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THE EVOLUTION OF THE ANAMNIOTA.

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"Since the days when Gegenbauer and Thatcher and Balfour propounded their views on the origin of the limbs, vertebrate morphology has not been standing still. Great increases have been made in our knowledge. Now, in considering the working hypotheses of these earlier days of morphology, we should remember that increase in our knowledge may greatly alter our point of view, and it seems in my humble opinion that it is conducive to progress, not so much to search for new detailed facts which may bolster one or other of existing hypotheses, as to endeavour to make an impartial survey of the facts as we know them and then to consider carefully whether the body of facts so surveyed seems to suggest a working hypothesis drawn up on the original lines or one drawn up on somewhat different lines."¹

Thus, without asking his permission, I call upon Professor Graham Kerr to provide an introduction to a paper on speculative morphology.

That which follows is an attempt to harmonize the facts of development and adult anatomy of the Anamniota. In no case, I am well aware, would I be justified in writing Q.E.D. at the end of any section or argument. Basing conclusions on unavoidably scanty circumstantial evidence, the student of evolution who adopts a dogmatic attitude or positive language, such as that italicized by Professor Kerr at the foot of page 278, betrays an unphilosophic mind or a partisan conviction. None of our working hypotheses can be proven, they are but statements of probabilities, and, as such, then, the conclusions arrived at herein are presented.

My conclusions are embodied in the diagram below, so that in it I present, as it were, a thesis which it is intended to defend in the following pages. The two most radical conclusions which it is intended to convey by the diagram are:

1. The Chondrostei are bony Elasmobranchs.
2. The Dipnoi are primitive amphibians.

¹ Kerr.—*In* The Work of J. S. Budgett, 4to., Cambridge, 1907, pp. 277-8.

This work is founded on the study of a fairly wide range of material which includes the following: (1) a very fine series of teleostean specimens, placed at my disposal by Dr. C. Anderson, Director of the Australian Museum; (2) *Chimera* and *Tandanus*, received from the New South Wales Fisheries Department; (3) *Callorhynchus antarcticus*, from the Hon. G. H. Thomson of Dunedin, New Zealand; (4) *Amia*, *Lepidosteus*, and *Acipenser*, as well as *Necturus*, *Pseudotriton*, *Notophthalmus* and *Amblystoma*, through Professor W. K. Gregory, from the American Museum of Natural History; (5) a large number of *Amblystoma tigrinum* in alcohol and several beautiful series of sections of the head of *Amphiuma*, from Professors C. Judson Herrick and H. W. Norris; (6) *Neoceratodus*, from Dr. T. Bancroft, Eidsvold, Queensland; (7) *Psephurus*, from Mr. A. De C. Sowerby, Shanghai, China; (8) *Lepidosiren*, through Mr. Carl P. Schmidt, from the Field Museum of Natural History, Chicago; (9) various anurous amphibians and a number of elasmobranchs collected by myself and my friends.

I have to acknowledge my indebtedness to the gentlemen and institutions mentioned above and to thank them for their assistance.

From this list it will be gathered that I have not been able to dissect for myself either of the recent crossopterygians, or *Protopterus*, and that I have also had to rely entirely on the work of others for my knowledge of the anatomy of the gymnophiones; for the rest I have been able to study at first hand the structures of representatives of all the forms discussed.²

The embryological material has not been so varied: (1) sections of the head of embryonic Trout and *Sparus*; the lengths of these were not known, but they were all stages prior to the formation of bone; (2) longitudinal sections of the head, 8 mm. in length, of an unidentified shark, and well advanced as to the

² Since this paper was finished Professor H. W. Norris placed me further in his debt by presenting me with several very fine sets of transverse sections of gymnophione heads, and I received a skull of *Polypterus* from Ward's Natural Science Establishment, Rochester, New York. I have also had the opportunity of working out very completely the development of the chondrocranium of the lizard *Physignathus lesueurii*, Gray, and that of the common fowl, as well as one stage in the development of the chondrocranium of the Frogmouth, *Podargus*.

EXPLANATION OF THE DIAGRAM.

Pregnathostomes.—The salient features of these are briefly reviewed in the text.

Archignathostomes.—Protovertebrata which have the first visceral arch essentially similar to the rest of the arches, but functioning at times as a jaw. The foregut has a dorsally situated glandular caecum.

Neognathostomes, or *Astylic Gnathostomes*.—The first arch is definitely modified to act as a jaw, but is held in place, fore and aft, by fibrous unions only.

Archistylica.—Gnathostomes in which the maxillary arch is in cartilaginous union with the trabecula anteriorly, in the ethmoid region; probably a feature of many Pre- and Protapulmonates.

Prepulmonates.—Archistylic Gnathostomes in which, it is assumed, the dorsal glandular caecum of the foregut is large and flaccid.

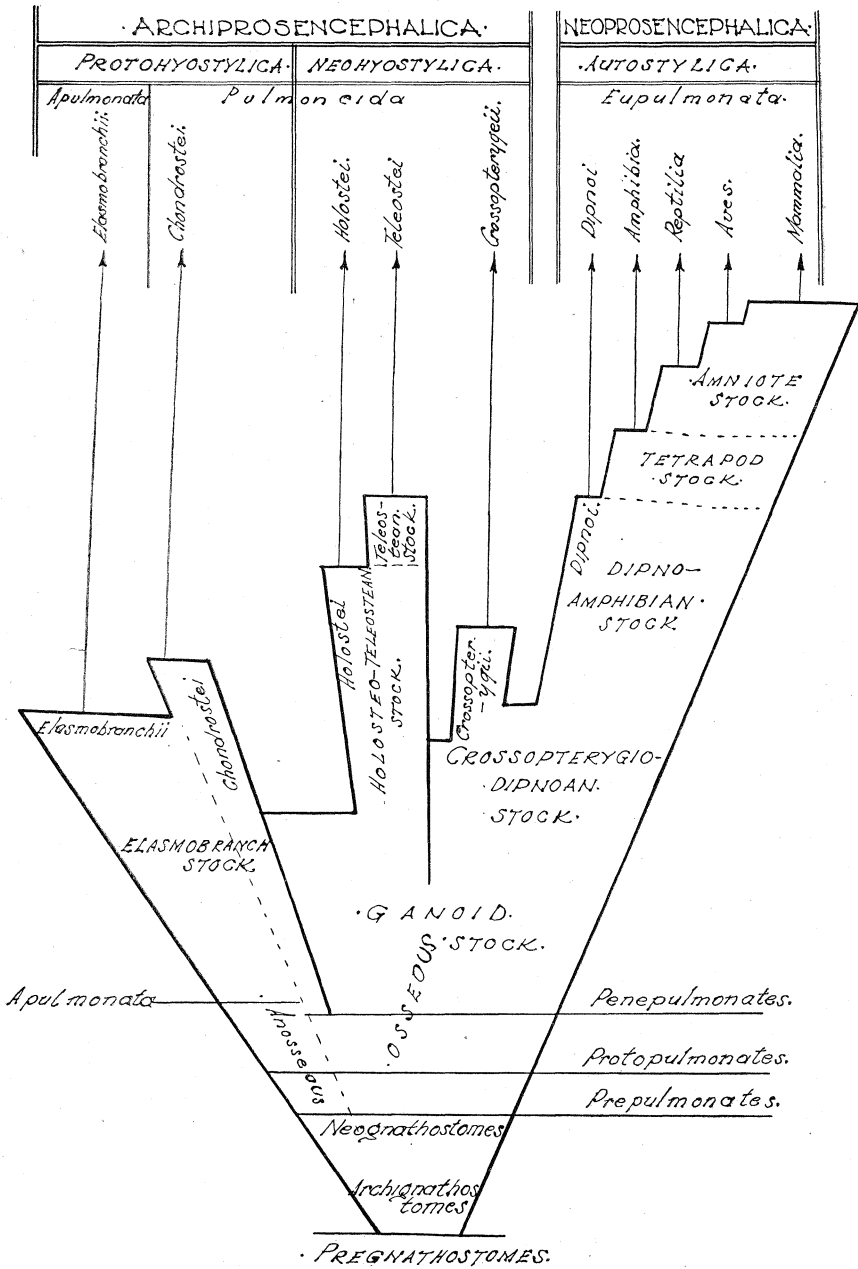
Protapulmonates.—In this stage of the evolution of the lung, it is assumed that the dorsal caecum now contains gases, but has as yet no function to perform relevant thereto.

Penapulmonates.—It is assumed that now the "almost-lung" has gained control of its gaseous contents by muscular and/or glandular activity.

Apulmonata.—It is assumed that the caecum has become aborted.

Pulmoneida.—Greek: eidos—like.

The terms used at the top of the diagram are fully discussed in the text.



For explanation see foot of preceding page:

chondrocranial structures; (3) complete sets of embryos of *Hyla aurea*, *Hyla caerulea* and *Lymnodynastes peronii* from the deposition of the eggs up to the appearance of the forelimbs, collected, a few each day. From these latter I have prepared sections which enable me to state that the phenomena of development of the chondrocranium is so closely similar to that described by Parker and Gaupp in *Rana* that I do not deem it useful to publish any further account of my findings.

Though this embryological material is scanty, its study has enabled me to understand embryological literature and drawings as I should not have done without it.

The Elasmobranch Age.

1. *The Pregnathostomes.*

Before we discuss the evolution of the fishes and amphibians it is desirable that we attempt to form some idea of the structure of the early vertebrates, pregnathostomes, from which they have evolved. We have been taught to believe that in its development each animal "climbs its own genealogical tree," and there is little reason to doubt that we have been taught aright. Now, if in our studies of embryology we find certain structural features appearing in all the vertebrates, then, even if these features be evanescent in some forms, we feel justified in concluding that the features in question were present in the common ancestor of all the forms studied.

Not only is this so, but, remembering that the adult is but the last stage in the life history, we are equally justified in assuming that structures possessed by adult forms in common were also inherited.

Two striking illustrations. Because all vertebrates *are* vertebrate, we assume a vertebrate ancestor. Because all amniotes have an amnion, we assume an amniotic ancestor for the group, distinct and different from that of the Anamniota, though, as just pointed out, tracing their ancestry further back we find that they have both sprung from a common stock.

It is believed that if we sift carefully the evidence provided by the life histories and adult anatomies of the Anamniota we shall be able to arrive at the probable structure of the various ancestors as we trace backwards the converging lines of similitude.

Before proceeding to an analysis of the life histories it will not be out of place to enumerate those structural features which we are all agreed must have been present in the ancestral vertebrate stock.

The Archi- or Protovertebrata, pregnathostomes, were provided with a segmented nervous system, whose central stem was enclosed in a more or less continuous vertebral column. The anterior end of this system had become enlarged, in consonance with the importance of certain organs of special sense, eyes, olfactory organs, the organs of equilibration, and probably tactile organs. Respiration was effected by a series of gills, which were related to clefts in the body wall anteriorly; these clefts opened into the fore end of the gut. The gill clefts were supported by skeletal arches, and in relation to these and their respiratory function a system of muscles had been developed, whereby the clefts

could be opened and closed. Herein was an added cause for the increased complexity of the anterior end of the nerve stem, to which was also added certain oculomotor nerves. There was a well developed blood vascular system with the motor power restricted to a short segment of the main vessel, a primitive heart. The intestine was slightly, if at all, convoluted, it was provided with a definite set of muscles whereby the anterior orifice was enabled to function as a mouth, under voluntary control, and a sphincter ani, which probably acted entirely reflexly. Hepatic and pancreatic glandular tissues were present and poured their products into the gut. A coelomic cavity was well developed. The excretory system was a pronephros composed of coiled tubulo-glandular tissue; it probably emptied into the hind gut. Only one gonad, male or female, was present.

It is further agreed that the body was fish-like, and that its muscles were arranged metamerically, and also that the anterior end of the nerve stem was enclosed in a cartilaginous capsule, the chondrocranium, which had built into it the capsules for the organs of special sense, and was more or less continuous with the vertebral column.

It is also agreed that dorsal and ventral fins were present, and in all probability paired anterior and posterior fins.

These, then, are the generally conceded attributes of the archi-vertebrata. Our problem is to discover by what modifications the various fishes and the amphibia were evolved, and how these are related one to another and to the ancient stock from which they have evolved.

2. *The Evolution of the Jaws.*

That I begin with certain cranial structures is not because I regard them as of pre-eminent importance, but because I am more familiar with cranial structures than with any others.

