one of these ribs is an ordinary dorsal, agreeing in every respect with those described above. Another is remarkable in that the rib is very wide, the outer edge being carried out on a thin web of bone which gradually subsides into the shaft near the distal end. The third rib has a massive tubercle and capitulum, which lie close together in such a way as to show that the transverse process of the vertebra to which they were attached projected little if at all from the side of the centrum. From the articular region the rib continues as a deep thin strip of bone whose lower edge is thickened, rounded, and forms a very gentle curve. The upper edge of the bone proceeds outwards, roughly parallel to the lower edge, for a distance of about 4 cm.; it is then suddenly cut into by a step so that the depth of the rib is lessened; distally the border continues so as slightly to increase the depth of the rib. This rib is seen by comparison with D.M.S.W. 33 to be a sacral.

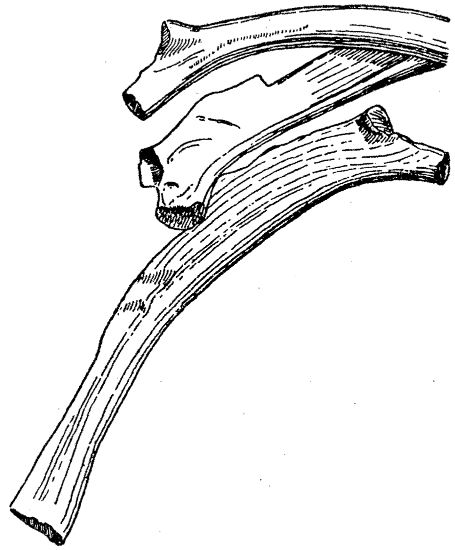

FIG. 24.—*Eogyrinus Attheyi.* A typical dorsal, the last dorsal and the first (?) sacral rib, × $\frac{1}{3}$. Newcastle Museum, No. D.M.S.W. 32.

D.M.S.W. 33 retains many incomplete dorsal ribs which agree with those described above; these are in general displaced and cannot be referred to their own vertebræ. Lying underneath the last dorsal and the three sacral vertebræ, however, are four ribs of the right side, which obviously retain their natural position with respect to one another, and have slipped down as a whole for a distance of about 4 centimetres from their natural articulation.

The first of these ribs, on careful examination, is seen to agree very nearly with the second rib of D.M.S.W. 32, described above; like that element, it is a wide thin strip of bone supported by a capitulum and tuberculum, which are here even closer together than in the former specimen; this rib has been folded on to itself and then crushed flat, so that it is now a channel-shaped bone with its inner and outer edges approximated, the apparent outer border being really the mid-line of the anterior face.

The next rib, the first sacral, has powerful tubercular and capitular articulations lying close together; from them the rib extends outward as a deep sheet with a thickened and rounded lower edge. The upper border has a step about 3½ centimetres distal to the tuberculum. This step is overhung by a projecting point; from it the outer border continues, approaching the inner edge, so that distally the rib is of nearly circular section. This rib has a total length of some 15 centimetres.

The second and third sacral ribs agree in general structure with the first; their articular faces are, however, somewhat further apart, they are shorter, and in the third the step is considerably more proximal than in the two which precede it.

That these ribs are sacrals is quite certain. The sacral vertebræ are definitely determined by their position between the dorsals and caudals in a naturally articulated column. The articular surfaces of the sacral ribs agree exactly with those on the sacral vertebræ and differ entirely from those of any of the dorsal and caudal vertebræ. Thus, in this specimen, and from the less complete evidence of D.M.S.W. 32 in Eogyrinus, we have a sacral arrangement which differs from that in any other known Tetrapod in that the ribs are elongated and double-headed, extremely resembling dorsal ribs. It is certain that these remarkable sacral ribs did not articulate with the inner surface of the ilium, but that that bone lay on their outer surface, its upper edge being, perhaps, received in the step which exists in their upper borders, and the bones being attached to one another by muscles. The relation of the pelvis to the sacral ribs must, in fact, have been very similar to that of the scapula to the pectoral ribs.

Consideration of the structure of the Embolomer pelves, described later in this paper, will render the possibility of this arrangement obvious.

The shoulder girdle of an Embolomerous Amphibian is represented in Newcastle by an excellently preserved and well exposed, but isolated example, D.M.S.W. 34, part of which was figured by Hancock and Atthey as *Pteroplax*. Their interpretation is, however, quite incorrect and their figure very poor and incomplete. The specimen is contained in two slabs of shale which just touch at a spot in the middle of the right scapula, their relative position being obvious from the direction of the striæ on this bone and the anterior edge of the right clavicle. In this specimen the interclavicle is concealed by other bones except for its edges. These only suffice to show that it is relatively very small, rhomboidal, and without a long posterior stem.

The left clavicle is complete, the right lacks a little of its dorsal end. The bone is a flat sheet, with nearly parallel anterior and posterior margins. The lower part of its outer surface bears an ornament of pits and grooves quite similar to that of the skull of Eogyrinus, and differing from that of all the other Amphibian skulls which have been found at Newsham. The lower border of the bone is straight and meets the anterior border at an angle of about 45°; it passes into the anterior and posterior borders by rounded corners.

Both cleithra are in position rigidly attached to the clavicles. The left lacks its upper end, the right has both ends preserved but has a piece missing from the middle ; its length is, however, certain.

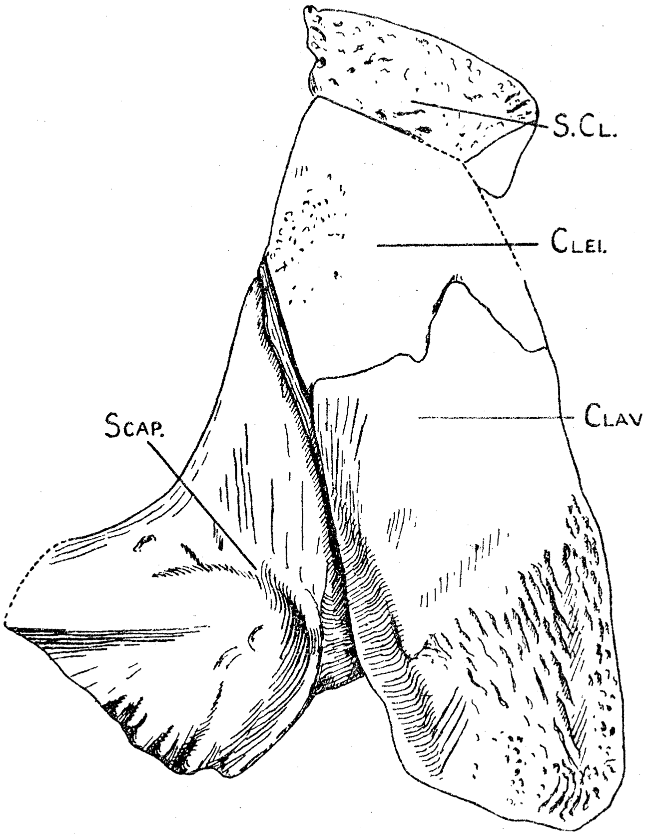

FIG. 25.—*Eogyrinus Attheyi.* Right side of the shoulder-girdle, the interclavicle being omitted × 4/9. Reconstructed from Newcastle Museum, No. D.M.S.W. 34.

The cleithrum is a flat bone much resembling the clavicle. Ventrally it is applied to the inner surface of the clavicle, passing downward for more than half its posterior edge ; on the cranial edge it does not extend quite so far. The upper part of the outer surface of the cleithrum lies in the same plane as that of the clavicle and on the left side is shown to have a shallow ornament of the usual type. The visceral surface of the upper end of the cleithrum has a depressed strip, for the attachment of another bone running along its upper and anterior border.

The clavicle with the attached cleithrum thus forms a rigid plate of bone with parallel anterior and posterior borders. This plate is about 24 cm. long and 8 cm. wide ; the maximum thickness of the two bones is about 1 cm.

Both scapulæ are preserved, they being the bones interpreted by HANCOCK and ATTHEY as interclavicles. Each has a long blade with roughly parallel anterior and posterior margins, terminating in a point dorsally and expanding to the glenoid region below. The outer face of the bone, toward the anterior edge, bears a large elongated roughened area, by which it was obviously attached to the inner surface of the cleithrum. It seems impossible that the scapula touched the clavicle at any point.

