

SPECIALIZATIONS IN EARLY VERTEBRATES

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Summary. — In association with a previous paper (1960) current opinions on the evolution of the vertebrates are critically examined and are shown, in important respects, to be inconsistent with known, well established facts. A selection of these facts, gained mainly from the comparative anatomical studies of the early vertebrates made by STENSIÖ and others, are presented and the views on the evolution of the vertebrates advanced in 1960 are further elaborated. The available evidence, including new information, warrants the following conclusions.

The cyclostomes (Agnatha) do not include the ancestors of the gnathostomes. Several of the most important specializations (nasohypophysial complex, gills, branchial arches and braincase), which distinguish these two major stems of the Vertebrata were fully developed in their oldest reasonably well-known representatives and in certain respects, the cyclostomes are more advanced than the gnathostomes. The acquisition of internal gills very early in the phylogeny of the cyclostomes prevented the development of jaws of gnathostome type.

The earliest arthrodires were not primitive cyclostome-like creatures. They were highly-specialized, typical gnathostomes, and the view that the arthrodires are the most primitive gnathostomes and ancestral to the teleostomes lacks foundation. The accepted picture of vertebrate evolution is thus fundamentally incorrect.

The recent petromyzontids differ widely from the myxinoids in the structure and function of the rasping tongue, and in many other features. Many of the structural characteristics of the petromyzontids were present in the late Silurian cephalaspids and most probably the two major cyclostome stocks were well established and quite separate at the end of the Cambrian, about 500 millions of years ago. The distinctive features of these stocks must have arisen in the Cambrian or earlier, and prior to this, before the separation of the vertebrates into cyclostomes and gnathostomes, the many qualities common to all vertebrates must have arisen. The Vertebrata therefore must be a most ancient group of animals, but not even the oldest-known, fossil forms give us any information as to their origin and relationships. We do not know when or under what conditions the vertebrates arose.

What we do know is that the vertebrates, when they appear in the fossil record, in the Ordovician, or, more commonly in the late Silurian and early Devonian were divided into a number of clearly defined main

groups. No single group is more primitive than any other and in no case can one group be derived from another.

Most of the main vertebrate types represented in the Middle Devonian or earlier are still in existence and by comparing early and recent representatives it is possible to form an opinion as to the evolutionary changes that have taken place in each of these groups during 400 million years or more. The investigation of early forms has thus given us a much widened perspective of vertebrate evolution.

Detailed comparisons of this nature, carried out since 1927, have invariably demonstrated that these groups, in all respects available for study, have changed very little or sometimes not at all during their known geological history. Ample examples of this remarkable stability, which applies even to inconsiderable structural features, such as the collarstud-like formation in the coelacanthids, have been given.

Another important fact, well documented by the geological history of the coelacanthids, is that the successive formation of new species and new genera in combination with considerable changes in environment over prolonged periods of time has had no noticeable influence on the evolutionary process. If we disregard the spectacular effect of the retrogressive development of the skeleton and other, still unexplained, parallel evolutionary trends, the recent *Latimeria* hardly differs more from the Devonian genera than these genera differ from each other.

This most remarkable reluctance to change over vast periods of time, which is encountered in all the groups of vertebrates that have remained aquatic, characterizes also the two stocks which include the tetrapods and their piscine ancestors. In their internal anatomy the porolepiforms and the osteolepiforms had independently reached the tetrapod stage of organisation by the beginning of the Devonian. In each of these groups of aquatic animals, quite typical fish in external appearance, numerous specializations have been discovered which with no or inconsiderable changes have been retained in their present-day tetrapod descendents.

The tetrapod limb arose in the piscine ancestors of the tetrapods and was present in a practically complete form within the paired paddles of our Devonian, osteolepiform forerunners. With some justification we can say that the old problem of the origin of the tetrapod limb has now been solved, but with equal justification we can say that it is still unsolved. It has only been pushed back in time, and we have to admit that we do not know why, when, or under what conditions this highly-specialized structure, and other intricate pre-requisites for a life on land, arose.