Since the review of the phylogeny of the Dipneusta by Dollo³ and of their anatomy, development and classification by Bridge,⁴ our knowledge of their embryology has been increased by Agar⁵ and Kerr⁶ and by several contributions of a comparative nature from Edgeworth during the years 1911 and 1926, which are of especial value. Kellicott⁷ has given us a very valuable paper on the development of the respiratory and vascular systems of *Neoceratodus*.

In the five tables which follow, the facts in connection with the development of the palato-pterygo-quadrate arch have been collected. Two of these tables are taken direct from Edgeworth,⁸ the others are largely compiled from his work. In the tables of my own compilation I have added a column giving the authority for the fact recorded. In some of these cases I have with confidence accepted the fact and authority from Edgeworth without troubling to confirm it.

³ Dollo.—Bull. Soc. Belge Geol. Pal., ix, 1895, pp. 79-128.

⁴ Bridge.—In Cambridge Natural History, vii, Fishes, 8vo., London, 1904.

⁵ Agar.—Trans. Roy. Soc. Edin., xlv, 1906, pp. 49-54.

⁶ Kerr.—Quart. Journ. Micro. Sci., xlvi, pp. 417-459.

⁷ Kellicott.—Mem. N.Y. Acad. Sci., ii, 4, 1905, pp. 135-249.

⁸ Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.

TABLE I.
The palato-quadrate cartilage first appears

In	As an independent cartilage not attached at any point to the neural cranium.	Attached to the trabecula or ethmoid plate.	Authority.
<i>Petromyzon</i>		+ ⁹	Parker
<i>Scyllium</i>	+		Edgeworth
<i>Heterodontus</i>	+		"
<i>Acipenser</i>	+		Parker
<i>Polypterus</i>	+		Budgett
<i>Amia</i>			Swinerton
<i>Lepidosteus</i>		+ ¹⁰	Parker
<i>Gymnarchus</i>	+		Assheton
<i>Gasterosteus</i>	+		Swinerton
<i>Belone</i>	+		"
<i>Zoarcia</i>	+		"
<i>Salmo</i>	+		Winslow
<i>Neoceratodus</i>	+		Edgeworth
<i>Lepidosiren</i>		+ ⁹	Agar
<i>Protopterus</i>		+ ⁹	Agar ¹¹
<i>Ichthyophis</i>	+		Peters
<i>Menopoma</i>	+		Edgeworth
<i>Siren</i>	+		Gaupp
<i>Triton</i>	+		Edgeworth
<i>Hyla</i>	+?		Kesteven
<i>Limnodynastes</i>	+		"
<i>Rana</i>	+		Gaupp
<i>Amblystoma</i>	+?		Edgeworth
<i>Salamandra</i>	+?		"
<i>Plethodon</i>	+?		"
<i>Spelerpes</i>	+?		"
<i>Hynobius</i>	+?		"
<i>Megalobatrachus</i>	+?		"
<i>Salamandrella</i>	+?		"
<i>Ranodon</i>	+?		"
<i>Amphiuma</i>	+?		Winslow
<i>Necturus</i>	+?		Platt
<i>Desmognathus</i>	+?		Wiedersheim

In the case of the forms marked "?" the youngest stages studied have had one or two attachments between the neural cranium and the palato-quadrate, but, inasmuch as that in several amphibians an originally free palato-quadrate has been observed to become attached by one, two, and three processes successively, one is justified in assuming that, had earlier stages been studied in these other cases, they also would have been found to have the palato-quadrate entirely free at its first appearance.

TABLE II.

The order in time of attachment of the Quadrate, in dipnoans and amphibians, to the cranium by ascending otic, and basal processes.

It is not claimed for this table that it conveys a final statement of the facts set out; on the contrary it is believed that, with more complete series of early embryos, most, if not all of the forms, would be found to gain attachment to the cranium by the three processes in succession. The table presents the present state of our knowledge, as far as I have been able to abstract the literature. The order of sequence of attachment is indicated by the numerals; where the same numeral appears in two or more

⁹ In these cases the palato-quadrate bar first appears as a spur or lateral process of the hinder end of the trabecula.

¹⁰ In this form the palato-quadrate is attached *ab initio* to the lateral cornu of the ethmoid.

¹¹ Several other fishes might have been included in the table, but every case known in which the bar is not originally quite free has been, I believe, included in the table.

columns, it simply means that, in the youngest stage I have found an account of, two or more attachments were already established.

Forms.	Ascending process.	Otic process.	Basal process.	Authority.
<i>Neoceratodus</i>				
<i>Protopterus</i>	?	?	1	Agar ¹²
<i>Lepidosiren</i>	2	1	2?	Agar ¹²
<i>Amblystoma punctatum</i>	1	2	3	Edgeworth
<i>tigrinum</i>	1	2	3	"
<i>Triton</i>	1			Gaupp
<i>Siredon pisciformis</i>	1	2?	3?	Gaupp, Stöhr
<i>Desmognathus</i>	1	1	1	Edgeworth
<i>Spelerpes</i>	1	1	2	Wiedersheim
<i>Plethodon cinereus</i>	1	1	1	Edgeworth
<i>Amphiuma tridactylum</i>	1	2	2	Winslow
<i>Megalobatrachus maximus</i>	1	2	2	Wiedersheim
<i>Menopoma</i>	1	1	2	Edgeworth
<i>Hynobius nebulosa</i>	1	1	2	"
<i>Salamandrella keysertingii</i>	1	1	2	"
<i>Ranodon</i>	1	1	2	"
<i>Necturus</i>	1	2	3	Platt
<i>Siren</i>	1	1	1	Parker, Edgeworth
<i>Rana</i>	1	2	3	Gaupp, Parker
<i>Hyla cærulea</i>	1	2	3	Kesteven
<i>aurea</i>	1	2	3	"
<i>Limnodymastes peronii</i>	1	2	3	"
<i>Ichthyophis</i>	1		2?	Winslow
<i>Siphonops</i>	1		2	Edgeworth

TABLE III.

The ascending process of the quadrate is always attached to a trabecular derivative, but at varying levels, as follows:

Forms.	At the level of cranial base.	To the trabecular wall.	To the <i>tænia marginata</i> .	Authority.
<i>Neoceratodus</i>		+ ¹³		Edgeworth
<i>Protopterus</i>	+?			Agar
<i>Lepidosiren</i>	+			
<i>Salamandrella</i>		+ ¹³		Edgeworth
<i>Ranodon</i>		+ ¹³		"
<i>Cryptobranchus</i>		+ ¹³		"
<i>Menopoma</i>		+ ¹³		"
<i>Hynobius</i>		+ ¹³		"
<i>Amblystoma</i>		+ ¹³		Winslow
<i>Spelerpes</i>		+		Wiedersheim
<i>Desmognathus</i>		+ ¹³		Edgeworth
<i>Plethodon</i>		+		"
<i>Amphiuma</i>		+ ¹³		Winslow
<i>Siren</i>		+		Parker
<i>Triton</i>		+ ¹³		Gaupp
<i>Siredon</i>		+		"
<i>Rana</i>		+ ¹³		"
<i>Hyla</i>		+ ¹³		Kesteven
<i>Limnodymastes</i>		+ ¹³		"
<i>Ichthyophis</i>			+	Winslow
<i>Siphonops</i>			+	Edgeworth

There is a continuity, temporary or permanent, between the palato-quadrate and trabecular cartilage in the following forms, and always at, or close to, the cranial base: *Acanthias*, *Notidanus*, *Petromyzon*, some, if not all, *Heterodontidae* and the *Holocephali*. In some of these the attachment rises on the side wall well above the base level, but in all the primary attachment was, as stated, at or near the base level.

¹² See also Edgeworth.—Trans. Roy. Soc. Edin., liv, 1926, pp. 719-720.

¹³ Below the centre of the height of the wall.

TABLE IV.*

In	Trabecula.	Junction of trabecula and parachordal.	Basal plate.	Perfacial commissure.	Floor of auditory capsule.
<i>Protopterus</i>	+				
<i>Leoidosiren</i>	+ ¹⁴				
<i>Acanthias</i>	+ ¹⁴				
<i>Notidanus</i>	? + ¹⁴				
<i>Lepidosteus</i>	+ ¹⁴				
<i>Ceratodus</i>		+			
<i>Menopoma</i>			+		
<i>Megalobatrachus</i>			+		
<i>Siren</i>			+		
<i>Siphonops</i>			+ ¹⁴		
<i>Ichthyophis</i>			A joint		
<i>Amblystoma</i>				+	
<i>Necturus</i>			+		
<i>Triton</i>					+
<i>Salamandra</i>					+
<i>Desmognathus</i>					+
<i>Spelerpes</i>					+
<i>Plethodon</i>					+ ¹⁴
<i>Amphiuma</i>					+
<i>Hynobius</i>					+
<i>Salamandrella</i>					+ ¹⁴
<i>Ranodon</i>					+ ¹⁴
ANURA					+ ¹⁴

* From Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.

Note.—The amphibian forms have been arranged so as to bring together those having similar attachments, and this arrangement is quite out of accord with their natural classification.

TABLE V.*

		Dipnoi	Monimostylic	Streptostylic					
		<i>Necoceratodus</i>	+						
		<i>Protopterus</i>	+						
		<i>Lepidosiren</i>	+						
				Larva		Adult			
				Monimostylic	Semi-streptostylic	Monimostylic		Semi-streptostylic	
¹⁵ Urodela	<i>Amphibia</i>								
Amblystomidae	<i>Amblystoma punctatum</i> and <i>tigrinum</i>			+			+		
Salamnadridae	<i>Triton cristatus</i>			+			+		
	<i>Salamandra atra</i>			+			+		
Plethodontidae	<i>Desmognathus fuscus</i>			+			+		
	<i>Spelerpes bislineatus</i>			+			+		
	<i>Plethodon cinereus</i>						early + adult	older + adult	
Amphiumidae	<i>Amphiuma tridactylum</i>			+			+		
Hynobidae	<i>Hynobius nebulosus</i>			+ ¹⁶ earlier					+
	<i>Salamandrella keyserlingii</i>			+ earlier					+
	<i>Ranodon sibericus</i>			+					+
Cryptobranchidae	<i>Megalobatrachus maximus</i>			+			+		
	<i>Menopoma alleghaniense</i>			+			+		
Proteidae	<i>Necturus maculatus</i>			+			+		
Sirenidae	<i>Siren lacertina</i>			+			+		
Anura	<i>Rana</i>			+					
Gymnophiona	<i>Ichthyophis glutinosus</i>								+ streptostylic
	<i>Siphonops braziliensis</i>						+		+

* From Edgeworth.—Journ. Anat., lix, 1925, pp. 225-264.

Edgeworth draws attention to the fact that those forms which I have italicized are monimostylic in both larval and adult stages, and that with the exception of the gymnophionians all three dipnoans and every amphibian studied is monimostylic in the early stage.

¹⁴ Subsequently a joint.

¹⁵ The classification of Dunn is here followed.

¹⁶ s. *Hynobius keyserlingii*.

Important facts which appear in the tables may be summarized as follows:

1. With the exception of *Petromyzon*, *Lepidosteus* and two of the Dipnoi there is actual, or circumstantial, evidence that the mandibular arch arises independently, not attached at any point to the chondrocranium, in every anamniote whose development has as yet been studied.

2. In the exceptional cases the connection of the primordium of the arch is with the trabecula where it occurs posteriorly.

3. In every amphibian in which the first attachment of the mandibular arch posteriorly has been observed, that attachment is by the ascending process. In no case has an otic or basal attachment been found without an attachment by the ascending process as well. True, in late larval stages it is not uncommon to find the ascending process absorbed and the basal attachment still present; this probably happens in all Anura, but also in all of them the ascending process is probably the first to gain attachment to the chondrocranium.

4. The ascending process is never attached to a parachordal derivative, but always to the trabecular wall (usually at or near the cranial base), or, in the gymnophiones, to the *tania marginata*.

Not uncommonly the earliest attachment of the ascending process is to the low trabecular crest, but it is never carried dorsad with the upward growth of the crest; that grows past it, as it were.

5. The attachment by a basal process is later than that by the ascending process.

6. The point of "basal" attachment is to various parachordal structures or the otic capsule in the Amphibia, but to a trabecula in the fishes and Dipnoi.

7. The varying position of the basal attachment in the Amphibia shows no agreement with their natural grouping.

8. We can recognize a primary and a secondary streptostylic condition in the Amphibia.

As stated above, it is generally agreed that the pregnathostomes had a chondrocranium into which the special sense capsules had already been incorporated, and that the visceral arches were not differentiated. Sooner or later, however (archignathostomes) the first arch must have become modified. Presumably, because of its position in front of the others, it functioned as a jaw before there was any modification.