The glenoid end of the scapula widens very rapidly. The anterior edge immediately below the end of the facet for the cleithrum is carried out into a massive irregular process, ending in a series of blunt prominences. The main part of the lower end of the bone is separated from this process by a strong rounded ridge, behind which lies a shallow concavity, presumably the glenoid cavity. This cavity is not in any way separated from the rest of the outer surface which stretches caudally and ventrally from it. The lower margin of the bone is thick and its outer surface bears a series of short massive ridges which are directed toward the glenoid cavity. This scapula is not perforated by any foramina in the glenoid region, but a pit lying dorsal to the glenoid may mark the position of a small foramen.

In addition to the bones just described, D.M.S.W. 34 shows four others which must belong to the shoulder girdle. Only one of these is perfect, but they all agree in the possession of the following features :—each is an excessively thin (under 1 mm.) sheet of bone whose visceral surface is smooth, whilst the outer surface bears a shallow ornament of pits and ridges.

The only complete bone forms an irregular parallelogram, the outer surface along two edges being depressed, lacking ornament, and the depression being terminated by a sudden step rising to the normally ornamented outer surface. These rabbets are undoubtedly for the attachment of other bones. The least incomplete of the other three bones is obviously the pair to that described above.

That these four unusual bones are dermal elements is obvious from their sculpture ; that they do not belong to the skull or lower jaw is equally well proved ; the definite evidence that the complete element has articulated with others shows that they are not mere scattered scutes, and in any case they differ *in toto* from the ventral squamation of the Embolomeri. There remains therefore only the natural conclusion that they belong to the isolated shoulder girdle with which they were found.

The complete element is appropriate in size for articulation by the rabbet along its longer edge with the upper end of the cleithrum which has a similar depression, and when so placed the rabbet along its shorter edge extends freely in front of the cleithrum.

In this position the bone agrees exactly with the supracleithrum of an osteolepid fish in all its relations, including the direction of overlap. The bone which formerly articulated with the anterior end of the supracleithrum, the post-temporal, must be represented by one of the incomplete bones present in the specimen.

In connection with the discussion of this very remarkable shoulder girdle it must be remembered that the inner side of the tabular horns of *Palæogyrinus* and *Pteroplax cornutus*, shows evidence, in the presence of an articular surface, that a post-temporal element did occur in these forms. The type specimen of *Pholiderpeton scutigerum*, HUXLEY, which is closely related to Eogyrinus, retains a strange bone (fig. 26) which can only belong to the shoulder girdle. It is not homologous with any of the bones described above and can only be a post-temporal. The long spike at its anterior end is massive and is scarfed presumably for attachment to the tabular horn. The wider hinder end is thin and seems quite suitable for attachment to the supracleithrum described above.

An isolated interclavicle from Newsham, D.M.S.W. 34, agrees in size and shape with the visible margins of the concealed interclavicle of D.M.S.W. 36, it is of relatively very small size, rhomboidal in shape, and in every way suitable for articulation with the caudal and ventral corners of the clavicles in that specimen.

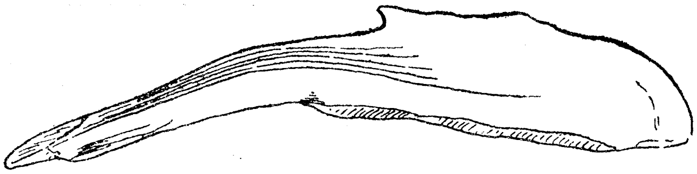

FIG. 26.—*Pholiderpeton scutigerum,* HUXLEY. Post-temporal × 4/9. Type specimen, Bradford Museum.

There is no direct evidence to show to what animal the shoulder girdle just described belongs. It is clearly Amphibian, because it differs from that of all the fish found with it in the possession of an interclavicle, in the details of its structure, and in its ornament. It is of very large size, far exceeding even the largest specimens of Orthosaurus. Its ornament agrees exactly with that of the skull of Eogyrinus, and differs from that of all the other Amphibia found with it, and it is of a size exactly appropriate to the skull D.M.S.W. 27, which is the type specimen of that form.

Pelvis.—The Embolomerous pelvis is very scantily represented by coal-measure material. The best example (fig. 27) was found in the same coal seam at Pictou, Nova

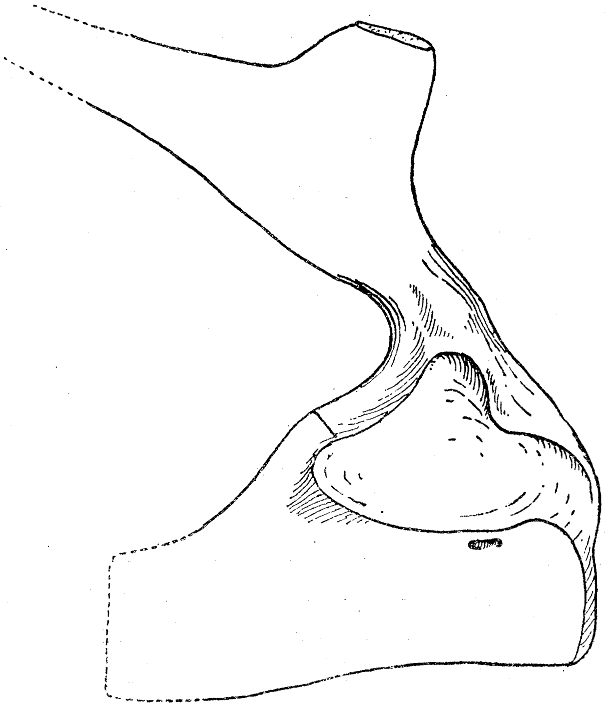

FIG. 27.—*Embolomerous Amphibian.* Outer side of pelvis × $\frac{2}{3}$. Pictou, Nova Scotia, B.M.N.H.

Scotia, as the type specimen of the Loxommid *Baphetes*, but is not in any way connected with that individual.

The ilium unites with the pubis and ischium in a normal triradiate suture, over which lies the acetabulum, marked off by raised ridges. Further dorsally the bone contracts to a narrow shaft of approximately circular section, above which it expands into a broad but thin blade, whose posterior end is extended into a long process. The upper border of the bone bears a dorsally-directed process anteriorly.

The pubis is a small bone, meeting its fellow and the ischium in continuous sutures, and perforated by a small foramen.

The ischium is a larger bone, also forming a symphysis, and with the whole of its anterior border in contact with the pubis. There is no trace of any facet for attachment of sacral ribs on any part of the ilium.

An isolated ilium (No. 62,936, Neilson Collection, Royal Scottish Museum), from the coal measures of CARLUKE, agrees closely with this pelvis, as do those of Pholidogaster, Cricotus, and those referred by FRITSCH to Macromerium. In none of these does the ilium show any marks of attachment to the sacral ribs.

This type of pelvis is entirely appropriate to the sacral arrangement of Eogyrinus. The long sacral ribs of that form lay below the elongated ilium, and that element was attached to them by muscles exactly as the scapula is attached to the pectoral ribs.

D.M.S.W. 28, part of the type individual of Eogyrinus, retains a femur. This bone is considerably crushed, lacks part of its distal end, and is exposed from the dorsal and partly from the ventral surface. It has a semicircular head, set straight on the end of the bone, and of slight thickness, so that the articular face is shallow. The shaft is rounded, there being no pronounced adductor crest as in Eryops. The bone is, in fact, rather strikingly like the femur of Dimetrodon.

Reconstruction and Habits.—From the material described above I have made the restoration of Eogyrinus reproduced in fig. 28. In this drawing the skull and lower jaw represent the type specimen. The vertebral column and ribs are from D.M.S.W. 33, whose individual elements agree in size and structure with similar bones belonging to the type individual. The shoulder girdle is a drawing of D.M.S.W. 34, reduced in the same proportion. The femur is that of the type specimen.

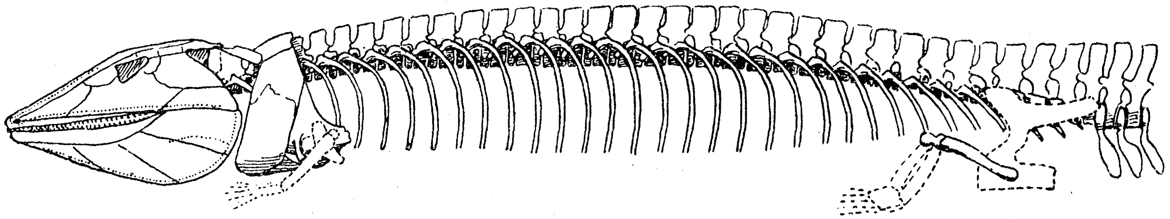

FIG. 28.—*Eogyrinus Attheyi*. Reconstruction of the skeleton about $\frac{1}{18}$ natural size.

The number of presacral vertebræ is uncertain. Twenty-six are preserved in

D.M.S.W. 34, the more anterior showing no evidence of being near the skull. I have thus allowed thirty-two.