The earliest, and without doubt the most important, phases in the history of the vertebrates are thus wrapped in obscurity. Not only the many important structures common to all vertebrates, for instance the six eye-muscles with their special innervation, but also the specializations distinguishing gnathostomes and cyclostomes and the various groups, have arisen before the vertebrates began to appear in the fossil record with

reasonable frequency, some 4-500 million years ago. When we think we study evolution on the basis of fossils, it is in fact only more or less inconsiderable modifications of these ancient structures that we are studying. The major evolutionary changes took place in the unknown past.

(Résumé français à la fin de l'article.)

The popularly accepted picture of the evolution of vertebrates, even today, is that of a tree where man and other mammals, together with recent fish, amphibians, and reptiles represent the uppermost branches. The picture leads us to believe that man developed from a mammalian ancestor, that these mammals developed from a primitive reptile, that reptiles developed from a primitive amphibian, that amphibians developed from a jawed fish, and that jawless cyclostomes constitute the ancestors of the jawed fishes or gnathostomes (fig. 1; JARVIK, 1960, figs. 1, 2). But what real proof is there for the acceptance of this line of succession?

The recent cyclostomes have no jaws or paired fins, they lack an exoskeleton and, as in the vertebrate embryo, their endoskeleton is made up of cartilage. Accordingly the anatomists of the latter half of the 19th century elaborated the view that the cyclostomes are to be regarded as the most primitive vertebrates and the forerunners of the gnathostomes. The next stage in evolution, it was believed, was represented by the sharks as they, while still retaining a cartilaginous endoskeleton, had developed jaws, paired fins and a primitive exoskeleton represented only by simple scales (placoid scales) in the skin. From the sharks and their relatives (classified together as the *Chondrichthyes*) arose in the first place, the bony fishes (the *Osteichthyes*) which had developed a bony exoskeleton, and then arose in order, amphibians, reptiles and birds, mammals, and finally man. Up to this stage paleontology played no or little part in the elaboration of these ideas. However, when the fossil vertebrates gradually became better known it turned out that the earliest vertebrates, instead of being cartilaginous, generally have a strongly ossified skeleton. This discovery, one would have thought, would have removed the very foundation of the anatomists' family tree but by a remarkable coincidence the paleontologists arrived at fundamentally the same conclusions as the anatomists, although they used an entirely different basis for their conclusion, viz. the appearance of the various groups in the fossil record. The latter demonstrated that the oldest known vertebrates, the Ordovician and Silurian ostracoderms, were jawless forms, or *Agnatha*,

related to the recent cyclostomes, and the first gnathostomes to appear in the geological record, in the late Silurian times, were the sharklike placoderms. Then followed, in the Devonian, a great variety of fish and after this so called age of fishes came, in the Carboniferous and Permian, the age of amphibians, succeeded in the Mesozoic era by the age of reptiles. The placental mammals did not appear until in the Tertiary, the age of mammals, and not until quite recently, probably only a few hundred thousand years ago, our own species, *Homo sapiens*, came into the picture. This succession from fish to man in the fossil record agreed so well with the anatomists' conception of verte-

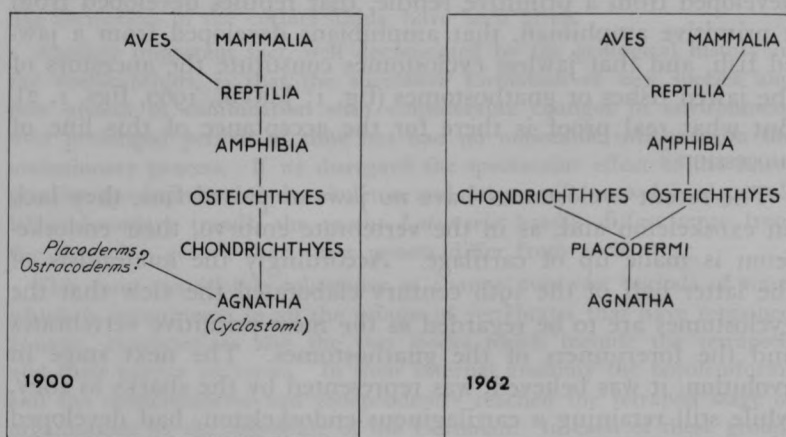


FIG. 1.