As a result of this function it became modified so that its upper half on each side moved as a single entity, and likewise its lower half; this resulted in the loss of any joints there may have been in the upper and lower segments, and in the perfection of the joint between the two halves.

This stage is surely represented by the early embryos of all but a few of the Anamniota, wherein we find the maxillo-mandibular arch arising quite independently of all other skeletal structures; similar to, and yet recognizably different from, the other arches.

I have ventured to designate these hypothetical early vertebrates "neognathostomes," and the condition of the mandibular arch "astylic." It is assumed that in the neognathostomes the primitive jaw was still attached in a manner similar to the other visceral arches, and that neither upper nor lower jaw was yet more fixed than upper and lower halves of the other arches. Notwithstanding this, the lower half will have been the more mobile, for the upper would

have been limited in its dorsi-ventral range by the fibrous union of its upper and anterior end with the under side of the chondrocranium.

It would appear that in the further modification of the arch, the upper end of the mandibular segment early became structurally continuous with the lateral expansion of the ethmoid, for we find cartilaginous or procartilaginous continuity here at some time in the development of representatives from most groups of anamniotes. It is of constant occurrence throughout the Anura, very generally present in larval stages of the Urodela and in those urodeles in which the continuity is broken there is, as also in the gymnophiones, evidence that such continuity has been but recently lost from the ontogeny. The anterior structural continuity of the palato-pterygoid and the ethmoid plate has been recorded in several Teleostei, as a temporary condition in early embryonic life, and among the elasmobranchs it is found in the adult Holocephali, and it is not improbable that the anterior articulation of various selachians will be found to have been preceded by cartilaginous or procartilaginous continuity, as demonstrated for *Acanthias* by Sewertzoff.^{16a} Amongst the surviving ganoids *Lepidosteus* is apparently alone in presenting the continuity here under review.

Discussing the various modifications in the forward attachment of the palato-pterygoid, Edgeworth¹⁷ concludes that: "These phenomena indicate an ancestral Urodelan condition in which the pterygoid process was continuous anteriorly with the trabecula. . ."

In view of the facts detailed above it would seem reasonable to assume that the primitive forms in which this forward attachment was present in the adult condition, were ancestral, not only to the urodeles, but to all the fishes as well, and it is not improbable that this was the first definite attachment of the arch. Holding this belief, I have designated these hypothetical ancestors "Archistylica" or "archistylic gnathostomes." This question will be dealt with in greater detail later.

There was now developed a definite fixed upper jaw and moving lower jaw. The articulation between the two was not yet fixed in any definite manner, but moved with the rest of the visceral arches. The need for fixation of this joint was imperative, and modification of the posterior relations of the arch took place in two directions. On the one hand the upper segment of the second arch was impressed into the service of the first and the hyoid (protohyostylic) suspension resulted, on the other hand the posterior end of the mandibular arch developed certain special processes whereby it became directly attached to the chondrocranium (autostylic suspension).

It is, of course, possible that the hyostylic suspension was antecedent to the autostylic, but I am of the opinion that this was not so, for on that hypothesis the complete elimination of the hyostylic phase from the history of the autostylic forms, with the single exception of *Neoceratodus*, seems inexplicable in view of the fact that both astylic and archistylic conditions are clearly recognizable in so many of them.

In this connection, and supporting the view taken, it may be mentioned that amongst the earliest known fossil vertebrata we find both hyostylic and autostylic forms.

^{16a} Sewertzoff.—Festschr. Kupffer, 1899, pp. 281-320.

¹⁷ Edgeworth.—Journal Anat., lix, 1925, p. 234.

There is not wanting evidence that there are two kinds of hyostylism, and two kinds of autostylism;¹⁸ in addition *Lepidosteus* and *Megalichthys* present one, if not two, other types of suspension, which are neither autostylic nor hyostylic, but may be a combination of both.

It seems reasonable, then, to assume that the two outstanding types of mandibular fixation found in the Anamniota have been independently derived from the archistylic condition.

An analysis of the further modification of the suspension will involve us in an examination of the modern groups of anamniotes; this will be attempted later.

I turn next to a consideration of the probable course of evolution of the swim-bladder and lung.

3. *The Evolution of the Lungs.*

Kerr¹⁹ sees in the swim-bladder of the fishes a modified lung. His history of the probable evolution commences with a "primitive condition of a lung, communicating with the pharynx by a ventrally placed glottis" The reason for this belief is to be found in the concluding portion of this same sentence: "for we have seen that the embryonic rudiment of the organ in the most archaic forms possessing it is a typical lung-rudiment." The archaic forms here referred to are *Polypterus* and the dipnoans, and it should be noted before proceeding further that the Heterocerci are equally as ancient as the Crossopterygii and Dipnoi, and that the surviving archaic Actinopterygii have well developed swim-bladders opening into the fore-gut *dorsally*.

It will at once be conceded that the primitive lung must have evolved from something much more simple, and if that something much more simple was, as Bridge²⁰ suggests, a glandular caecum opening dorsally into the fore-gut, I cannot understand why this could not have been modified to act either as a swim-bladder or as a lung directly, without first evolving as a lung and then becoming further modified to act as a hydrostatic organ.

Bridge does not enlarge on his suggestion, but on a previous page (p. 298) he implies that the swim-bladder may be represented among selachians "by a small caecum embedded in the dorsal wall of the oesophagus and communicating with its cavity" which was described in *Mustelus*, *Galeus*, and *Acanthias* by Miklouho-Maclay. I have not been able to find other references to these structures; it would be interesting to ascertain whether they are of common occurrence in the adult or embryonic stages of the elasmobranchs.

There is one set of facts that would appear to render highly probable the past occurrence of the beginning of the air-bladder and lung in the pro-elasmobranch stock. It is as follows: In so many features do the Chondrostei* resemble the elasmobranchs that they may be justifiably

* Throughout this paper I have used the term Chondrostei as Zittel²¹ does, but, excluding the Belonorrhynchidæ, which appear to be misplaced here on account of their diphyccercal tail. The well developed opercular apparatus of the Palæoniscidæ and Platysomidæ surely indicate that these fish were hyostylic after the manner of the Teleostei (neohyostylic).

¹⁸ The autostylism of the Holocephali is a very different thing to that of the Dipnoi and amphibians.

¹⁹ Kerr.—Text Book of Embryology, 1919, Vol. ii, p. 173.

²⁰ Bridge.—In The Cambridge Natural History, vii, 1904, p. 309.

²¹ Zittel.—Text Book of Palæontology, transl. C. R. Eastman, 1902.

termed elasmobranchs which possess both an air-bladder and true bones. These are no mere parallelisms, but real identities of structure which indicate a much closer relationship for the Chondrostei to the elasmobranchs than to any bony fishes. Now, if this be correct, it follows that since the Chondrostei are derived from the elasmobranch stock and have in common with the other bony fishes a swim-bladder, then we are justified in assuming that, prior to those modifications which gave rise on the one hand to the elasmobranchs and on the other to the bony fishes, there was present in the parent stock the potential swim-bladder.

This question of the relationships of the Chondrostei will be returned to later; for the present it will be taken as established that they are more truly elasmobranchs than teleostomes.

We have then evidence that the swim-bladder has evolved from some structure that was present in the common stock from which both teleostomes and elasmobranchs have evolved; that structure, it is further assumed, was a glandular caecum situated above and opening dorsally into the fore end of the gut.

The history of its evolution was, perhaps, somewhat as follows: It would be foolish to speculate as to its original function, but sooner or later, owing to its flaccid walls, open mouth, and dorsal situation, it came to act, quite passively, as a trap or receptacle for gases gulped in with the food or resulting from putrefaction in the gut. This interfered with its original function, and resulted in its becoming aborted, or developing an ability to deal with the new conditions. In the latter case there resulted an air-bladder with the power of controlling its gaseous contents by glandular activity and/or muscular action. From this condition there evolved on the one hand the various types of swim-bladder and on the other the lungs.

In the diagrammatic presentation of my thesis which appears on an earlier page, it will be seen that I have recognized pre-, proto-, and pene-pulmonate stages in the evolution of the air-bladder, and differentiated between apulmonate, eupulmonate and pulmoneid resultants of the final stages in the evolution. These latter will be returned to later.

The foregoing considerations lead us to believe that the dipnoans, ganoids and elasmobranchs are but different groups derived from one common family.

A study of the geological record leads one to the further belief that the family flourished during the Silurian age, and that at the close thereof it was already differentiated into those groups which were soon to yield the dipnoans and the various orders of the ganoids and elasmobranchs, and one is finally led to the belief that this Silurian vertebrate fauna presented a general elasmobranch facies.

To the student of the evolution of the Vertebrata the Silurian was the elasmobranch age.

We turn now to a consideration of the segregation or differentiation of the members of this fauna into dipnoan, ganoid and elasmobranch groups, that took place during the early Mesozoic; and this may be aptly termed the teleostome age.

The Early Mesozoic or Teleostome Age.

1. *The Elasmobranchs and the Chondrostei.*

The Chondrostei undoubtedly combine the features of the Elasmobranchi and the Teleostomi, and in explanation thereof one has to choose from two

alternatives; either they have retained the elasmobranch features inherited from their ancestors or they have reverted thereto. If the Chondrostei be classified as teleostomes, then there must be more or less tacit assumption that they have reverted to the elasmobranch type. This must surely be so, because it seems very probable that the teleostomes have evolved from an elasmobranch-like stock. By so much as they have departed from the stock type have they become teleostomes.

Now the Chondrostei have departed from the stock type to the extent of having acquired a swim-bladder and true bone, but herein they have moved along a road common to both dipnoans and teleostomes; they are certainly not dipnoans; neither, it is believed, are they teleostomes.

Parker²² says of the skull of *Acipenser* that "the development of the basis cranii and cranial walls is very similar to what is seen in the selachians; and the after modifications are essentially alike, except that in the sturgeon the cartilage is very massive, and the occipito-cervical articulation is not formed. The separation of a large symplectic, and a lesser interhyal segment, the complex metapterygoid plate, and the partial ossification of the visceral arches, are all modifications which separate this from the selachian type."

Budgett²³ (1901) speaks of the suspensorial apparatus of the larval *Polypterus* as exhibiting a condition "exactly intermediate between that of the hyostylic selachians and the Teleostei."

Whilst it would appear that Edgeworth²⁴ has finally demonstrated the soundness of Gegenbaur's theory, and shown that the hyomandibular of the *Selachii*, teleostomes and *Ceratodus* are truly homologous, it is yet a fact that there are the two distinct types of hyostylism, as implied in the quotation from Budgett.

The hyostylism of the Chondrostei is of the selachian type, and that this is no reversion, but a true genetic character, is surely evidenced by the relation of muscle C₂hd (Edgeworth²⁵).

Bridge²⁶ briefly reviews the characters of Chondrostei as here restricted, and differentiates between characters typically elasmobranch (primitive) and those due to degeneration. His primitive characters are all of them found in most, if not all the elasmobranchs, whilst every one of his characters of degeneration may, with equal justification, be regarded as a distinct advance on those of the acanthode elasmobranchs.

Bridge remarks that from an evolutionary point of view it is significant that the Chondrosteidæ do not make their appearance until the Palæoniscidæ are approaching extinction. It is equally, and to my mind more, significant that they make their appearance in the Lias, thus replacing the Acanthodei, which die out soon after the Lower Permian.

The peripheral distribution of the cranial nerves in *Amia*, *Lepidosteus*, *Polyodon*, *Scaphirhynchus*, and *Acipenser* was reviewed by Norris. It is noteworthy that throughout the review it was found convenient to discuss *Amia* and *Lepidosteus* together and the other three forms together. Norris uses the term "Ganoid" as one of convenience rather than of exactness, and states that "the

²² Parker.—Philosophical Transactions, clxxiii, 1882, 443-492.

²³ Budgett.—The Work of J. S. Budgett, 4to., Cambridge, 1907.

²⁴ Edgeworth.—Journ. Anat., lx, 1926, pp. 173-193.

²⁵ Edgeworth.—*Loc. cit.*, pp. 190-191.

²⁶ Bridge.—In Cambridge Natural History, vii, Fishes, 1904, pp. 489-490.

fishes so designated have certain nervous as well as other similarities, which mark them off rather sharply from the shark-like forms on the one hand, but less distinctly from true teleosts on the other."