The position of the shoulder girdle depends on the assumption that the post-temporal of Eogyrinus was of corresponding size to that of the closely-allied Pholiderpeton. The presence of a quite distinct neck in Embolomeri is confirmed by the skeleton of Cricotus figured by Case 1911, and that of Pholidogaster figured by Huxley, in both of which there is a considerable length of vertebral column lying in advance of the shoulder-girdle.

The ventral squamation, undoubtedly composed, as is that of Cricotus, of very numerous rows of scales arranged in chevrons, with their points in the mid-ventral line and directed forward, is omitted.

The restoration of the pelvis follows the common Embolomer pattern. The tail was undoubtedly very long, probably exceeding the whole presacral part of the body.

Regarded as a whole, Eogyrinus is remarkable for its relatively small head, extremely long body of circular section, and powerful laterally compressed swimming tail. The limbs, if we may judge from the femur, were relatively very short and feeble, extremely inefficient as agents for support and propulsion on land.

All the known remains of carboniferous Labyrinthodonts have been found in rich fish beds, and it may almost be stated that all such horizons in the coal measures will, if sufficiently completely explored, be found to yield their remains.

Rich coal-measure fish beds almost invariably have a characteristic lithological type. They are cannel coals of greater or less inorganic content, ranging from such commercially workable deposits as that at Pirnie into black shales and blackband ironstones. Such rocks are rare in the coal measures ; they are very usually associated with normal coal seams and are found in lenticular masses of very variable extent. The present occasion is not one on which I am called on to discuss their mode of origin in detail, but it is necessary for my purpose to state that a careful consideration of all the relevant evidence leads me to believe that they represent deposits of detrital matter, largely of organic origin, laid down in pools which lay in the middle of the great continuous coal forests. These pools were sometimes of very considerable area, up to three or four miles in diameter, of some depth, and relatively long lasting. Their waters contained a thallophytic flora from whose remains some of the mass of cannel coal was built up, and in them swam large numbers of fish, ranging from small Palæoniscids to great Rhipidistia, Dipnoi and Elasmobranchs, several feet in length. The Embolomeri must have lived habitually in these pools, swimming about by their long tails and balancing themselves by their limbs. They are usually of very large size, capable of holding their own with even the largest fish, and having the advantage of these creatures in that when a pool dried up they could travel overland to a new lake, much as eels pass from ditch to ditch nowadays. That the Embolomeri did actually spend the greater part of their life in the water is shown by the great development of lateral-line sense organs which characterises them, by their great flattened tails, and by the inefficiency of their limbs for progression on land.

Diplovertebron punctatum, FRITSCH, 1885.

= *Gephyrostegus bohemicus*, JAEKEL, 1902.

The type material of this form consisted only of certain scattered bones, amongst which premaxillæ, maxillæ, a dentary, several vertebræ, an interclavicle, and an ilium were figured by FRITSCH. Subsequently JAEKEL figured a compressed but otherwise beautifully perfect skull as *Gephyrostegus.* He did not recognise any resemblance between his material and *Diplovertebron*, but the fact that it is clearly an embolomerous form and the great similarity which its premaxilla, maxilla and dentary present, both in size and structure, to the corresponding bones of the type renders their identity most probable.

The best existing specimen is, however, contained in a slab of oil shale from Nyran which is in my own possession. This specimen shows an impression of the ventral surface of a skeleton, in the main naturally articulated, and complete except for the tail and the distal parts of the hind legs, which are cut by the edge of the slab. The actual preservation is extremely good, every detail even of the minute scales of the ventral surface being clearly shown on squeezes.

The skull is present complete, but was slightly disarticulated before burial. The ventral surface of the table is shown, partly overlapped by the bones of the left cheek, which remain in natural articulation with each other and with the maxilla, lachrymal, and prefrontal. A single nasal and both premaxillæ show the shapes of these bones perfectly. The outer surface of the left and the inner surface of the right mandible are well shown, and scattered remains of the palate can be determined.

From this material there is no difficulty in reconstructing the dorsal and side views of the skull, as in fig. 31 of the restored skeleton. The skull so restored is of characteristically anthracosauroid type with the squamosal attached to the table only by ligaments, and with the orbit in the middle of the length and surrounded by the usual series of bones, the lachrymal agreeing with that of Palæogyrinus in extending to the nostril in the way usual in the early reptiles.

It is quite clear that the palate was of normal embolomerous structure, with large Pterygoids covered with small close-set denticles.

The lower jaw is proved to possess a post-splenial and a series of three coronoids, each bearing a patch of small teeth as in Eogyrinus. The pre-articular is of great length, stretching forward nearly to the symphysis.

It is thus certain from the structure of the skull and lower jaw that the animal was an embolomerous form. In structure it agrees exactly with Gephyrostegus, but the shape and proportions are somewhat different. As my skull is less than half as large as JAEKEL'S

I attribute these differences to youth, and do not regard them as making specific identity of the two forms improbable.

Of the vertebral column no trace remains except the faint impressions of some central elements in the mid-dorsal region. It is clear that the counter slab must have contained the actual bones, but it is probable that the vertebræ were only lightly ossified. A nearly complete series of ribs is present, which shows that there were about twenty-five pre-sacral vertebræ. These ribs appear to be similar throughout the column : they are long, slender and considerably curved. In most cases their proximal ends terminate abruptly without widening, but in one or two specially favourable examples there is an indication of two heads ; the tuberculum lying laterally of the capitulum as in the Eogyrinus rib in fig. 24. There is evidence that the sacral ribs were long as they are in Eogyrinus, but it is impossible to be certain of the number of sacral vertebræ.

The shoulder girdle is perfectly shown. The interclavicle is a very large flat bone, whose shape may be described as a rhomboid, whose anterior corner is widened out into a broad expansion with a segmental anterior border. The lateral corners give attachment to the clavicles and the hinder end is produced backward into a gradually widening tongue of bone, with a bluntly pointed termination. This bone agrees with that of the type figured by FRITSCH in most respects.

The clavicle consists of a narrow vertical rod, attached to the anterior border of the cleithrum, whose lower end turns inward at right angles to the shaft and underlies the interclavicle. This part of the bone is slightly widened, and bears an ornament consisting of ridges radiating from the point where the bone turns upward. The cleithrum is a long, strap-shaped bone, whose upper end is a little widened and turned backward so as to overhang the upper end of the scapula.

The scapula, being a cartilage bone, has been a good deal crushed and shows little structure. It is of considerable size, but ossification does not seem to have spread into the sub-glenoid part of the structure.

The pelvis is represented by good impressions of the left and less complete right ilia and ischia. There is no trace of the pubes, and these bones, as in so many Amphibia, must have been unossified.

The ilium has an expanded acetabular region, with its lower border divided into facets for the ischium and pubis. The acetabulum is overhung by a thickened mass of bone as it is in the majority of Palæozoic Tetrapods, and the whole acetabular region is connected to the dorsal part of the bone by a contracted and rounded neck. The dorsal part of the bone bears a long backwardly directed blade and has a small dorsal prominence anteriorly. Thus, it closely resembles the ilium of the type figured by FRITSCH and also all other known embolomerous ilia, such as the original of fig. 27.

The ischium is a large flat plate of bone, which obviously met its fellow in the middle line, and was in contact with an unossified pubic region in front.

Both forelimbs are present, the left, which lies on the ventral surface of the body, showing a quite perfectly-preserved hand. The humerus is a massive bone with expanded ends which are placed at a considerable angle with each other. The material does not admit of any detailed description, but makes it clear that the bone much resembled the immature humerus of Cricotus figured by CASE, 1915, fig. 36, *c*, *d*, *e*, *f*.

The radius and ulna are featureless bones, the latter considerably the longer and more massive. The carpus is entirely unossified, and, judging from the undisturbed left arm, very short.

The hand is five fingered. The first metacarpal is very short, the third and longest being twice its length and the fifth half as long again. The phalangeal formula is 2, 3, 3, 3, 4, the terminal phalange being small, sharp pointed and claw-like in each case. In the complete hand the third and fourth fingers are of nearly equal length, and the fifth not much shorter, whilst the thumb may almost be described as rudimentary.