The family tree of the vertebrates in its simplest form. To the left the conception gained by the anatomists of the nineteenth century (see also Jarvik 1960, fig. 1). To the right the opinion still held by Romer and others (from Romer 1962b, p. 35; cf. Jarvik 1960, fig. 2).

brate evolution that it forms today one of the corner-stones of the theory of evolution. Because of this remarkable agreement paleontologists had no reason to doubt the theory that evolution had proceeded from a primitive agnathous form to primitive sharklike forms and they had therefore only to substitute ostracoderms for cyclostomes and placoderms for recent sharks in the main line of succession to arrive at a family tree satisfactory to all (fig. 1). Under the influence of the theory of evolution and on the presumption that animals appearing in older geological strata are generally more primitive than those appearing later, paleontologists have tried to find a place for every known fossil vertebrate in this monophyletic family tree with

the result that a great number of evolutionary lines, added as branches to the tree, have been distinguished.

The accepted conception of the monophyletic origin of the vertebrates from a common Ordovician or possibly Cambrian ancestor tends to overrule our thoughts when dealing with problems concerning the anatomy, ontogeny, phylogeny, etc. of the vertebrates. The view, too, that the cyclostomes are the most primitive vertebrates and the sharks the most primitive living gnathostomes is deeply rooted in our minds. But are these views correct and are they founded on well established facts?

Objections can justifiably be raised against many fundamental details in the accepted family tree. Several of the assumed stem-groups or ancestral forms are nothing more than imaginary creations, a result of wishful thinking evoked by the theory of evolution, while many evolutionary lines are founded almost exclusively on the geological time factor. But a more important question is whether current views of vertebrate evolution are correct even in their principal or basic features. Has it, for instance, ever been proved that the forms generally classified as the *Agnatha* (ostracoderms and recent cyclostomes) are more primitive than the gnathostomes, and do we know that they include a form ancestral to all the vertebrates with jaws? Have we not perhaps been too impressed by the word « jawless », too impressed by the fact that the gnathostomes most likely evolved from ancestors without jaws and the seeming solution in the fact that the *Agnatha* as a systematic unit comprises forms which all lack jaws of the type characteristic of the gnathostomes? It may also be asked whether the views that the placoderms are the most primitive gnathostomes, and include the common ancestor of all other gnathostomes, rests on evidence other than geological data. Also, what evidence is there for the generally accepted view that the paleoniscids represent the common stem-group of the actinopterygians other than the fact that the oldest known actinopterygians happen to be paleoniscids?

These are only a few of the questions that can be asked regarding the fundamental conceptions embodied in the accepted family tree. Certainly no scientist of today can deny that vertebrates, like invertebrates and plants, have been subject to considerable change during geological time and we certainly have to admit an evolution from the primitive to the more specialized in the history of the Earth. However, if we want to get a true picture of what really happened during the enormous

span of geological time we can not rely too much upon the geological time factor. What we need in the first instance is the most detailed and reliable knowledge of the fossil that can be gained through the use of the most modern methods of paleontological investigation. Only after having these basic facts at our disposal, and after comparison with recent animals, both larval and adult, can we hope to begin to understand and interpret the many intricate structural features that emerge. In other words our basic evidence must be of a comparative anatomical nature.

Comparative anatomy, at least in the classical sense, is not very popular today and this is perhaps one of the reasons why so many present-day scientists have accepted the current views without deeper reflection. Fortunately there are exceptions and objections have not been lacking. In the last few years, for instance, several writers have raised doubts as to the monophyletic origin of the mammals; an increasing number of scientists adopt the view that the reptiles are di- or polyphyletic, while as early as 1933 HOLMGREN, on the basis of the ontogeny of the tetrapod limb, arrived at the conclusion that the recent amphibians must be diphyletic. However, it is above all the thorough comparative anatomical investigations of early vertebrates of the Ordovician, Silurian and Devonian that have weakened the accepted views as these investigations have led to what is in many respects a new theory of the evolution of the vertebrates (SÄVE-SÖDERBERGH, 1934; JARVIK, 1960). Some of these facts are of primary importance in the elucidation of the problem of the origin of the vertebrates, and this opportunity will be used to present some of the essential new data. In doing so use will be made mainly of easily understandable examples chosen from among the main groups of early vertebrates.