This, I take it, is a general statement whose form was determined rather by accepted views than by the observations made, for on a later page we meet the statement: "In their cranial nerves the Chondrostei are plainly shark-like," and again, describing the origin of the trigemino-facial complex: "In *Polyodon*, *Scaphirhynchus* and *Acipenser* the 5th and 7th roots are more closely compacted than in *Amia* and *Lepidosteus*, i.e., are more shark-like."

It is concluded that the Chondrostei are really a group of the Elasmobranchii, and that it were well to place them along with the Acanthodei.

Returning again for a moment to the two types of hyostylism, there can be little doubt that the elasmobranch type is the more primitive, and we are justified in believing that the teleostome type is a direct modification thereof. Since the two types are characteristic, it will be helpful in descriptive work and discussion if we have separate designations for them. The primitive may be aptly termed protohyostylic, and the teleostome type neohyostylic.

2. *The Crossopterygii, Dipnoi, and Amphibia.*

There appears to be such general agreement that these groups are more nearly related one to another than to other fishes that little need be written under this head.

1. We have Kerr's considered statement—quoted below (p. 181)—relevant to the phenomena of development in the three groups.

2. External gills are developed in all the members of the three groups, and in no other forms.

3. The anterior, stomodeal portion of the buccal cavity arises in a similar manner in crossopterygians, Dipnoi and urodeles, and is more or less characteristic of these forms.

4. The crossopterygian lung approaches that of the Dipnoi more closely than does that of other fishes, and the glottis opens ventrally into the fore-gut as in the dipnoans and amphibians.

5. The arteries to the lung are derived from the fourth pair of efferent branchial vessels as in the dipnoans. Herein the Crossopterygii share a character with *Amia*.

6. The skull of the Crossopterygii presents striking resemblances to that of the amphibian. Kesteven²⁷ has written: "The Ganoids present three distinct types of cranium, the Elasmobranch is represented by the Acipenserids, the Amphibian by the Crossopterygii and the Teleostean type by the Holostei."

Both Watson and Gregory depend very largely on cranial structures to support the contention that the Amphibia are derived from crossopterygian ancestors.

3. *The Dipnoi and the Amphibia.*

With the exception of Kerr, Edgeworth, and Kellicott, recent writers have agreed that the ancestors of the amphibians must be sought among the crossopterygians, and to this group they also look for the ancestors of the dipnoans.

²⁷ Kesteven.—Journ. Anat., lxi, 1926, p. 120.

Apparently Cope²⁸ first expressed these views, and they were independently arrived at by Kingsley.²⁹ They were adopted by Dollo³⁰ and Bauer³¹ and stated again at great length by Kingsley³² in 1900.

Bridge³³ derives both dipnoans and amphibians from some "crossopterygian ancestor with Elasmobranch tendencies" and is of the opinion that they "subsequently became modified in certain respects on parallel lines."

Kerr³⁴ expresses his views thus: "I may here merely indicate that on the whole the general phenomena of development in *Polypterus* show frequent striking resemblances with what occur in Dipnoans and in the lower Amphibians. I believe that these resemblances are sufficient by themselves to indicate the probability that the Teleostomes, the Dipnoans and the Amphibians have arisen in phylogeny from a common stem, which would in turn probably have diverged from the ancestral Selachian stock. The ancestors of the Amniota probably diverged about one or about several points from the region of the stem common to Dipnoi and Amphibia." While admitting such vague speculative conclusions, we are, in my opinion, here, as in other phylogenetic speculations, absolutely debarred from making such statements as that the "Amniota are derived from the 'Amphibia' or the 'Dipnoi' from the 'Crossopterygii'."

Edgeworth,³⁵ writing of the posterior relations of the pterygo-quadrate in dipnoans and Amphibia continues: "This and many other phenomena, both skeletal and muscular, show that Dipnoi and Amphibia are descended from a common ancestral stock with a primarily fixed pterygo-quadrate (a monimostylic condition)."

Gregory³⁶ is of the opinion that the "known Dipnoi are all excluded from direct ancestry to the Amphibia by the specialized character of the dentition, including the complex radially arranged tritorial plates on the roof of the mouth and on the inner side of the mandible and the loss of marginal teeth on the premaxillæ, maxillæ and dentaries." In his concluding paragraphs Gregory applies the name "Osteichthyes" to the primitive common ancestor of the dipnoans, Actinopterygii and Crossopterygii, and believes that from this stock the above three groups became differentiated, and that from the last the Tetrapoda evolved.

Watson³⁷ finds in a "curious type of tooth change . . . a strong additional reason for regarding the Tetrapoda as derived from" the crossopterygian fishes.

Broom,³⁸ following Watson, makes two of those statements which Kerr, I think rightly, says we are "absolutely debarred from making." He writes: "The skull in some types [Cotylosaurian], such as *Seymouria*, agrees strikingly with that of the large Carboniferous Stegocephalians such as *Loxomma*, and there can be little doubt that the Cotylosaurs are directly descended from such Carboniferous forms, as these latter have themselves sprung from Devonian Crossopterygians as maintained by Watson."

²⁸ Cope.—Amer. Phil. Soc., Proc., 1892, xxx.

²⁹ Kingsley.—Refers, in Tuft's College Studies, No. 6, 1900, p. 250, to a paper published in 1892, which I cannot trace.

³⁰ Dollo.—Bull. Soc. Belge Geol. et Pal., ix, 1895, p. 79-128.

³¹ Bauer.—Anat. Anz., xi, 1896, p.

³² Kingsley.—Tuft's College Studies, No. 6, 1900, pp. 203-274.

³³ Bridge.—In Cambridge Natural History, vii, Fishes, 1904, p. 519.

³⁴ Kerr.—In The Work of J. S. Budgett, 4to., Cambridge, 1907, p. 274.

³⁵ Edgeworth.—Trans. Roy. Soc. Edinb., liv, 1926, p. 720.

³⁶ Gregory.—Annals New York Acad. Sci., xxvi, 1915, pp. 317-383.

³⁷ Watson.—Mem. Proc. Manchester Lit. Phil. Soc., lvii, 1912, p. 5.

³⁸ Broom.—Phil. Trans. (B), ccvi, 1914, p. 8.

With the single exception of Bridge, and to a lesser extent Dollo, all these writers arrive at their conclusions from the study of a limited number of features of anatomy, osteology, or development.

My interest in this problem arose in the following way. Some few years ago I commenced the study of the skull in the fishes, with a view to arriving at a comprehensive review that would harmonize the modifications which it presents, and of determining the homologies of its components with those of the tetrapod skulls. After having, as I thought, cleared the way of difficulties by the discovery that the so-called premaxillæ and maxillæ of the teleostean skull were really labial bones not represented in the tetrapod series, I³⁹ still found that it was impossible to harmonize the structure of the skull of the Chondrostei and dipnoans with that of the rest of the bony fishes. My search for the explanation of that impossibility has led to the present contribution. Very naturally my first idea was that, had I sufficient knowledge, the difficulties would melt away and that I should come to an understanding of the apparent differences. The contrary has happened, and I am now convinced that the correct explanation is that different evolutionary roads have been followed, and that as a result there are now in existence three distinct types of cranium among the bony fishes (including the Dipnoi as such).

From these years of study I find that I am almost, but not quite, in agreement with Kerr and Edgeworth.

I am of the opinion that the archistylic prepulmonate gnathostomes yielded two great divisions, the elasmobranchs and Chondrostei on the one hand and the teleostomes and Dipnoi on the other ("Ganoid stock" of the diagram). This latter group, to which I would restrict the term Osteichthyes, next yielded the Actinopterygii on the one hand and the Crossopterygii and Dipnoi on the other.

In the Crossopterygii we see the result of a conflict between inherited potential and acquired potential; in the result they have failed to advance along those lanes which yielded the dipnoans, but, the inherited potential gaining the upper hand, they have been halted at the commencement of that career, and have remained fishes. The Dipnoi, on the other hand, have been impelled along roads of evolution which ultimately led to the amphibians.

I am, indeed, absolutely convinced that the dipnoans are the most primitive amphibians that we know. This is not to say that I deem the amphibians to have been derived from the dipnoans as we know them. (No one, as far I am aware, derives the urodeles from the gymnophiones or the Anura from the urodeles, or *vice versa*, though many writers have expressed convictions as to which of these is the most primitive).

In arriving at this conclusion I am especially swayed by the form and development of the brain, the type of autostylism, the form and development of the heart, and arterial and venous systems, and the possession of a true pelvic girdle.

There can be little doubt that the amphibian ancestors must have possessed all these features, wherein the dipnoans differ fundamentally from the rest of the fishes, and therefore it appears that we must conclude that they approach

³⁹ Kesteven.—Journ. Anat., lvi, 1922, pp. 307-324. RECORDS AUSTR. MUSEUM, xv, 1926, pp. 132-140.

nearer to the amphibian stock than any of the fishes, even if we still argue the question whether we shall regard them as fishes or amphibians.

Having stated my conclusions, I proceed to discuss the evidence on which they are founded.

"The relations (similarities?) of the Dipneusti to the Amphibia are somewhat deceptive, and it seems improbable that the former group stands in the direct line of the amphibian descent. In most of their structural features not directly or remotely associated with air breathing the Dipneusti are true fishes, and the striking resemblances which they present to the amphibians in the vascular system and lungs seem to be rather the outcome of physiological convergence, associated with adaptive and parallel modifications in structure, and due to the influence of a similar environment, than indicative of direct ancestral relations. With more reason it may be inferred that both the Dipneusti and the Amphibia have been derived from some primitive crossopterygian ancestor with elasmobranch tendencies, and subsequently became modified in certain respects on parallel lines" (Bridge⁴⁰).

This quotation is taken from the only review I have been able to find of the phylogeny of the dipnoans, written by one who has studied the group in its entirety; that is to say, by one who has studied, not only the adult features of the recent and fossil forms, but also the anatomy and development of the recent forms, and also the anatomy and development of the other groups of fishes. One cannot but conclude that the views expressed are directly traceable to an uncritical reading of Dollo's work on the phylogeny of the dipnoans, for there was surely ample evidence scattered through the previous pages of his review of the anatomy and development of the fishes to have corrected the concluding inferences.

The paragraph is a little ambiguous, and it may be that I have misunderstood it. He states his conviction that the resemblances are not due to direct ancestral relationship, but suggests that both forms have been derived from some (one?) primitive crossopterygian. Surely we have here direct ancestral relationship, and, if so, why postulate modification along parallel lines? Why not assume that the features in common were already present or evolving in that common ancestor? It will be shown later that this is the more reasonable assumption, and from it will follow the conclusion that the common ancestor was not a crossopterygian, but a fish that, in certain features, was more primitive than any known crossopterygian, and yet presented many, if not all, of the distinctive features of the dipnoans, not, perhaps, so well developed as in the dipnoan, but, nevertheless, recognizable.

There are a large number of characters wherein the dipnoans resemble the amphibians more than other fishes do, and, though the contrary has been argued, not one of them is devoid of phylogenetic significance. I give a list of the characters in question and discuss the more important of them.

Adult Features.

The mode of swimming.

Autostylic and monimostylic suspension of the maxillo-mandibular arch.

The fenestration of the nasal roof.

The homology of the supra-orbital bone with the amphibian prefrontal.

⁴⁰ Bridge.—*In* Cambridge Natural History, vii, Fishes, 1904, p. 519.

The form of the brain.
 The possession of internal nares.
 The division of the auricle into right and left halves.
 Certain features of the arterial system.
 Certain features of the venous system.
 The possession of true external gills.
 The form of the air-bladder and its function.
 The structure and position of the glottis.
 The possession of an epiglottis.
 The possession of a true pelvic girdle.
 The mating call.

Embryological and Larval Characters.

The general course of the development.
 The development of the external form.
 The mode of development of the two-chambered auricle.
 The origin of the amphibian characters in the arterial system.
 The origin of the amphibian characters in the venous system.
 The mode of origin of the cerebral hemispheres.
 The early form of the chondrocranium.
 The development of the buccal cavity.
 The form of the pituitary involution.
 The development of the flask glands.
 The development of the cement organs.
 The history of the palato-quadrate.
 The history of certain cranial myotomes and their derived muscles.

The mode of swimming.—"When we consider the *clumsy movements* of the only existing fish retaining this type of fin (*Ceratodus*) . . ." (Kerr⁴¹). This is the only reference I can find in literature to the peculiarity of the mode of progression of *Neoceratodus* through the water. Whereas the great majority of fish appear to strike the water with the tail, a few of weak muscular development in the caudal region, and practically all fish when sick and exhausted, appear to undulate through the water much as a snake travels over the ground. In these cases the body flexures are, so far as my observations serve me, but two in number, producing a very wide open S-curve. Now the swimming motions of *Neoceratodus* recall these undulations; there is a complete absence of the tail "stroke," but more than that, the undulations follow one another so that there appears to be a sequence of them, and they recall in a most striking manner the wagging of the "tadpole's" tail.