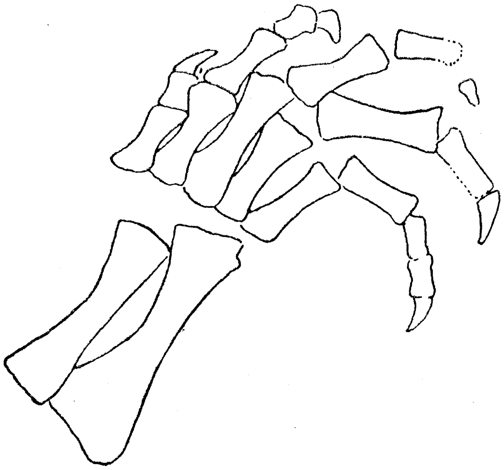

FIG. 29.—*Diplovertebron punctatum*, Dorsal surface of the left manus, reversed in drawing, so that it now appears to belong to the right side. Reduced from a camera lucida outline at a magnification of 24 diameters. × 5 approx.

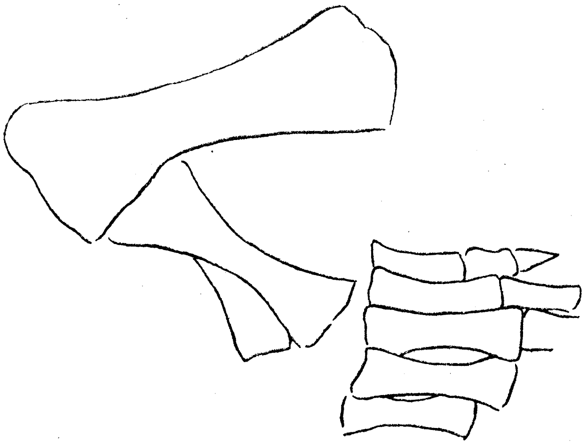

FIG. 30.—*Diplovertebron punctatum*. The left hind leg × 3 approx.

This hand is the only one known belonging to an Amphibian which shows, with complete certainty, the presence of five fingers. Its phalangeal formula is unique, and is perhaps most readily explained as reduction from the normal reptilian formula, which is known from the specimen of *Eosauravus copei* to have been established in pre-stephanian time.

Both femora are preserved, but give little information as to the structure of the bone. There is, however, reason to believe that, as in Eogyrinus, there was no marked adductor crest. The tibia and fibula are short and rather massive bones, with expanded extremities. The foot much resembles the hand in the general proportions of the metapodials, but in it the fourth metatarsal is of the same length as the third, and the first is a little less reduced.

The ventral surface of the animal from the shoulder girdle to the pelvis is completely covered with a continuous squamation of small scutes widened from side to side and short from back to front. These scales overlap one another from before backward, and from above downward, forming very definite transverse rows; in the region from the axillæ to the pelvis, these rows meet in the middle line so as to form chevrons, with their points directed anteriorly, whilst in the pre-axillary region there is on each side of the interclavicle a patch of exactly similar scales, which together form a set of chevrons placed in the opposite direction. There is no extension of the squamation on to the limbs. This squamation agrees exactly in its distribution with that of Cricotus and Archegosaurus, and in all probability with that of the reptile Solenodonsaurus.

The material allows of the restoration of the skeleton with certainty, fig. 31.

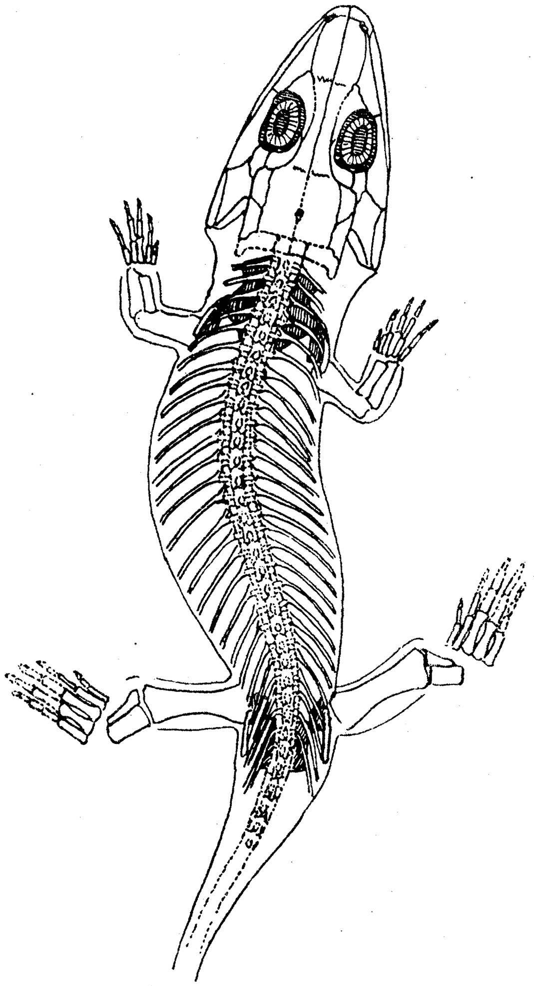

Fig. 31.—*Diplovertebron punctatum.* Restoration of the skeleton, founded entirely on a single articulated individual in the author's possession. × 4/3 approx.

The skeleton so reconstructed is remarkable for its lizard-like proportions. In the presence of a distinct neck, it differs from such Rachitomous forms as Cacops and from the Cotylosauria, and resembles the other Embolomeri; but in its general proportions, the shortness of the body and the comparatively large limbs, it recalls the land-living Rachitomi, and was undoubtedly thoroughly terrestrial in its habits.

It is important to notice that adaptation to a land life has produced in it a structure of the shoulder girdle identical with that of a terrestrial Rachitomous form, such as Cacops, a structure which I believe a necessary intermediate between a primary aquatic girdle, such as that of Eogyrinus, and a secondarily aquatic girdle like that of Cricotus or Pholidogaster.

Another very curious and contrasted change is the failure of the pubis to ossify. The other Embolomeri and the earlier Rachitomi all have well-ossified pubes, whilst all advanced Amphibia, no matter to what order they belong, lose the pubis, for unknown reasons, which can hardly receive any mechanical or directly adaptive explanation, because the animals in which the loss has occurred present great variations in habits and in the structure of their hind limbs.

Despite the work of H. MILLER, 1858, H. PANDER, 1860, R. H. TRAQUAIR, 1875, 1881, W. K. GREGORY, 1915, WATSON and DAY, 1916, E. S. GOODRICH, 1919, W. L. BRYANT, 1919, and E. A. STENSIO, 1922, the general structure of the Osteolepid fish still remains badly known, and I am thus driven to the necessity of giving a new, more complete, and, I hope, accurate account of their structure in order to have the necessary materials for comparison of them with the Embolomeri.

Although the structure of the dermal skull differs a good deal, even in important points, in the various members of the group, it is, as STENSIO has recently emphasised, reduceable to a common ground plan, which is very nearly retained in the form represented in figs. 2 and 3. This fish belongs to the group called by TRAQUAIR Osteolepis macrolepidotus, and the figures are drawn entirely from specimens from the Middle Old Red Sandstone of the Tynet Burn in my own possession. It is evident that the fish from Orkney, and even those from Gamrie and other Moray Firth localities, which are commonly included under the same name, differ considerably in structure.

The hinder part of the neural cranium is covered by a flat table consisting of parietal, supra- and inter-temporals rigidly attached to one another; to the hinder margin of this table is articulated a row of three bones, the tabulars and interparietal. In some forms a little triangular ossicle lies between the tabular and the supra-temporal.

The anterior border of the table is nearly straight and terminates abruptly, being attached to the frontals only by a ligamentous sheet, which in Megalichthys, and probably also in other forms, has its origin in a deep groove along the front margin of the parietal.

The anterior part of the neural cranium is covered by a complex shield of dermal bones. Of these the frontals, which surround the small pineal foramen, are always the largest. Small postfrontals are always attached to the hinder parts of the lateral margins of the frontals so as to form the lateral extremities of the straight hinder border of this part of the skull.

In front of the frontals is usually a pair of smaller elements very variable in size, which may meet in the middle line or may be separated by a median bone or bones; they may fuse with other bones, but when present as separate elements do not transmit any part of the lateral line apparatus. The anterior part of the upper border of the orbit is formed by two bones, the supraorbital and the prefrontal, also not perforated by a lateral line canal. Between these bones and the nasals lies a very variable series of bones, called by STENSIO the nasal series, through which the supraorbital lateral line canal runs forward. This row of bones may or may not meet the corresponding series of the opposite side in front of the group of bones, always including one or more median elements, which lies in front of the nasals. In any case the nasal series are separated from the premaxillæ by a series of small bones, the rostrals of STENSIO, through which runs the ethmoidal cross commissure and its backward continuation with the infraorbital canal.

Between the rostral series, the nasal series and the circumorbital bones lies another small group, whose exact structure is not shown clearly in Osteolepis. This group vanishes entirely in many later forms. Somewhere within it lies the external nostril. In Osteolepis from Tynet it lies high up. In Orkney specimens, referred to the same species, often low down, whilst in Diplopterus and Thursius it is in contact with the upper border of the extreme anterior end of the maxilla; whatever its position it is always single.