1. The oldest vertebrates recorded so far are a few tooth-like structures from the lowermost Ordovician of Esthonia (see JARVIK, 1960, fig. 6). According to ØRVIG (1958, p. 4) they are broken off tubercles of the exoskeleton of an astraspid, a group of the *Heterostraci* (see STENSIÖ, 1958, p. 176), elsewhere known only from certain Middle and Upper Ordovician strata in the United States of America. The American material of Ordovician vertebrates, besides various *Astraspida* and indeterminable remains, includes at least one other heterostracean group, the *Eriptychida*. Accordingly the *Heterostraci* were diversified and had a wide geographical distribution in Ordovician times (ØRVIG, 1958).

In the microstructure of the skeleton the Ordovician forms agree well with the post-Ordovician heterostraceans and they show practically all the types of hard tissues (calcified cartilage, bone, dentine, and enamel-like structures) characteristic of the later appearing ostracoderms. As regards the histologic structure of the skeleton they are typical vertebrates and in this respect they differ widely from the echinoderms and other invertebrates and from the still obscure and mysterious conodonts (ØRVIG, 1951, pp. 380-381; GROSS, 1954). The histologic structure of the skeleton thus gives no definite clues towards the solution of the problem of the origin of the vertebrates (see also LEHMAN, 1957).

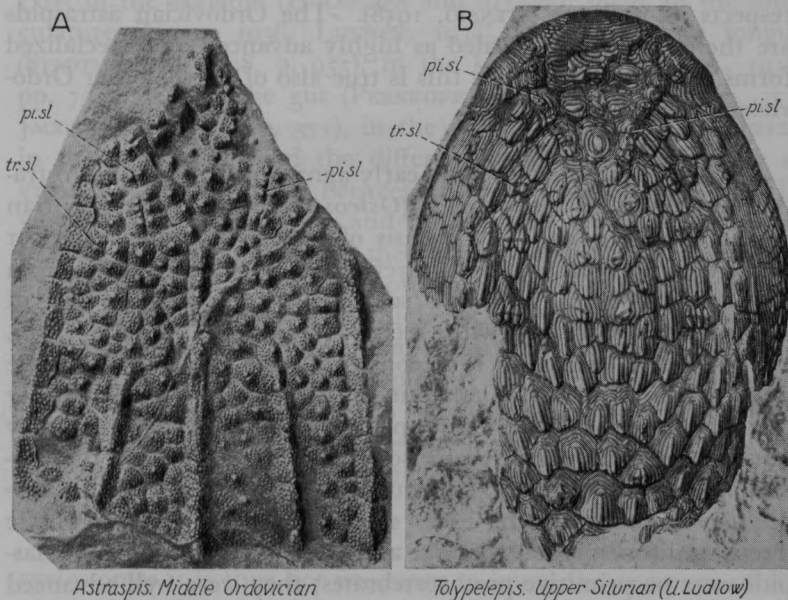


FIG. 2.

Imperfect dorsal shield of, A, an astraspid, *Astraspis desiderata* Walcott and, B, a cyathaspid, *Tolypelepis undulata* Pander, in dorsal views. A, photograph of latex cast made by ØRVIG (see Stensiö 1958, fig. 131). B, from Stensiö 1958, fig. 215.

pi.sl, pineal sensory line; *tr.sl*, transverse sensory line.

The most complete specimen of an Ordovician vertebrate found so far is an imperfect dorsal shield of *Astraspis*, shown in figure 2 A. As demonstrated by ØRVIG (see STENSIÖ, 1958, p. 358) this shield presents several sensory lines. This condition proves

not only that the lateral line sensory system was developed in this early vertebrate but it also implies that the modifications of the brain and cranial nerves connected with the development of this system had already taken place. Of still greater importance is the fact that the sensory lines in *Astraspis* run very much as they do in *Tolypelepis* (fig. 2 B) and other post-Ordovician cyathaspids. As in *Tolypelepis* there is thus, *inter alia*, a V-shaped pineal line (*pi.sl*) and several short transverse lines (*tr.sl*). This fact demonstrates that the astraspids, as far as the lateral line system was concerned, had become specialized in a similar way as the cyathaspids, and, judging from this and other conditions, it would seem almost certain that they had undergone the same specializations as the *Heterostraci* in other fundamental respects as well (see STENSIÖ, 1958). The Ordovician astraspids are therefore to be regarded as highly advanced and specialized forms. As far as we know this is true also of all the other Ordovician vertebrates.