It is a fact not without significance that this is the mode of swimming of practically all fish larvæ. Again I speak from personal observation, for I can find nothing in literature on the matter. The opportunities of a single individual for making such observations are of necessity limited as to the variety of forms observed. The youngest pelagic fish larvæ "wiggle" through the water; as they increase in size the number of flexures of the body become less. Growing a little older, the youngster will, when frightened, start off with a jump, wiggle

⁴¹Kerr.—*In* The Work of J. S. Budgett, 1907, p. 277.

rapidly for a little space and then seem to be propelled through the water with the body held rigid; closer observation discovers the tail striking the water with a lateral and oblique stroke. The adult starts off with a similar jump, the result of a powerful lateral sweep of the tail, and then continues with a rigid body.

Since it is characteristic of larval forms, "wiggling" or undulatory progression may be regarded as having been the primitive mode of swimming, and there is ample confirmation of this inference in the metameric arrangement of the longitudinal musculature. The interest of these phenomena to our present problem lies in the fact that alone among the compact vertebrata, the adult dipnoans and the amphibians retain an archaic mode of swimming. Is this evidence that in their common ancestry there was none which had developed the tail as the organ of swimming?

The autostylic and monimostylic suspension of the maxillo-mandibular arch.—The mode of attachment of the quadrate to the neurocranium in the dipnoans is essentially and in *Neoceratodus* identically the same as in the amphibians, excepting only the aberrant *Ichthyophis* and *Siphonops*. Herein the lung-fishes differ, it may be said, fundamentally from the rest of the fishes and resemble the frogs. As this matter will be returned to in the next section it may be left for fuller discussion there.

The fenestration of the nasal roof.—The similarity noted here and the fact that it did not extend to other fish was noted by Bridge.⁴² Having described the fenestration, in a footnote he remarks: "With the exception of the Dipnoi, this curious fenestration of the nasal roof occurs in no other vertebrates except certain Urodele Amphibia, and affords another instance of the many homoplastic modifications which are to be noted in the two groups." It is a fact that, as he further notes, this fenestration has been observed, but hardly more than indicated, in certain selachians.

Like several of the other features, which are here passed in review, wherein the lung-fishes resemble the amphibians more than any other of the fishes, this is not advanced as being in itself of phylogenetic significance, but considered in conjunction with all the others it lends weight, and receives weight. It is certainly significant that so "many homoplastic modifications" are found in the Dipnoi, whilst none are found in the ganoids which lived side by side with them. Why, one cannot but ask, are the resemblances between the crossopterygians and amphibians regarded as of phylogenetic import, while those between Dipnoi and amphibians must be deemed merely homoplastic?

The homology of the supra-orbital bone with the amphibian prefrontal.—This is a homology maintained by Bridge,⁴³ but Kesteven⁴⁴ has maintained the homology of the teleostean ectethmoid and the amphibian prefrontal; if he be correct, this feature is not a peculiarity of the dipnoans.

The form of the brain.—Herein we have a feature which is unquestionably of phylogenetic import. Here, in the Dipnoi, we have the inception of those modifications of the cerebral hemispheres which culminate in the mammalian neopallium. It is quite beyond question that, whereas there is a fundamental

⁴² Bridge.—Trans. Zool. Soc. Lond., xiv, 1898, pp. 325-376.

⁴³ Bridge.—*Loc. cit.*, pp. 332-333.

⁴⁴ Kesteven.—Journ. Anat., lvi, 1922, p.

similarity in the brains of all other fishes, there is an equally fundamental departure from that type in the dipnoan brain, and that we must turn to the amphibians for a similar brain, and, further, that having so turned, we find the similarity between dipnoan and amphibian brains as complete as that between the rest of the fishes among themselves.

The possession of internal nares may be merely a homoplastic variation, but equally it may have been derived from an ancestor common to the gnathostomes possessing them. As far as my reading serves me, it would appear that the dipnoi are the only animals below the Amphibia so endowed.

The division of the auricle into right and left halves.—That this does not occur in other fish is, of course, not in need of telling, but, together with the form of the lung and the related modifications of the arterial and venous systems, it has been regarded as the result of parallel modification under the drive of similar environment. On the other hand, it is equally well known that in certain of the ganoids, especially *Polypterus*, the air-bladder acts as a subsidiary respiratory organ (Budgett⁴⁵). There is not wanting evidence that in the Teleostei also the air-bladder acts as a subsidiary respiratory organ (Jobert⁴⁶). Although this is so, it is also a fact that in neither *Amia*, *Lepidosteus*, *Polypterus* nor the teleosts investigated by Jobert is there any indication of those modifications of the heart and vascular system which, in the dipnoans, resemble the amphibian arrangement. We have here, then, circumstantial evidence that there was nothing in the mere assumption of a respiratory function by the air-bladder to condition variations in the vascular system after the amphibian pattern; some other circumstance or factor must be invoked. Since it *did* work in the same manner on both dipnoans and amphibians, it is at least not unreasonable to postulate "inherited potential."

The arterial system.—Bridge⁴⁷ briefly reviews the arterial systems of the dipnoans as follows: "As in so many other features of its anatomy, *Neoceratodus* exhibits in its arterial system abundant evidence of the widespread affinities of the group to which it belongs. In its branchial arterial system *Neoceratodus* presents a singular combination of features which, individually, are characteristic of Amphibia and Elasmobranchs. Special amphibian features may be noted in the origin of the afferent branchial arteries almost simultaneously from the anterior end of the conus arteriosus; in the origin of a lingual artery from the efferent vessel of the first arch; and in the derivation on either side of a pulmonary artery from the fourth epibranchial artery. Agreement with Elasmobranchs is to be found in the presence of two efferent branchial vessels in each branchial arch, although the relations of these vessels are more primitive than in most adult Elasmobranchs, inasmuch as the two efferent vessels of the *same* arch unite to form an epibranchial artery; and also in the origin and distribution of the anterior and posterior carotids. Lastly may be mentioned the fact that *Neoceratodus* agrees not only with the Amphibia, but also with those generalized Teleostomi, *Polypterus* and *Amia*, in the mode of origin of the great arteries for the air-bladder" (from the fourth pair of efferent branchial vessels). This last is described as a "significant resemblance" (p. 338).

⁴⁵ Budgett.—Proc. Zool. Soc., 1903, pp. 10-11.

⁴⁶ Jobert.—Ann. Sci. Nat. (6), vii, 1878.

⁴⁷ Bridge.—In The Cambridge Natural History, vii, Fishes, 1904, p. 339.

"Of the two remaining Dipnoi, the arterial system of *Protopterus* is better known than that of *Lepidosiren*, but in both cases further research is needed before a satisfactory comparison can be made with *Neoceratodus* and other Vertebrates. It is evident, nevertheless, that both genera differ from *Neoceratodus* in approximating more closely to the Amphibia than the lower fishes, in so far as the branchial part of the arterial system is concerned." [*Lepidosteus* in its arterial system is said to offer "a singularly interesting transition from the Elasmobranch to the Teleost" (*l.c.*, p. 334).]

In this comparative review Bridge was struck by the dual nature of the similitudes of the arterial system, those wherein it resembled the amphibian on the one hand and those wherein it resembled the elasmobranch on the other; characters new and characters archaic.

Of the new characters, conceivably, the origin of pulmonary arteries from the fourth pair of efferent branchial vessels may be causally "post hoc" to the assumption of respiratory function by the air-bladder, but not so the peculiar origin of the lingual artery or the bunching together of the afferent branchial vessels at the anterior end of the conus arteriosus; else why has it not happened in *Polypterus* and *Amia*? In both of these the air-bladder functions as a respiratory organ supplied by pulmonary arteries similar to those of *Neoceratodus*.

The venous system.—Features of this system which may be regarded as pointing to a common ancestor for the dipnoans and the Amphibia are the renal-portal vein, the inferior vena cava and the anterior abdominal vein. Bridge⁴⁸ writes: "Less is known of the venous system of *Protopterus* [than of that of *Neoceratodus*], but it is certain, nevertheless, that it presents a more advanced grade of evolution . . . , and, except for the doubt as to the existence of the anterior abdominal vein, it is essentially similar to that of a Urodele Amphibian in which the right posterior cardinal vein has aborted." There is no evidence that any of these features is merely a homoplastic variation.

The external gills.—Herein the Dipnoi share a distinction with the Crossopterygii as well as the Amphibia, and we are to assume that the feature was present in their common ancestor, but it is not evidence that the ancestor in question was more crossopterygian than dipnoan in character.

The form of the air-bladder and its function.—Although the air-bladder of *Polypterus* is more complex than that of other ganoids, and to that extent it stands as an intermediate stage between the dipnoans and other fishes, it is not of great phylogenetic significance because it has not associated with it those other modifications of the respiratory and vascular systems which in their totality bring about the striking resemblance between the dipnoans and the amphibians. In the case of *Polypterus* the increase in the complexity of the walls of the air-bladder is a single isolated modification, and, moreover, one that may with justice be regarded as resulting from the influence of the environment; although the resemblance is marked, it well may be an analogous modification and not a homologous one. The development of a glottis might also be regarded as but another part of the same modification. On the other hand, the ventral position of the glottis cannot be so regarded; there are forms with air-bladder almost as complex and a dorsal glottis. It is believed that this position of the glottis is

⁴⁸ Bridge.—*In* The Cambridge Natural History, vii, 1904, p. 327.

evidence of the existence of closer relationship between the Crossopterygii and the dipnoans than between the former and other ganoids. There is other evidence in support of this belief.

The possession of a fibro-cartilaginous epiglottis by two of the dipnoans is not, in itself, significant, but being superadded to the glottis it is; unless we assume that it was evolved *pari passu* with the glottis, it surely pushes the origin of the glottis further back in time. Does it not indicate that the respiratory function of the air-bladder in the dipnoan ancestry was so well established that already there was diversity in the superadded structure amongst the members of the group?

The mating call of Neoceratodus is essentially similar to that of the frogs. I know of no fish with a mating call.

The development of the cerebral hemispheres.—Kerr (1902), when describing the development of the brain of *Lepidosiren*, describes the hemispheres as arising as "two separate lateral bulgings of the wall of the thalamencephalon" and notes that herein the development of the brain of *Lepidosiren* presents features of fundamental importance to a proper understanding of the morphology of the vertebrate brain generally. Professor Kerr returns to this question in his account of the development of *Polypterus* (1907), and his remarks are worthy of quotation in full.⁴⁹

"As has been pointed out elsewhere, I hold the view of von Baer, Reichert, Goette and Studnička that the true cerebral hemispheres *as seen in Vertebrata from Dipnoi upwards*, are to be looked upon as primitively paired structures—as lateral evaginations of the wall of the primitive fore-brain, developed doubtless in order to give space for the great increase in the mass of nerve matter in this region correlated with the increasing development of the olfactory organ. I find it difficult to realize how anyone can fail to be convinced that this is the correct view to take of the morphology of the hemispheres, *looking at their mode of development in the Dipnoi and Amphibia* and to their adult relations in the higher forms where that potent disturbing factor—the yolk sac—is present. In *Polypterus* a quite similar increase takes place in the mass of nervous matter forming the sides of the primitive fore-brain, but in this case there is no evagination of the brain wall to form hemispheres, beyond the small pair of olfactory lobes. Room is found for the nervous mass in other ways: (1) the side wall becomes greatly thickened to form the so-called 'basal ganglia'; (2) the thalamencephalon increases much in length and (3) the thickened portion becomes slightly invaginated instead of being evaginated. The nervous material which corresponds with the whole of the hemisphere in the higher forms—including the pallium or mantle—lies in the thickened wall of the thalamencephalon. What is ordinarily termed the pallium in the Crossopterygians is nothing more nor less than the roof of the thalamencephalon, which is of course epithelial here as elsewhere. The conditions in Actinopterygian Ganoids and Teleosts are obviously similar to those in *Polypterus*: what is ordinarily called the pallium in these forms is simply the epithelial roof of the primitive fore-brain, while the so-called basal ganglia are thickened walls including what corresponds to the whole of the hemispheres in higher forms." Kerr concludes by pointing out that Studnička "has already given utterance to exactly the same views."

⁴⁹ Kerr.—In *The Work of J. S. Budgett*, 1907, pp. 195-284.