The whole structure of the dermal shield of the ethmoidal region can only be made out in specimens in which it is viewed from below, because the cosmoid layer which forms the external surface becomes quite continuous very early in life.

The orbit is surrounded by a ring of circumorbital bones, the post-orbital, jugal, lachrymal, pre-frontal, supra-orbital and post-frontal. The post-frontal contains the junction of the supra and infra-orbital canals, and the latter traverses the post-orbital, jugal and lachrymal passing on into the rostrals.

The cheek is covered by a variable number of plates, only one in the Tynet Osteolepis, two in *Osteolepis macrolepidotus*, and as many as five in Holoptychius. The maxilla is long and underlies and is rigidly attached to the series of circumorbital bones and the cheek.

The neural cranium of the Osteolepids was first, though quite inadequately, described by ROHON; later, and again misleadingly, by myself and H. DAY and by E. A. ANDERSON; and, finally, more successfully by W. L. BRYANT. Dr. BRYANT'S description is, as Dr. STENSIO informs me and as I have been able to confirm, from an examination of the original material, inaccurate in certain respects, but was the first to bring out the main features of the very remarkable structure correctly.

I have material from Tynet Burn which allows of a description of the structure in *Osteolepis macrolepidotus*. (See fig. 1).

The bony neural cranium of all Osteolepids consists of two disconnected parts, the fused occipital and otic region and the ethmo-sphenoidal region.

In Osteolepis the basioccipital consists of a very delicate ossification surrounding the notochord, and ending anteriorly at a point far behind the posterior surface of the basisphenoid. From its upper surface rises a continuous mass of bone which completely surrounds the hind brain and the labyrinths. The exoccipital and supraoccipital region is fully ossified and forms a tube, widening as it is traced forward until it comes into contact with the dermal roof of the skull, apparently at the junction of the parietal and the interparietal. From this point forward the roof of the neural cranium is continuous and forms a gently curved surface, which is in contact with the table of the skull over its whole extent, except for a pair of depressions, lying surrounded and mapped out by the three semi-circular canals. The otic capsule extends laterally of the horizontal canal as a gradually narrowing paroccipital process, which is finally truncated by a vertical surface which bears an articular facet for the head of the hyomandibular. Somewhat mesially of this facet and immediately below the horizontal semi-circular canal, the process is perforated horizontally by a jugular canal.

In front of the otic capsule the hinder part of the brain case has no bony floor, but its side walls are formed by massive bony prolongations of the pro-otic region, whose lower margins bear strong laterally-directed flanges which pass outward to the ends of the paroccipital processes. These side walls are connected together by a thin bony roof. Finally, they end abruptly at the joint between the parietals and frontals.

In front of the otic capsule this side wall is perforated by two foramina, which open forward and outward. The larger of these lies just dorsal to the anterior opening of the jugular canal and no doubt transmitted part of the VII^th^ nerve, certainly the Hyomandibular trunk, and perhaps also, though less probably, the palatine branch. The other foramen is much smaller and lies further forward, it can only have transmitted an ophthalmic branch of the lateralis system.

The anterior part of the brain-case consists of a continuous ossification extending forward from the hinder border of the frontals to the ethmoidal region, which is entirely filled by it. For descriptive purposes, this mass may be divided into ethmoidal, orbital and sphenoidal regions.

The sphenoidal region consists of a short but powerful bone whose posterior surface is formed by a concave condyle which faces backward, and was, no doubt, during life occupied by the anterior end of the notochord and by a cartilaginous part of the basis cranii which connected the basisphenoid with the basioccipital. From the sides of this bone a pair of powerful scoop-like basipterygoid processes project outward.

Dorsally the basisphenoid supports a pair of processes which form side walls to the brain case, and are themselves split longitudinally so as to form a deep groove, presumably continued forward by a canal for the ophthalmic nerve.

The orbital region is composed essentially of a vertical septum, whose lower edges are turned outward into low ridges, which posteriorly pass into the basipterygoid processes, whilst anteriorly they swing outward and form the hinder borders of the ethmoidal region.

The brain-cavity passes far forward and must then divide into two canals, each of which opens into the inner wall of an olfactory chamber. The side wall of the interorbital plate is shown to be perforated by three foramina, others, not visible, having certainly been present. The posterior foramen lies low down, not far in front of the basipterygoid process. In the figure I have labelled it for the oculo-motor nerve, but it is perhaps more probable that it actually transmitted the pituitary vein.

In front of this foramen lies a much larger opening for the optic nerve, and the third foramen, which lies very anteriorly, and high up, may be the anterior opening of the ophthalmic canal. The whole of the orbital region is underlain by a fused, tooth-bearing parasphenoid.

The ethmoidal region is a very extensive mass of bone whose upper surface is in contact with the dermal bones of the snout, whilst the ventral surface was in life nearly covered by the prevomers.

Widely separated in this mass lies a pair of nearly spherical cavities for the olfactory capsules. Each of these has a foramen for the olfactory nerve opening into its mesial wall, its lateral surface is perforated by a small oval external nostril, which leads out between dermal bones to the exterior, whilst the ventral floor is perforated by a small triangular internal nostril, which lies only just within the bone at its lateral margin. These openings are constantly present, but in one specimen only there is an additional lacuna, passing backward into the orbit.

This very remarkable brain case is in all essentials identical with that of the Upper Devonian Cœlacanth, Diplocercides, described by STENSIO, and if allowance be made for the increased tropibasism and decreased ossification which they present, also with that of all other Cœlacanths. Its most remarkable feature, the long unossified stretch of basis cranii separating the basisphenoid from the basioccipital, is clearly functionally connected with the hinge which extends across the dorsal surface of the skull, between the frontals and parietals. The whole arrangement is presumably an adaptation designed to decrease the stresses developed in the skeleton of a powerful, rapacious fish with long jaws, during the process of catching prey.

The neural cranium of Osteolepids and Cœlacanths is thus very clearly marked off from that of all other vertebrates, but, if allowance be made for the hinge, presents very definite resemblances, especially in the character of the otic region to those of the Embolomeri and the Dipnoi, whilst it differs even here very considerably from that of all the Actinopterygii.

A comparison with Macropoma shows quite clearly that the pituitary fossa lay within the basisphenoid between the basipterygoid processes, and the position of the pineal foramen confirms the view that the Thalamencephalon lay in the hinder part of the anterior section of the neural cranium. Thus, it is certain that the fifth nerve passed out through the triangular notch which lies between the dorsal parts of the two divisions of the brain case. The hind and mid-brains thus formed a region of extraordinary length, much as in the living Dipnoi, and the cerebral hemispheres must also have been long and narrow as in the Dipnoi and Amphibia.

The palate of the Osteolepids has hitherto only been known from the incomplete accounts of TRAQUAIR, 1875, WATSON, 1913, WATSON and DAY, 1916, and BRYANT, 1919. Materials of *Megalichthys* in Newcastle, and of *Eusthenopteron* in Edinburgh, allow me to give a complete account of the structures in those two forms.

The pterygoid of Megalichthys is a large bone which in the adult condition, and indeed in individuals which have not yet reached one-quarter of the ordinary size, includes regions which in most forms, and probably in development in Megalichthys, belong to the palatine and transverse bones. It consists of a deep quadrate ramus, which stands nearly vertically in the skull (fig. 31). This part of the bone has a free ventral border which forms the inner side of the large sub-temporal fossa; anteriorly this border sweeps outward and becomes the hinder margin of the palatal part of the bone. The palatal plate lies horizontally in the skull, with its outer edge in contact with the maxilla for the greater part of its length; this margin is thickened but the attachment is not a sutural one.

The inner margin of the palatal plate, as it is traced backward, gradually turns dorsally until it finally rises abruptly to form the anterior border of the quadrate ramus.

The admesial part of the palatal plate is thick, and the whole of its ventral surface is covered with a granulation of close-set small teeth. That broad lateral strip of it, however, which is presumably really formed by the palatine and transverse bones, is much thinner and devoid of shagreen. It bears two tusks and the pits for their replacing teeth; the whole arrangement of pit and tooth is entirely identical in all details with that of the homologous teeth in *Orthosaurus*, described above on page 212. Between these two sets of teeth there is a depression in the bone, which presumably received the first coronoid tusk of the lower jaw. The sets of tusks are preceded and succeeded by similar pits for the other coronoid tusks.