2. The best known of the early agnathous vertebrates (ostracoderms) are the cephalaspids (*Osteostraci*) of the late Silurian and early Devonian. On the basis of studies of a great number of excellently preserved and carefully prepared specimens from Spitsbergen, several grinding series and wax models, and of thorough comparisons with recent vertebrates, STENSIÖ (1927, 1958, 1964 b) was able to reconstruct even the most delicate structures in the internal anatomy of these previously practically unknown animals. In the first place it was established that they had a typical vertebrate brain (see also STENSIÖ, 1964 a), the normal set of cranial nerves, habenular ganglia, pineal organ, hypophysis, olfactory organ, eyes, six eye-muscles, endolymphatic ducts, auditory organs, visceral arches, gills, etc. The cephalaspids were no primitive protovertebrates; they were well advanced and typical vertebrates in all known respects.

However, of still greater interest is that the cephalaspids, as demonstrated by STENSIÖ, had become specialized in a great number of anatomical features and, that in most of these features they agree strikingly with recent petromyzontids, in particular with the *Ammocoetes* larva, but differ from myxinoids and all other recent vertebrates. These most remarkable facts prompted the following important conclusions (see also JARVIK, 1960, fig. 7):

a) That the recent petromyzontids are closely related to the cephalaspids and in all probability the specializations common

to these two groups were developed in their common ancestor, that is in the Silurian or earlier.

b) That the recent cyclostomes are diphyletic in origin.

In the first place it must be strongly emphasized that the recent petromyzontids and myxinoids, anatomically, differ widely from one another, a condition which seems generally to be completely ignored by those writers who, mainly because of the presence of a « rasping tongue » (ROMER, 1962 a, p. 223) still maintain that the recent cyclostomes are monophyletic. Many students have demonstrated the profound differences in practically all the organ systems of these two groups. Such differences exist in the skeleton (HOLMGREN and STENSIÖ, 1936), in the musculature (NISHI, 1938; LUTHER, 1938), in the rasping tongue (STADTMÜLLER, 1938, p. 955), in the kidneys (BROEK, etc., 1938, pp. 733, 738), in the gut (PERNKOPF and LEHNER, 1937, p. 353; JACOBSHAGEN, 1937, p. 571), in the gills (RAUTHER, 1937, p. 212), in the brain, etc., and the differences are in most respects so great that a comparison between the two groups is difficult. In view of these well-known and indisputable facts it seems very hard indeed to uphold the theory of a monophyletic origin of the cyclostomes. Since we know, in addition, that many of the special anatomical features which characterize the recent petromyzontids and distinguish them from the myxinoids were developed in the Silurian cephalaspids, it is obvious that the petromyzontid and myxinoid stocks must have been separate at least since the Silurian, and that the myxinoids originate from ancestors which differ widely from the cephalaspids and related forms (anaspids).

In order to demonstrate the diphyletic origin of the recent cyclostomes it is thus not necessary to know the ancestors of the myxinoids. However, if we accept the now well documented view of STENSIÖ (1958, 1964 b) that the myxinoids are closely related to the *Heterostraci*, it would mean that the separation of the petromyzontid and myxinoid stocks had occurred before the time (lowermost Ordovician) when the heterostraceans began to appear in the geological record, that is, in the Cambrian or earlier. At this time, probably already in the Precambrian, many of the specializations characteristic of the petromyzontids and the myxinoids, respectively, must have been developed. Let us now consider some of these very early specializations.