Clearly we are compelled to conclude that the form and mode of development of the cerebral hemispheres are features wherein the Dipnoi differ fundamentally from the fishes and resemble the amphibians.

Gregory⁵⁰ finds that the Dipnoi and Crossopterygii were derived from a common ancestor, and concludes his paragraph thus: "Nor should the difference in brain structure of these modern forms outweigh the above-mentioned resemblance, for there is no evidence that the brains of the Devonian Crossopterygii were any more divergent from each other than were the other parts of the body."

With this conclusion I am unable to agree. If our knowledge of the recent dipnoans were confined to fossil skeletal structures only, we would unhesitatingly classify them along with the rest of the dipnoans, and we should find that they all differed from the crossopterygians in one fundamental respect—they are autostylic, while the Crossopterygii are without exception neohostylic. In the very nature of the problem we can have no direct evidence as to the form of the Devonian brains, but it is surely more likely that the Devonian dipnoans resembled the recent in this respect, having inherited this brain form from an earlier ancestor, from whom also the Amphibia inherited it. If this view be not accepted, we must accept one of two alternatives: (1) the dipnoans and amphibians independently developed this type of brain; (2) this type of brain was possessed by the common ancestor of the crossopterygians, dipnoans and amphibians, but the crossopterygians reverted to the ichthyic type.

Neither of these alternatives is acceptable.

With a view to emphasizing the character of the fore-brain, it is proposed to designate the whole of the fishes "Archiprosencephalica" and the rest of the Anamniota and the Amniota "Neoprosencephalica."

The history of the palato-pterygo-quadrate.—The significance of the autostylic condition of the Amphibia and of the Dipnoi was discussed by Huxley,⁵¹ Bridge,⁵² Dollo,⁵³ Goodrich,⁵⁴ and Luther⁵⁵ (1909, 1913, 1914), all of whom agreed that the autostylism was a secondary character. According to Edgeworth, Fürbringer was the first to cast doubts on the correctness of this view. He was "of the opinion that the primitive condition was one in which the mandibular and hyoid bars articulated separately with the cranium" (Edgeworth⁵⁶).

Edgeworth's opinion on the question is as follows: "The sum of these skeletal phenomena suggests that Selachii, Batoidei and Teleostomi are descended from autostylic and monimostylic ancestors in which there was a pterygo-quadrate united to the chondrocranium at three points. The anterior end was probably fused with the ethmoid region. The middle region was probably fused with the trabecula by a basal process. The otic process was probably fused with the auditory capsule. This condition was lost and a streptostylic one was developed. *Heptanchus* is autostylic, the others amphistylic or hostylic, whilst various traces are left in developmental phenomena or in adult anatomy of what existed in the past" (*loc. cit.*, p. 257).

⁵⁰ Gregory.—Ann. New York Acad. Sci., xxvi, 1915, p. 325.

⁵¹ Huxley.—Proc. Zool. Soc. Lond., 1876, pp. 24-59.

⁵² Bridge.—Trans. Zool. Soc. Lond., xiv, 1898, pp. 325-376. *In* Cambridge Natural History, vii, Fishes, 1904.

⁵³ Dollo.—Bull. Soc. Belge Geol. Pal., ix, 1895, pp. 79-128.

⁵⁴ Goodrich.—*In* Lankester, A Treatise on Zoology, ix, 1909.

⁵⁵ Luther.—*Fide* Edgeworth, Journ. Anat., lix, 1925, pp. 225-264.

⁵⁶ Edgeworth.—Journ. Anat., lix, 1925, pp. 225.

In the main I find myself in agreement with Fürbringer and Edgeworth, though I cannot agree with the latter that any of the hyostylic elasmobranchs or teleosteans have descended from autostylic ancestors. I would point out that he has himself collected and produced evidence that, with the exception of *Lepidosteus*, *Petromyzon*, and two of the dipnoans, every anamniote, not excluding the Holocephali, sufficiently studied has an originally quite free palato-pterygoquadrate cartilage (see Table I, antea, p. 172). This should surely be interpreted to indicate that the primitive condition was a streptostylic condition. I cannot agree, however, that this primitive streptostylysm was a hyostylysm.

Dollo wrote of the autostylysm of the Dipnoi: "c'est un pure conséquence de l'adaptation à un régime triturateur très accentue (mylodont), dans un but de consolidation de l'appareil masticatoire.

1. En premier lieu, la morphologie démontre, certainement, sans réplique, que les Vertébrés autostyliques dérivent de Vertébrés hyostyliques.

Et l'Embryologie confirme cette conclusion."

This statement is supported by a quotation from Cope wherein Huxley is stated to have shown that the Batrachia are hyostylic in early stages and become autostylic in later stages of development.

I have sought in vain for the embryological evidence that gives confirmation to the statement that autostylic vertebrata are derived from hyostylic forms.

Kerr,⁵⁷ too, is among those who believe that the primitive condition was one in which there was an attachment of the mandibular arch posteriorly.

He states that "the usually accepted idea of the mandibular arch is to regard it as a half-hoop shaped cartilage resembling the other arches, to which is added a forwardly projecting outgrowth—the palato-pterygoid bar—which forms the primitive upper jaw skeleton."

I have not met elsewhere this idea of an *added* palato-quadrate, nor can I find justification for the suggestion in the facts.

There is, of course, growth in length of the maxillary segment of the first arch as there is growth in length of the mandibular, or as there is growth from the centre both ways in length of the branchial and hyoid arches, but this growth in length of the dorsal segment of the first arch is not fundamentally greater than in the other arches and does not suggest the addition of anything not added in the growth of the other arches.

In its most primitive form, in the early embryos of elasmobranchs, the dorsal and anterior end of the first arch is almost in contact with the trabecula behind the rudiment of the nasal sac, lying close to the edge of the future mouth. With increase in size of the individual and the increasing gape, the upper and lower segments of the arch are lengthened proportionately, becoming segmented one from the other in the middle of the length of the arch just as do the other arches.

As the upper segment grows forward it retains its close relation to the trabecula, and in some cases becomes temporarily continuous therewith, but it should be noted that this point of temporary continuity, or articulation, is not back close to the posterior end of the trabecula near the otic capsule, but anteriorly near the nasal capsule, either in front of, beneath, or behind it.

⁵⁷ Kerr.—Text Book of Embryology, ii, 1919, p. 320.

The hinder end of the upper segment of this first arch does not become approximated to the skull base, but becomes attached to the lower end of the upper half of the second arch, hyomandibular.

Turning now to the amphibians, it is clearly the forward end of the arch which so commonly becomes attached to and continuous with the lateral expansion from the forward end of the trabecula immediately behind the nasal capsule, whilst it is from the hinder end that are produced those processes, ascending, otic, and basal, whereby the posterior end of the bar becomes knit to, and continuous with, the trabecula, otic capsule, and parachordal cartilages.

This hinder end is the morphological centre of the original arch, and is the point of fission into upper and lower segments; it is not, as stated by Kerr, "the dorsal portion of the original arch" (*loc. cit.*, p. 320).

Now, of all the points of cartilaginous continuity, temporary or permanent, which have been noted between the rudiment of the mandibular arch and the neurocranium, this anterior one between it and the trabecula in the neighbourhood of the nasal capsule is the only one which has been found to occur in every one of the major divisions of the Anamniota, hence I have been led to believe that it is the most primitive.

In 1884 Cope⁵⁸ described the structure of the skull of *Didymodus* and in the general discussion arising out of this study he expressed it as his opinion that the Holocephali were the most primitive of the elasmobranchs and traces thence the evolution of all the other fishes, the dipnoans and the amphibians. In the course of this discussion he quite plainly indicates that he regards the fixed upper jaw of the Holocephali as the primitive condition, for he says that these forms have not yet "differentiated a suspensorium."

Portion of Kingsley's⁵⁹ comment hereon is as follows: "In this there are several important errors. In the first place the assumption that the monimostylic condition is the more primitive is at variance with every known fact relating to the comparative anatomy and embryology of the visceral arches."

I believe that there is no room for doubt that the maxillo-mandibular apparatus has been evolved from a visceral arch essentially similar to the arches behind it, and similar to the branchial arches as we see them to-day. If this be so it is surely unreasonable to assume that the primitive jaw was one in which the mandibular segment was in structural continuity fore and aft with the neural cranium. There must have been transitional stages between the original arch and the attached arch; there was surely the slightly modified, the more modified, and the completely metamorphosed arch.

If an originally "floating" visceral arch has become structurally continuous with the cranium at two points, it is not unreasonable to assume that the nearest point of contact was the first to be converted to the continuous state; undoubtedly the dorsal end was the nearest. Thus far I have the support of Kerr, but we differ as to what shall be interpreted as representing the original dorsal end of the arch in the amphibians.

Again, if the maxillo-mandibular apparatus has evolved from a visceral arch by the development and improvement of a joint at the point of division into dorsal and ventral halves, as a first or early step, then surely, as the first arch

⁵⁸ Cope.—*Proc. Amer. Phil. Soc.*, xxi, 1884, p. 585.

⁵⁹ Kingsley.—*Tuft's College Studies*, No. 6, 1900, p. 248.

must have been attached to the second by muscular and fibrous tissue, the evolution of the protohyostylic condition should have been possible directly, without the intervention of a preliminary autostylic condition. Indeed had we but a few more examples of the incorporation of a portion of the hyoid arch into the basal attachment of the mandibular arch, as in *Neoceratodus*, we should have to assume that this was the primitive method of suspension. It is only the complete absence of any indication of the inclusion of any separate cartilages in the processes of attachment of the autostylic forms that justifies the assumption that this type of suspension has also been evolved directly from a primitive gnathostome as one of the original modes of fixation of the upper jaw posteriorly.

In the Teleostei we see the development of a metapterygoid process that may well be regarded as an incomplete attempt at autostylism, and, indeed, we have no evidence that it was not in this way, without any structural continuity between the maxillary and hyomandibular segments, that autostylism was developed.

In the present state of our knowledge, the final decision as to whether the greater probability is that the autostylic is an original or secondary mode of fixation of the maxillo-mandibular joint, must be by the personal equation. I am of the opinion that it has been evolved from a primitive suspension from the second arch, without that arch becoming modified to act as the suspensorium of the first.

However, whatever be the decision on this point, Edgeworth has left us little room for doubt that the autostylism of the Dipnoi and amphibians is a feature of fundamental importance in which these creatures differ from the fishes. This he has proven not only by his clear demonstration of the essential similarity and identity of the three processes of attachment, but also by his demonstration of the modification in the mode of development of the muscles of mastication in the amphibians and dipnoans on the one hand and the fishes on the other. His conclusion quoted above (p. 181) is fully justified by his evidence.

Though his main contention, as just stated, appears completely justified by his evidence, it is not so clear that he is correct in regarding the basal attachment as the most primitive, and the *processus ascendens* as being "probably a later phylogenetic development."⁶⁰

It must be pointed out that throughout the Amphibia, the *processus ascendens* is the first to develop, and that, with the exception of *Siphonops* and *Ichthyophis*, it presents identical relations throughout the class. On the other hand the basal process develops later, becomes attached later and presents varying relations to the neural cranium, as to its point of attachment, and to the nerves, and finally these variations show absolutely no relation, in their occurrence, to the natural grouping of the creatures themselves. (See Tables II, III and IV, antea.)

Our knowledge of the development of the processes of attachment in the Dipnoi is incomplete; unless the development in *Lepidosiren* is similar to that of *Ceratodus* it would seem that there are three different modes of development. Edgeworth⁶¹ states that in *Neoceratodus* the palato-ptyergoid arises as an independent structure, and subsequently becomes attached by the same three processes as are found throughout the Amphibia. Agar⁶² has shown that in *Protopterus* the first chondrified portion is found as a spur from the trabecula behind the floor of the

⁶⁰ Edgeworth.—Journ. Anat., lix, 1925, p. 258.

⁶¹ Edgeworth.—Journ. Anat., lvii, 1923, pp. 238-244.

⁶² Agar.—Trans. Roy. Soc. Edinb., xlv, 1906, pp. 49-64.

gasserian recess. His description and illustration of his findings in *Lepidosiren* indicate that it develops quite otherwise in this form, for, although he speaks of a basal attachment, it appears quite certain that in the earliest stage he illustrates the only attachment is by the *processus oticus*, and that a *processus ascendens* is present in the next stage.

The condition in *Protopterus* is closely paralleled in *Petromyzon*, and, although I now think that one can place but little confidence in phylogenetic deductions based on the conditions in the cyclostomes, it is not entirely without significance that, as I have previously pointed out,⁶³ the so-called basal attachment of *Petromyzon* is in truth by a *processus ascendens*, as judged by its position and relation to the nerves.