Anteriorly the pterygoid shows (D.M.S.W. 44) a striated depression on the ventral surface, which in life overlapped the dorsal surface of the prevomer. The outer border of the pterygoid from this point forward separates from the maxilla, so as to leave a triangular notch, which is converted into a foramen, the internal naris, by the prevomer, premaxilla and maxilla.

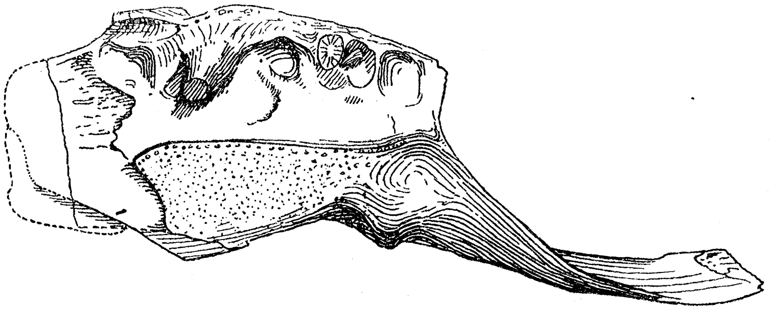

FIG. 32.—*Megalichthys.* Uncrushed right pterygo-palatine × $\frac{2}{3}$. Palatal surface. Newcastle Museum, No. D.M.S.W. 43.

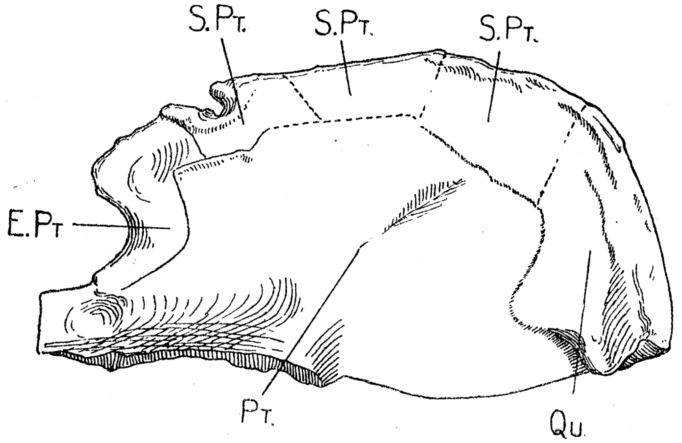

FIG. 33.—*Megalichthys.* Left pterygoidal complex with the palatal part broken away. Outer surface. Newcastle Museum, No. D.M.S.W. 48. Sutures in dotted line inserted from other specimens. × $\frac{2}{3}$.

The whole length of the inner margin of the pterygoid bears on its ventral, or, in the para-otic region, admesial face, a rabbet which articulates with a continuous series of cartilage bones. The most anterior of these bones overlaps the prevomer and no doubt came into contact with the olfactory capsule. It extends to the root of the anterior margin of the para-otic plate, when it is in contact with the next ossicle, the homologue of the Tetrapod epipterygoid, which I shall continue to distinguish by that name. This element rests on the anterior edge and inner surface of the pterygoid, standing nearly vertically in the skull; its anterior border is embayed by a wide notch, above which it is produced into a blunt process directed forward. It is immediately succeeded by another bone of the same series, which rests on the upper edge of the quadrate ramus of the pterygoid; this has a deep incision in its upper border, which must have transmitted the second and third branches of the fifth nerve. This element is succeeded by two more, which fill up the space between it and the quadrate. The quadrate itself is a comparatively large element, attached by the whole of its admedian surface to the outer side of the quadrate ramus of the pterygoid, along which it is drawn out into a short but quite definite pterygoid ramus; the mass of the bone stands transversely in the skull, its outer face being in contact with the pre-operculum and the quadrate jugal, and the whole of its lower margin forming a well-finished articular condyle.

The series of bones just described I shall call the suprapterygoids. The fact that they include the epipterygoid and the quadrate shows that they are ossifications in the palato-quadrate cartilage, and they form the only known instance of a complete replacement of that element by cartilage bones. That they are indeed substitution bones is fortunately confirmed by their structure. In Megalichthys the membrane bones are very massive, and are preserved in the Newsham shale in their full thickness and quite uncrushed. The cartilage bones, on the other hand, are feeble, consisting only of a thin superficial layer supported by a set of bony spicules; when preserved in the shale such bones are always crushed flat, the spicules showing through as low projections on the surface.

The shapes, numbers, and relations of these suprapterygoid bones are fixed by the following series of specimens:—

D.M.S.W. 48, pterygoid with the quadrate and all other suprapterygoid bones *in situ*, outer aspect.

D.M.S.W. 45, pterygoid with quadrate and fifth supra pterygoid *in situ*, fourth displaced, inner aspect.

D.M.S.W. 46, pterygoid with quadrate, fifth and third suprapterygoids *in situ*, second (epipterygoid), slightly displaced.

D.M.S.W. 47, pterygoid alone, inner surface.

It is now clear that no part of the pterygoid could have articulated with the basis cranii, but the base of the epipterygoid, which is not well exposed in any specimen, lies at exactly the right place to come in contact with the basipterygoid process, and in Eusthenopteron it can be seen to articulate with it.

In Eusthenopteron Bryant was only able to describe one element of the suprapterygoid series, and that, which he calls the metapterygoid, only very incompletely. Indeed his whole restoration of the palate is not very satisfactory.

No. 1897, 51, 206, Royal Scottish Museum, is a quite perfectly-preserved pterygoid complex of Eusthenopteron, with the maxilla in natural articulation. The specimen belongs to the right side and its palatal surface is perfectly exposed. This view does not appear to have been seen by Dr. Bryant.

The pterygoid is exactly as he has described it, differing only in its more slender shape from that of Megalichthys. Its outer border is rigidly attached by suture to the large ectopterygoid and smaller palatine. The former of these bones bears two rows of teeth, of which the outer lies along the margin of the bone and is composed of small, sharp-pointed teeth, apparently of circular section. On the admedian side of this row is another, which, in the two specimens available by me, consists of two alternative couples of large tusks with a crown of lozenge-shaped section. These teeth have been described by Bryant, but in his restoration (fig. 4) he makes them far too numerous. The palatal surface of the ectopterygoid is smooth and depressed below the shagreened neighbouring part of the pterygoid.

The palatine is a bone agreeing exactly in its general character with the ectopterygoid; it bears a row of small teeth along its outer margin, and supports a single alternative couple of large tusks. In front of the anterior of these teeth the smooth palatal surface of the bone is excavated by a hemispherical pit for the reception of an enlarged tooth in the lower jaw. It is probable that the foramen in this bone recorded by Bryant, and regarded by him as a nostril, is really only an exceptional development of this pit. This specimen shows a series of suprapterygoid ossicles, which begins

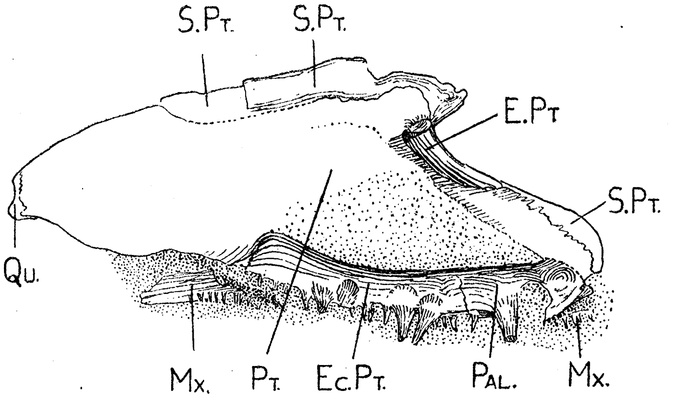

Fig. 34.—*Eusthenopteron*. Pterygoidal complex with the maxilla in natural articulation. Left side, palatal and admesial surface. Royal Scottish Museum, No. 1897, 51, 206.