Turning now to the evidence for an attachment by a *processus basalis* in the fishes, this evidence is very scanty, and fails to convince that it was of general occurrence in ancestral forms.

In *Acanthias* Sewertzoff discovered that, prior to the establishment of the basal joint, there was continuity of the so-called basal process with the trabecula.⁶⁴ This basal joint is, however, so far forward that it can hardly be homologized with the basal joint of the amphibians and the dipnoans.

In *Lepidosteus* Veit found that the articulation of the maxillary rudiment with the basiptyergoid process is preceded by a continuity in embryonic cartilage. In this case there appears no reason to cavil at the identification of the joint with that in the Amphibia.

Unless the basal contact in *Gymnarchus* described by Assheton⁶⁵—and probably present in others of the Mormyridæ (if one may judge from their adult structure as described by Ridewood⁶⁶) and in the Symbbranchidæ—can be regarded as homologous with the basal attachment of the amphibians, we have but one single instance of such a continuity among the fishes.

The evidence for the homology of the spiracular cartilage and the otic process is more convincing. Personally, I incline to the opinion that the metapterygoid process of the Teleostei is also homologous with the spiracular cartilage, and therefore with the *processus oticus* of the dipnoans and the amphibians.

It would seem that W. K. Parker and Bettany had the same inclination, for in the figures illustrating the chapters on the development of the Elasmobranch skull they consistently indicate the spiracular cartilage with the letters "M.Pt.", and in the interpretation of the lettering these letters are translated "metapterygoid" (Parker and Bettany⁶⁷).

It therefore appears that either the attachment by the ascending process, or that by the *processus oticus*, is the most primitive of the three attachments of the amphibian autostylism posteriorly, but the evidence does not permit us to decide in favour of either.

It would be of interest to learn whether the evidence of Edgeworth's wonderful series of *Neoceratodus* is such that his oto-quadrates cannot be regarded as a spiracular cartilage. Neither he, Allis, de Beer nor Schmalhausen appear to have considered the little pellicle of cartilage in this light.

⁶³ Kesteven.—Journ. Proc. Roy. Soc. N.S.W., lix, 1925, p. 250.

⁶⁴ Sewertzoff.—Festschr. Kupffer, 1899, pp. 281-320.

⁶⁵ Assheton.—In The Work of J. S. Budgett, 1907, pp. 293-421.

⁶⁶ Ridewood.—Journ. Linn. Soc., xxix, 1904, pp. 188-217.

⁶⁷ Parker and Bettany.—The Morphology of the Skull, 1877.

The development of the vascular and respiratory systems.—Since writing the earlier part of this section—the Dipnoi and the Amphibia—I have received a copy of Kellicott's paper. From that I learn that both he and Semon have expressed views relative to the evolution of the Dipnoi similar to my own, though they did not regard the Dipnoi as primitive amphibians.

To my mind Kellicott's thorough and detailed work should have established the views of himself and Semon, and the scant attention bestowed upon his work by subsequent writers on the evolution of the Tetrapods, is a distinct reflection upon their ability to appreciate work in other branches of comparative anatomy and embryology than their own specialties.

This review, of the features of anatomy and phenomena of development in the Anamniota which bear upon the evolution of the various groups, would be incomplete without a summary of the features of importance under the above heading, but for me to undertake such a review when Kellicott has presented the facts so well and briefly in his "General Conclusions" would be foolishness. I therefore quote that section from his work almost at length.⁶⁸

"It was stated in the Introduction that the immediate object of this investigation was to test embryologically the evidence, based upon anatomical considerations, for certain supposedly Elasmobranch and Amphibian characters seen in the adult vascular system of *Ceratodus*. Throughout the course of this paper, as the development of the vascular and respiratory systems has been reviewed, the embryological evidence has necessitated continual subtraction from the list of real Elasmobranch resemblances and continual addition to the list of Amphibian characters. For instance, the Elasmobranch similarities seen in the arrangement and distribution of the carotid arteries and the connection between the anterior carotid artery and the vessels of the hyoid arch, the double efferent branchial artery, the hyoidean gill, all prove to be in the nature of parallelisms and are preceded by Ganoid or Amphibian arrangements; the arrangement of the veins of the head and of the lateral cutaneous veins resembles as closely the Amphibian as the Elasmobranch. On the other hand the Amphibian resemblances in the adult system all have been confirmed—the origin of the afferent branchial arteries, the arrangement of the epibranchial arteries, the relations of the lingual artery, the abdominal vein, the renal-portal vein, are typically Amphibian, and, excepting in the Cyclostomes, it is only in the Amphibian group (*Necturus*) that there is a continuity between the cardinal veins and the branches of the caudal vein, comparable with the arrangement in *Ceratodus*.

"Furthermore, embryologically the similarities to the Elasmobranchs were only in such characters as are common also to the Amphibia, for instance, the method of formation of the primitive aortic arch and the arrangement of the lateral cutaneous veins. But the Amphibian resemblances are extremely numerous—the method of mesoblast formation, the hypoblastic nature of the cardiac endothelium and the details of its formation, the development of the thyroid body, nearly all of the numerous details of the formation and development of the heart, the arrangement of the visceral arches, the nature of the gill-pouches and gills, the presence of elongate "larval gills," the arrangement of the afferent branchial arteries and their relations to the conus, the early development of the branchial arteries, the formation and relations of the hyomandibular artery, the develop-

⁶⁸ Kellicott.—Mem. New York Acad. Sci., ii, 19055, pp. 243-244.

ment of the lingual artery, the formation and relations of the carotid arteries throughout a long period, the relations between the posterior cardinal veins and the pronephros, the later condition of the posterior trunk veins, the development of the inferior jugular veins, the development of the abdominal vein, the arrangement of the vitello-intestinal vein and the formation from it of the hepatic and subintestinal veins, the formation of the hepatic-portal vein and its relations with the subintestinal vein, the development of the lung—in all of these respects, to enumerate only the more important, there is close, usually exact correspondence between *Ceratodus* and the Amphibia.

“Characters more or less intermediate between Elasmobranch and Amphibian arrangements are the number of gill pouches, the development of the efferent branchial arteries which resembles the Ganoid rather than the Amphibian, the arrangement of the interrenal veins, and the frequent anastomoses between the posterior cardinal veins. . .

“The immediate object of this investigation as stated above is, of course, really a part of the larger question of the relationships of the Dipnoi. It is unwise to attempt exact or complete statements in the entire absence of knowledge concerning the development of the Crossopterygii, especially since such knowledge is soon to be expected, but it is absolutely impossible to believe that the Amphibian resemblances seen in *Ceratodus* in the development of the vascular, respiratory and urinogenital systems, as well as throughout the early processes of development, are in the nature of parallelisms. In the light of their embryology, it is impossible to believe that the Dipnoi and the Amphibia are not closely related and that they have not travelled for a time along the same path at some period during their history.”

When to this striking evidence are added the facts that these two groups are eupulmonate, autostylic, and neoprosencephalic, differing in all three respects fundamentally from the rest of the Anamniota, it may be fairly claimed that Kellicott's conclusion is as completely proven as circumstantial evidence *can* prove it.

Finally, it is also contended that all the recent work on the development of the Crossopterygii and Dipnoi has indicated that the latter are more nearly akin to the Amphibia than to the former, and that this fact should be admitted in classifications by assigning the Dipnoi a place among the Amphibia.

The Evolution of the Cheiropterygium.

The evolution of the cheiropterygium is so wrapped in obscurity that Kingsley's⁶⁹ summary—“No known facts of either embryology or palæontology throw any certain light on the matter”—is still very true. The latest survey of the question that I am acquainted with is that of Gregory,⁷⁰ who briefly reviews the previous work.

It must be admitted that Gregory is correct in his statement that: “The endoskeleton of the pectoral limb of the Rhipidistian offers the only remote approach to the tetrapod type hitherto known among recent or fossil types”; and whilst one notes that he is in agreement with Patten, Broom, and Watson as to

⁶⁹ Kingsley.—Outlines of Comparative Anatomy of Vertebrates, 3rd Edition, Philadelphia, 1926.

⁷⁰ Gregory.—Annals New York Acad. Sci., xxvi, 1915, pp. 317-383.

which elements shall be regarded as homologous with humerus, radius, and ulna, one also notes his choice of the word "remote" and feels that therein he was wise.

Gregory further expresses the opinion that the basal and central line of pieces in the fin of *Eusthenopteron* are probably homologous with the mesaxial series of *Neoceratodus*, and no reason is apparent why one should not agree with this suggestion.

There is other evidence that the dipnoan fin was the starting point for the evolution of the tetrapod limbs, which, so far as I am aware, has not heretofore been advanced. I find that among the large number of fins which I have been able to dissect, the dipnoan fin alone is provided with a segmented musculature, the segments of which are placed along the length of the fin, on both sides thereof, so that the segments can be flexed independently.

This extension of the muscle along the length of the fin was probably the first step in the development of the effectually jointed limb; certainly such an extension must have preceded the modification of the skeleton, and in all probability it caused the modifications. This excursion of the muscles along the axis of the fin was a more important factor in the evolution of the limb than the mere development of a fleshy muscular lobe at its place of origin from the body. The muscles of this basal lobe could but actuate the fin as a whole, and condition the more perfect development of the single joint. The fleshy lobe of the rhipidistian fishes was no greater than, if indeed it was as large as those of such typical forms as *Parascyllium collare* amongst the sharks and *Periophthalmus barbatus* amongst the Teleostei.

The evidence is, indeed, so scanty that theorizing on the evolution of the tetrapod limbs amounts to little more than speculation, but the following summary is at least not unreasonable.

The primitive limb was probably an archipterygium as defined by Gegenbauer, and it may have been derived from an external gill as postulated by Kerr. The concentration of muscle fibres at the base of the archipterygium caused the shortening and broadening of the structure with the ultimate development of the various types of ichthyopterygia. The development of muscular tissue along the length of the archipterygium and its segmental arrangement led to the improvement of the joints between the skeletal units, and to the development of the cheiropterygium.

Though it may be that the homologies of the proximal pieces of the fin of *Eusthenopteron* are as suggested by Gregory and others, it is equally probable that the fin presents an early stage in the transition from the form with a single piece next the proximal element and those with three or more which are typical of the recent fishes.

Anomalous Structures and Resemblances.

In the preceding pages I have endeavoured to pass in review those phenomena of development and features of adult anatomy which in the Anamniota appear to throw light on the vexed question of their mutual relations. From this review certain phenomena and mutual similarities have been omitted, either because they are completely discordant with any scheme of relationship of the various groups, or because they throw no light of any kind on the questions that have been discussed.

Some of the more anomalous of these facts, however, should be briefly reviewed, if only that their anomaly may be emphasized, and the need of further investigation pointed out.

1. One of these anomalous facts has been already mentioned in passing in paragraph 5, page 180.

2. The features of gastrulation of the Teleostei closely resemble those met with in the elasmobranchs. But Kerr⁷¹ believes that we must regard this as a phenomenon of convergence, seeing that the general evidence of morphology points a much closer relationship to the ganoids than to the recent elasmobranchs. In the surviving ganoids (p. 47) "the gastrulation clearly belongs to the same general type as that of the Lampreys, Amphibians and Lung-fishes. That of *Acipenser* seems nearly to resemble that of *Polypterus*, and that of *Amia* and more especially that of *Lepidosteus* to point towards the mode of gastrulation found in the modern Teleosts."

It seems probable that all these forms present a primitive vertebrate mode of gastrulation, more or less modified by the quantity of yolk present. Clearly, if the mode of gastrulation of *Acipenser* resembles most nearly that of *Polypterus*, one cannot seize on, as being of phylogenetic significance, the resemblance of that of *Amia* to that of the modern teleosts. *Acipenser* is more closely related to the elasmobranch stock than to any of the ganoids. Again, Kerr has himself stated his opinion that *Polypterus*, in its embryology, more nearly resembles the amphibians and dipnoans than any of the ganoids.

3. The history of the palato-pterygoid arch in *Lepidosteus* is to me absolutely an enigma. In the early stages it presents what appears to be complete homology of structure and relation with the amphibian arch. On the other hand, the investing and replacing bones later developed clearly indicate a close relationship to the modern teleosts. Further than this, *Lepidosteus* stands absolutely alone in the adult articulations of the pterygo-palatal arch, unless it be that a similar condition is present in *Megalichthys*, but on this point one cannot come to a decision from Watson's inadequate description of the joint with the basi-pterygoid process. As Watson makes no comparison of the bones with any of the surviving ganoids, the absence of any reference to *Lepidosteus* cannot be taken as an indication that one should not have been made.⁷²

4. In the development of the palato-pterygoid arch in *Gymnarchus* we have the phenomena of development in the Holocephali reproduced with remarkable approximation. In this case it is so obviously impossible to look to community of origin for an explanation of the phenomenon that with confidence we say this is clearly a case of analogy. I incline to the same view in the case of *Lepidosteus*.

5. The characteristic manner of formation of the buccal cavity of the Urodela and Dipnoi might be regarded as inherited from a common ancestor, but one cannot lay stress on this feature, because the more primitive mode of formation of the buccal cavity by "simple walling in of a special area of skin"⁷³ is found in forms more primitive and more advanced.

6. One might be tempted to seize upon the possession of a pronephros by ganoids, lung-fishes and amphibians as evidence of a common ancestor distinct

⁷¹ Kerr.—Text Book of Embryology, ii, 1919, p. 46.

⁷² Watson.—Mem. and Proc. Manchester Lit. and Phil. Soc., lvii, 1, 1912.

⁷³ Kerr.—*Loc. cit.*, p. 281.

from that of the elasmobranchs. But against this one has to remember that in many features the Chondrostei resemble more closely the selachians than other fishes. Sedgwick⁷⁴ pointed out that the pronephros appears to be reduced in forms having heavily yolked eggs and no real larval existence.

7. The Holocephali and lung-fishes present a peculiar and surely primitive character in the absence of segmentation of the secondary sheath of the notochord.

8. In cyclostomes and sturgeons the secondary sheath remains as a tough fibrous structure and does not become chondrified.

9. In crossopterygian ganoids dorsal and ventral ribs are present, in actinopterygian ganoids, teleosts, and dipnoans the ribs are ventral, whilst in elasmobranchs, amphibians, and amniotes they are dorsal (Kerr⁷⁵). Here we have a rib "pie"—to borrow a word from the printers—which it is quite impossible to sort with phylogenetic tweezers.

10. The case of the cyclostomes calls for special mention. They have, of course, in the past been very generally regarded as exceedingly primitive forms (a view which I have myself subscribed to), but are they? We know absolutely nothing of their ancestry, we do not definitely know of one single fossil representative of the group *Palaeospondylus* has been identified as an amphibian by W. J. and I. Sollas,⁷⁶ and Kerr sees in this identification confirmation of his own, which was that the little fossil is a larval dipnoan (Kerr⁷⁷).

As far as the head skeleton is concerned, it is arguable that the embryo is in some respects more advanced than the adult. The development of the palatoquadrate as a process of the hinder end of the trabecula is without parallel, except in two of the dipnoans. In these, that feature is surely the result of tachygenesis; the weight of evidence clearly indicates an independent origin as the primitive. Kerr (*loc. cit.*, p. 318) expresses the opinion that there is not sufficient evidence to doubt that the visceral skeleton of the cyclostomes is homologous with that of the gnathostomes. If, then, the cyclostomes be phylogenetically "pregnathostomes," how comes it that they have in the larval stage a more advanced palatoquadrate than most of the gnathostomes?

Such are the differences and such the points of resemblance of the cyclostomes, one to another, that it is not inconceivable that they are all degenerate forms of the same group of ancestors, and, whilst not actually polyphyletic, are yet not strictly homophyletic; perhaps homoiphyletic would convey the idea.

One cannot overlook the fact that a bilobed olfactory region of the brain related to an azygous organ is surely evidence that the organ in question was originally paired.

However, whatever be the truth in this question, it would be unwise to attempt to generalize on the evidence of the anatomy or development of these very especially isolated forms; for the present, at least, it would seem wiser to attempt to explain them by the mass of evidence presented by the development and adult form of the rest of the vertebrata than would be the converse.

⁷⁴ Sedgwick.—*Quart. Journ. Micro. Sci.*, xxi, 1881, pp. 432-468.

⁷⁵ Kerr.—*Text Book of Embryology*, ii, 1919, p. 303.

⁷⁶ Sollas.—*Phil. Trans. (B)*, cxvii, 1903, pp. 267-294.

⁷⁷ Kerr.—*Loc. cit.*, p. 310.

LITERATURE.

- AGAR, W. E.—The Development of the Skull and Visceral Arches in *Protopterus* and *Lepidosiren*. *Trans. Roy. Soc. Edin.*, xlv, 1906, pp. 49-64.
- ASSHETON, R.—The Development of *Gymnarchus niloticus*. *The Work of J. S. Budgett*, Cambridge, 1907, pp. 293-421.
- BAUER, G.—The Stegocephali. A Phylogenetic Study. *Anat. Anz.*, xi, 1896.
- BRIDGE, T. W.—On the Osteology of *Polyodon folium*. *Phil. Trans. Roy. Soc. Lond.*, clxix, 1878, pp. 683-733.
- On the Morphology of the Skull in the Paraguayan *Lepidosiren* and in other Dipnoids. *Trans. Zool. Soc. Lond.*, xiv, 1898, pp. 325-376.
- *Fishes in The Cambridge Natural History*, Vol. vii, 1904.
- BROOM, R.—On the Origin of the Mammals. *Phil. Trans. Roy. Soc. Lond. (B)*, ccvi, 1914, pp. 1-48.
- BUDGETT, J. S.—On some points in the Anatomy of *Polypterus*. *Trans. Zool. Soc. Lond.*, xv, 1901, pp. 323-358. (Also in Budgett Memorial Volume.)
- Note on the Spiracles of *Polypterus*. *Proc. Zool. Soc. Lond.*, 1903, pp. 110-11. (Also in Budgett Memorial Volume.)
- COPE, E. D.—On the Structure of the Skull in the Elasmobranch genus *Didymodus*. *Proc. Amer. Phil. Soc.*, xxi, 1884, pp. 572-590.
- On the Phylogeny of the Vertebrata. *Proc. Amer. Phil. Soc.*, xxx, 1892, pp. 278-281.
- DOLLO, L.—Sur la Phylogenie des Dipneustes. *Bull. Soc. Belge Geol. Pal.*, ix, 1895, pp. 79-128.
- EDGEWORTH, F. H.—On the Quadrate in *Cryptobranchus*, *Menopoma*, and *Hynobius*. *Journ. Anat.*, lvii, 1923, pp. 238-44.
- On the Autostylism of Dipnoi and Amphibia. *Journ. Anat.*, lix, 1925, pp. 225-64.
- On the Hyomandibular of *Selachii*, *Teleostomi* and *Ceratodus*. *Journ. Anat.*, 1926, pp. 298-308.
- On the Development of the Coraco-branchialis and Cucularis in *Scyllium canalicula*. *Journ. Anat.*, lx, 1926, pp. 173-93.
- On the Development of the Cranial Muscles in *Protopterus* and *Lepidosiren*. *Trans. Roy. Soc. Edin.*, liv, 1926, pp. 719-734.
- GAUPP, E.—Die Entwicklung des Kopfskelettes. *Hertwig's Handbuch*, 1905.
- GOODRICH, E. S.—Vertebrata Craniata in *A Treatise on Zoology*, Edited by Sir Ray Lankester. Part ix, Oxford, 1909.
- GREGORY, W. K.—The Present Status of the Problem of the Origin of the Tetrapoda, with Special Reference to the Skull and Paired Limbs. *Ann. New York Acad. Sci.*, xxvi, 1915, 317-383.
- HUXLEY, T. H.—Contributions to Morphology. Ichthyopsida—No. 1. On *Ceratodus Fosteri*, with Observations on the Classification of Fishes. *Proc. Zool. Soc. Lond.*, 1876, pp. 24-59.
- JOBERT.—Recherches Anatomiques et Physiologiques pour servir à l'Histoire de la Respiration chez les Poissons. *Ann. Sci. Nat.*, (6), vii, 1878, Art. 5, pp. 1-7.
- KELLICOTT, W. E.—The Development of the Vascular and Respiratory Systems of *Ceratodus*. *Mem. New York Acad. Sci.*, ii, 1905, pp. 135-249.
- KESTEVEN, H. LEIGHTON.—A New Interpretation of the Bones in the Palate and Upper Jaw of Fishes. *Journ. Anat.*, lvi, 1922, pp. 307-324.
- A Third Contribution to the Homologies of the Parasphenoid, Ectopterygoid and Pterygoid Bones and of the Metapterygoid. *Journ. and Proc. Roy. Soc. N. S. Wales*, lix, 1925, pp. 41-107.
- The Homology of the Ala Temporalis and of the Alisphenoid Bone. *Journ. Anat.*, lxi, 1926, pp. 112-131.
- Contributions to the Cranial Osteology of the Fishes. No. II. RECORDS AUSTR. MUSEUM, xv, 1926, pp. 132-140.
- KERR, J. GRAHAM.—The Development of *Polypterus senegalis*. *The Work of J. S. Budgett*, Cambridge, 1907, pp. 195-284.
- The Development of *Lepidosiren paradoxa*. *Quart. Journ. Micr. Sci.*, xlvi, 1902, pp. 417-459.
- Text Book of Embryology. Vol. II. Vertebrata, with the Exception of Mammalia. London, 1919.

- KINGSLEY, J. S., 1892 (article quoted on p. 250 of the following paper. I am unable to trace it.)
 ——— The *Ossicula Auditus*. Tuft's College Studies, No. 6, 1900, pp. 203-274.
 ——— Outlines of Comparative Anatomy of Vertebrates. Third Edition, Philadelphia, 1926.
- NORRIS, H. W.—Observations in the Peripheral Distribution of the Cranial Nerves of Certain Ganoids. *Journ. Comp. Neurology*, xxxix, 1925.
- PARKER, W. K.—On the Structure and Development of the Common Frog (*Rana temporaria*, L.). *Phil. Trans. Roy. Soc.*, clxi, 1871, pp. 137-211.
 ——— On the Structure and Development of the Skull in Sturgeons (*Acipenser ruthenus* and *A. sturio*). *Ibid.*, clxxiii, 1882, pp. 139-185.
 ——— On the Development of the Skull in *Lepidosteus osseus*. *Ibid.*, p. 443-492.
 ——— On the Skeleton of the Marsipobranch Fishes—Part I. The Myxinoids (*Myxine* and *Bdelostoma*). *Ibid.*, clxxiv, 1883, pp. 373-457.
- PARKER, W. K., and BETTANY, G. T.—The Morphology of the Skull. 8vo., London, 1877.
- PETER, K.—Die Entwicklung und funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus*. *Morph. Jahrb.*, xxv, 1898, pp. 555-628.
- PLATT, J. B.—The Development of the Cartilaginous Skull and of the Branchial and Hypoglossal Musculature in *Necturus*. *Morph. Jahrb.*, xxv, 1897, pp. 377-464.
- RIDWOOD, W. G.—On the Cranial Osteology of the Fishes of the Families *Mormyridæ*, *Notopteridæ* and *Hyodontidæ*. *Journ. Linnean Soc.*, xxix, 1904, pp. 188-217.
- SEDGWICK, A.—On the Early Development of the Anterior Part of the Wolffian Duct and Body in the Chick, together with some Remarks on the Excretory System of the Vertebrates. *Quart. Journ. Micr. Sci.*, xxi, 1881, pp. 432-468.
- SEWERTZOFF, H.—Die Entstehung des Selachierschädels. *Festschr. Kupffer*, 1899, pp. 281-320.
- STOHR, P.—Zur Entwicklungsgeschichte des Urodelenschädels. *Zeitschr. f. wiss. Zool.*, xxxiii, 1879.
- SWINNERTON, H. H.—A Contribution to the Morphology of the Teleostean Head Skeleton based upon a Study of the Developing Skull of the Three-spined Stickleback (*Gasterosteus aculeatus*). *Quart. Journ. Micr. Sci.*, xlv, 1902, pp. 503-593.
- VEIT, O.—Die Entwicklung des Primordialcranium von *Lepidosteus osseus*. Wiesbaden, 1911.
- WATSON, D. M. S.—The Larger Coal Measure Amphibia. *Mem. and Proc. Manchester Lit. Phil. Soc.*, lvii, No. 1, 1912.
- WIEDERSHEIM, R.—Das Kopfskelet der Urodelen. *Morph. Jahrb.*, iii, 1877, pp. 352-448.
- WINSLOW, G. M.—The Chondrocranium in the Ichthyopsida. Tuft's College Studies, No. 5, 1898, pp. 147-201.
- ZITTEL, KARL A. VON.—Text Book of Palæontology, 1902. C. R. Eastman, trans.