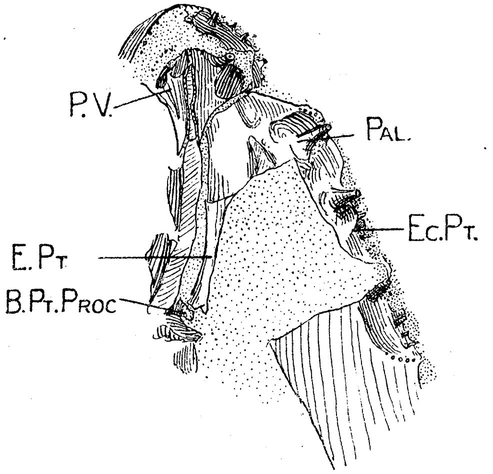

Fig. 35.—*Eusthenopteron*. Portion of the palate × ⅔. Stippled areas represent unremoved matrix. Royal Scottish Museum, No. 1897, 51, 201.

with an element bordering the inner and anterior edges of the pterygoid and extending so far laterally as almost or quite to touch the palatine. This is immediately followed by the epipterygoid, which stands nearly vertically in the skull, forming a thick rounded margin to the para-otic part of the pterygoid, and supporting admedially a very well-developed, cupped articular surface, which is seen in No. 1897, 51, 201, R.S.M., to articulate with the basipterygoid process. Dorsal to this articulation the epipterygoid is carried forward into a powerful process, already described and figured by BRYANT. Caudally of this extremity the epipterygoid is excavated by a notch, agreeing exactly with that in the third suprapterygoid of Megalichthys. Behind this its dorsal border is horizontal until the bone suddenly terminates at an apparent suture. The next suprapterygoid is, so far as it is exposed, a triangular bone ending behind in a point some distance in front of the quadrate. Thus in Eusthenopteron the continuity of the suprapterygoid series seems to be broken.

In No. 1897, 51, 206, the anterior end of the naturally articulated maxilla is seen to separate from the anterior part of the lateral margin of the palatine exactly as it does in Megalichthys, so as to leave a triangular notch. In No. 1897, 51, 201, the hinder end of the premaxilla leaves the outer margin of the hinder end of the prevomer, so as to leave a similar incision. As the anterior end of the maxilla is shown by other specimens to articulate directly with the hinder end of the premaxilla, in the intact skull a triangular opening surrounded by these four bones must be left ; this is the posterior naris, agreeing in all its relations with that of Orthosaurus.

The whole jaw apparatus thus receives very adequate connection with the anterior part of the neural cranium, because not only is the palate directly supported by its contact with the basipterygoid process, but its outer border is rigidly articulated with the maxilla, which is itself connected by a series of powerful membrane bones with the frontal, and hence with the anterior part of the neural cranium. As we have seen above, this region of the skull is capable of motion relatively to the occipital region ; it therefore necessarily follows that that connection of the jaw apparatus with the occipital part of the neural cranium which is provided by the hyomandibula will be relatively little important.

The hyomandibula was described by TRAQUAIR and by WATSON and DAY in Rhizodopsis, and by BRYANT in Eusthenopteron, and it is shown in its natural position, although only in section, in a remarkable specimen of Megalichthys. This skull, No. 28,308, Museum of Practical Geology, is the whole anterior part of a fish, preserved in an ironstone nodule quite undistorted and with all its elements in their natural relations. Unfortunately, all that can be seen of the internal parts is a section exposed on the posterior end (fig. 36).

The neural cranium here appears as a large continuous mass of superficially ossified cartilage, the lower part, basioccipital, is perforated by a large nearly circular notochordal pit, above which the irregular cavity of the brain case extends upward to an ossified supraoccipital region, which is widely attached to the parietals. From the sides of this mass a pair of slender processes pass outward and upward to the supra-temporals, with which the left is seen to come into contact; the right is cut more caudally and does not reach the skull roof. Between each process and the roof is an apparent post-temporal fossa. (In the specimen of Rhizodopsis described by WATSON and DAY this process rises to the skull roof, converting the fossa into a mere pit.)

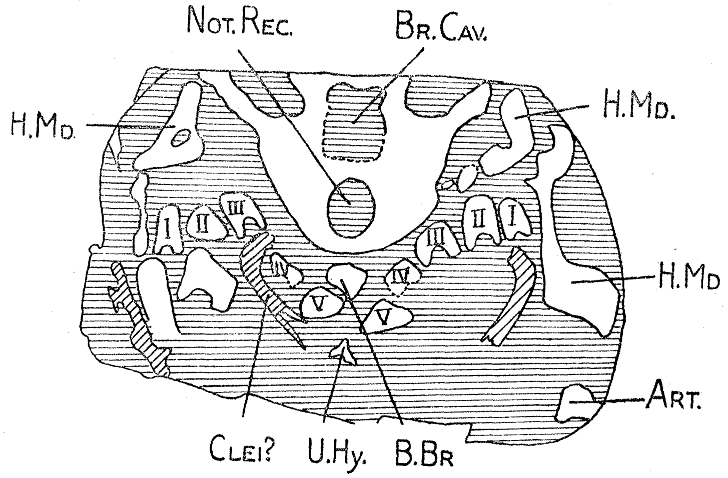

FIG. 36.—*Megalichthys*. Section exposed on the hinder surface of the head, No. 28,308, Museum of Practical Geology. × $\frac{2}{3}$.

The large but entirely superficially ossified hyomandibular is shown on both sides, the section of that on the left being about 0·5 cm. behind that on the right. On the left the bone is shown as an elongated mass nearly in contact with the outer extremity of the otic region and the dorsal surface of the skull; this mass widens below and is perforated by an oval foramen. The lower part of the bone is perhaps represented by a detached narrow strip.

On the right the hyomandibular is represented by two discrete areas. The outer extends from near the flat top of the skull to the quadrate region; its upper part shows a notch, presumably a continuation of the foramen shown in the other bone. Lateral to this it thickens and touches the operculum, probably without any real articulation with it. Below this broad head the bone becomes very slender in the section until it suddenly widens at the lower end.

In this section the branchial apparatus is represented by the sections in the cerato-branchial region of five pairs of gill arches, the fourth being smaller and less well ossified than either of the others. From the position of the section it seems to be certain that all these arches lie behind the hyoid, so that there is a full representation of all the visceral arches which occur in Vertebrates in development, and there is already a reduction of that arch which disappears during development in all Tetrapods.

The branchial apparatus is completed by the sections of two median elements, a large dorsal basibranchial, and a small ventral urohyal. The whole branchial apparatus is thus similar to that of the Cœlacanths, which are the only direct descendants of the Rhipidistia.

The lower jaw of the Rhipidistia was first correctly described by R. H. TRAQUAIR, but adequate illustrations, with a modern interpretation of its structure, are still lacking. The jaw of Eusthenopteron described by BRYANT departs so widely from that which occurs in the majority of forms that it cannot be used for general comparisons.

I give here an account of the lower jaw of Megalichthys, founded on a very large series, about one hundred, of complete jaws in Newcastle, together with D.M.S.W. 53, a detached dentary, exposed from within, with a misplaced anterior coronoid lying across it, and D.M.S.W. 54, a right pre-articular exposed from both surfaces, with a displaced anterior coronoid on its lingual surface. These two specimens clear up all doubtful points in the structure.

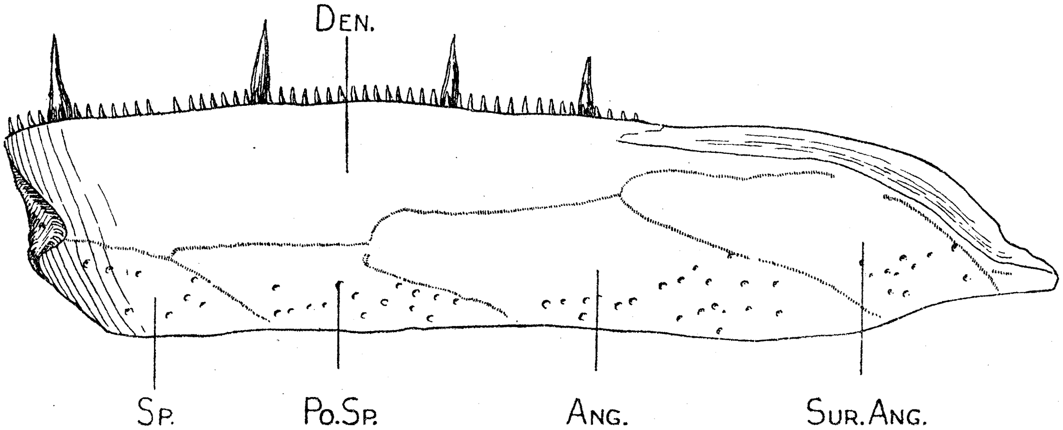

FIG. 37.- *Megalichthys.* Left ramus of the lower jaw. Outer surface. × $\frac{1}{2}$.

All the Newcastle jaws are crushed flat, but the uncrushed head in Jermyn Street shows that in life the section of a ramus was of considerable width, nearly equalling the depth.

The dentary is a long bone whose anterior end is thickened and supports a large tusk

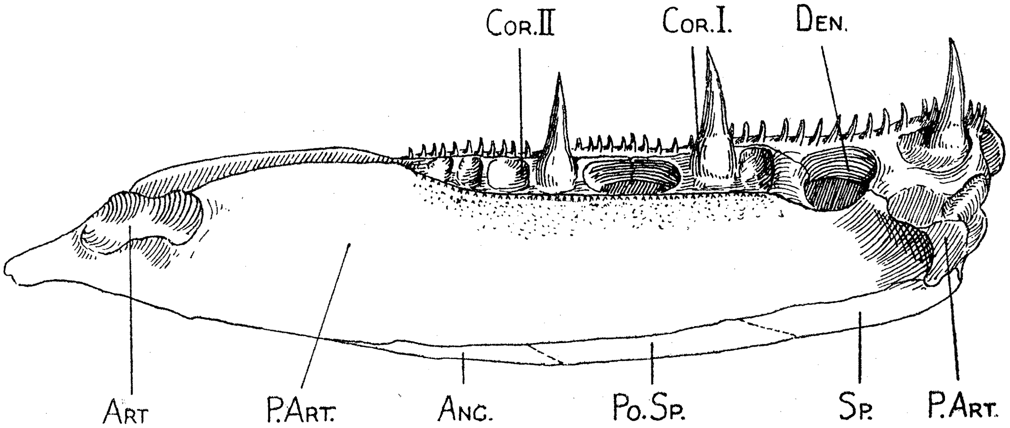

FIG. 38.—*Megalichthys.* Right ramus of the lower jaw. Inner surface. × $\frac{1}{2}$.

and the pit for its replacing tooth. This thickened region forms the upper part of the symphysis, and is strongly attached to the anterior end of the prearticular. Behind it the inner surface of the bone is smooth and recessed to form the anterior and outer borders of the first dental fenestra. Behind this opening the bone bears an articular face for the first coronoid. The remainder of the inner surface is not exposed in any specimen known to me. From the enlarged anterior tusk backward, the whole upper surface of the dentary is occupied by a continuous and uniform series of small, sharp-pointed teeth.

The lower border of the dentary never reaches the lower margin of the jaw, as it rests on the four infra-dentaries—the splenial, post-splenial, angular and sur-angular. These bones are all very much alike, and except for the first are entirely restricted to the outer surface of the jaw. The splenial has a small internal exposure on the inner surface where it articulates with the pre-articular; it appears to play no part in the symphysis. The sur-angular is clearly shown in D.M.S.W. 50 to cover the entire outer surface of the angular, which bears a well-developed cavity for articulation with the quadrate.

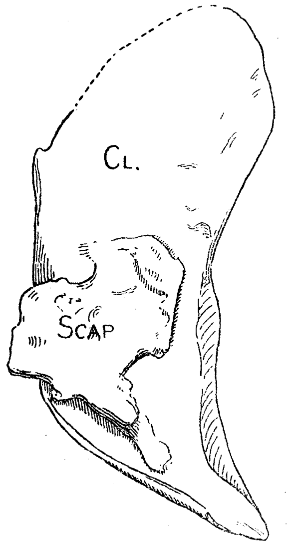

Fig. 39.—*Megalichthys.* Left cleithrum and scapula. Inner surface. × $\frac{2}{3}$.

Running from the articular to the dentary, along the upper margin of the bone here called sur-angular, there is a strip of bone whose outer surface is depressed below that of the rest of the surface. This region is separated by a groove agreeing in appearance with the sutures between the rest of the bones of the outer surface of the jaw. This thus appears to be a separate element not represented in Tetrapod jaws.

The pre-articular forms the greater part of the inner surface of the jaw, covering the inner surface of the articular and stretching forward to the symphysis. Its lower border joins the sur-angular, angular, post-splenial and splenial. Its upper border is free, although it is supported by the two coronoids which lie between it and the dentary, and by the thickened anterior end of the latter bone. The anterior end of the pre-articular has a powerful union with the dentary and forms the whole of the lower part of the symphysis. The anterior coronoid lies between the outer surface of the pre-articular and the inner surface of the dentary; its anterior border forms the hinder boundary of the nearly circular anterior dental fenestra, which leads down into the cavity of the jaw and houses the prevomerine tusk when the mouth is closed. This bone bears a single tusk and the pit for its replacing tooth.

The second coronoid exactly resembles the first in all its general relations. It lies caudal of it, separated by the second dental fenestra for the reception of the palatine tusk. The bone bears two tusks and the pits for their replacing teeth, and has in addition a depression for the ectopterygoid tusk. Its posterior margin is the anterior border of the suprameckelian fossa. It is conceivable that this second coronoid is really two, an unseen suture running through the depression in the middle of its length.

When the two rami of the lower jaw are articulated there is seen a lozenge-shaped depression over the symphysis, surrounded by the dentaries and splenials. No. 28,308, Museum of Practical Geology, shows that this depression is filled by a small, lozenge-shaped mental bone with a shining cosmine surface.

Summary and Conclusion.

In this paper the structure of four members of the Embolomerous group of Labyrinthodont Amphibia is described in detail. From being a group known only by descriptions of a few almost useless fragments, and by a series of forgotten descriptions of much better material, the Embolomeri become as well known as any other fossil vertebrates, and from their great age afford an invaluable point of departure in all discussion of phylogeny.

In the Croonian Lecture, which forms the first part of this paper, I have used them as a basis for a discussion of the mode in which an air-breathing life was first introduced amongst Tetrapods and of the conditions associated with its introduction.

My thanks are due to the Council of the Natural History Society of Northumberland, Durham and Newcastle-on-Tyne, whose collection of these Amphibia is the richest and most important in the world, and to Mr. E. L. GILL, the curator of their museum, who has rendered my work there both easy and pleasant. I am indebted also to Dr. KITCHEN, of the Museum of Practical Geology, Dr. TATTERSALL, of Manchester, Dr. EAGLE CLARK, of Edinburgh, and Dr. A. SMITH WOODWARD and the late Dr. C. W. ANDREWS of the Natural History Museum, for the use of materials in their charge, and to my assistant, Miss H. S. PEARSON, for much editorial assistance in the preparation of this paper.

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Explanation of the Reference Letters to the Figures.

Ang., angular.
Art., articular.
Art., *B. Pt.*, articulation on the epipterygoid for the basipterygoid process.
B.Br., basibranchial.
B. Sp., basisphenoid.
B. Oc., basioccipital.
B. Pt. Proc., basipteryoid process.
Br. Cav., brain cavity.
Cer. Br. I., 1st cerato-branchial.
Cer. Hy., cerato-hyal.
Cl. or Clav., clavicle.
Clei., cleithrum.
Cor. I, II, III, the three coronoids.
Den., dentary.
D.S.Oc., dermo-supraoccipital.
E. Pt., epipterygoid.
E. Pt. A., epipterygoid, ascending process.
E. Pt. Ot., epipterygoid, otic process.
Ec. Pt., ectopterygoid.
Ex. Nar., external nares.
Ex. Oc., exoccipital.
Fr., frontal.
H. Md., hyomandibular.
I. Cl., interclavicle.
I. Na., internasal.
I. Tem., intertemporal.
Int. Nar., posterior nares.
Ju., jugal.
L.L.J., left lower jaw.
Lac., lachrymal.
M.G., median gular.
Mx., maxilla.
Na., nasal.
Not. Rec., pit in the basioccipital for the notochord.
Op., operculum.
Orb., orbit.
P. Art., pre-articular.
P. Mx., premaxilla.
P.O., postorbital.
P. Tem., post-temporal.
P. Tem. F., post-temporal fossa.
P. V., prevomer.
Pal., palatine.
Par. Oc., paroccipital.
Par. Oc. Tab. F., facet on the paroccipital for articulation with the tabular.
Par. Sp., parasphenoid.
Po. Fr., post-frontal.
Po. Sp., postsplenial.
Pr. Fr., prefrontal.
Pr. O., pro-otic.
Pr. Ot., otic process of the epipterygoid.
Proc. B. Pt., basipterygoid process.
Ps. Fen. Ov., Pseudo-fenestra ovalis.
Pt., pterygoid.
Pt. Fr., post-temporal.
Pt. Par. Ot., parotic plate of the pterygoid.
Pt. R. Pal., palatal ramus of the pterygoid.
Pt. Sp., postsplenial.
Qu., Quadrate.
Qu. Ju., quadrato jugal.
R. L. J., right lower jaw.
S. Ang., sur-angular.
S. Cl., supracleithrum.
S. Mx., septomaxilla = os nariale.
S. Oc., supraoccipital.
S. Op., sub-operculum.
S. Pt., suprapterygoid.
S. Tem., supratemporal.
Scap. or Sc., scapula.
Sp., splenial.
Sp. Eth., sphenethmoid.
Sq., squamosal.
Sur.-Ang., sur-angular.
Tab., tabular.
U. Hy., urohyal.