3. As established long ago by DOHRN the naso-hypophysial complex undergoes remarkable changes in the ontogeny of *Petromyzon* (fig. 3 A-C). In early stages both the hypophysial invagination (*hyp*, RATHKE's pocket) and the primordium of the unpaired olfactory organ (*olf*) are situated close together on the ventral side of the head and in front of the stomodaeum inva-

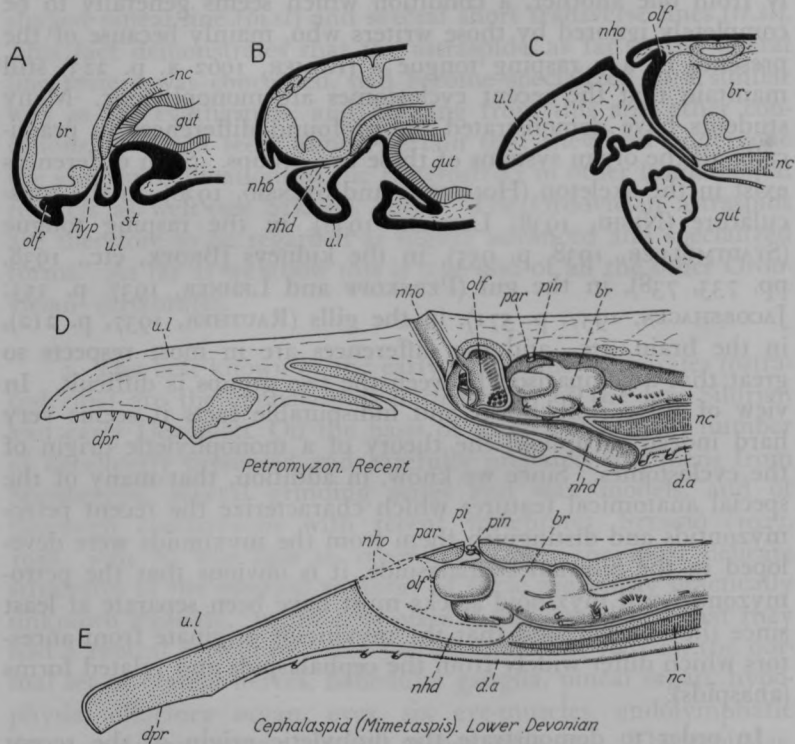


FIG. 3.

A-C, median longitudinal sections of the head of three stages in the development of the head in *Petromyzon*. A, the youngest and C, the oldest stage. After Dohrn (from Goodrich 1909, fig. 24). D, E, median longitudinal sections of the dorsal part of the head to show certain fundamental similarities between, D, *Petromyzon* and, E, a Devonian cephalaspid. D, compilation after Goodrich 1909, fig. 34 and Parker & Haswell 1962, fig. 121 (olfactory organ and brain). E, compilation mainly after Stensiö 1958, fig. 108 B (skeletal parts) and 1927, fig. 32 A (olfactory organ and brain).

ba, brain, *d.a*, dorsal aorta; *dpr*, supraoral depression, in *Petromyzon* and certain cephalaspids occupied by teeth opposed to those of the rasping tongue (see Stensiö 1958, p. 183, fig. 211); *hyp*, hypophysial invagination (Rathke's pocket); *nc*, notochord; *nho*, nasohypophysial opening; *olf*, olfactory organ; *par*, parapineal (parietal) organ; *pi*, pineal opening; *pin*, pineal organ; *st*, stomodeal invagination; *u.l*, upper lip.

gination (*st*). *At this stage the petromyzontids agree fairly well with the gnathostomes.* However, later in ontogeny considerable modifications occur resulting in the formation of a common unpaired naso-hypophysial opening (*nho*) on the top of the head. In connection with these changes the posthypophysial fold or « upper lip » (*u.l*), which in early stages separates the hypophysial and stomodaeum invaginations, grows considerably and forms the rostral part of the head (fig. 3 D).

In this respect the petromyzontids obviously are not primitive. In point of fact they are more specialized than the gnathostomes and, what is of a very great interest is that these most peculiar specializations had occurred already in the Silurian cephalaspidomorphs, both in the cephalaspids (fig. 3 E) and the anaspids.

The myxinoids, too, have become much specialized with regard to the naso-hypophysial complex, although in a different fashion. Not only does the naso-hypophysial opening become terminal in position, as a result of the intricate changes in ontogeny (see STENSJÖ, 1958, fig. 195), but in other respects as well the myxinoids differ considerably both from the petromyzontids and the fossil cephalaspidomorphs. In the *Heterostraci* there is no naso-hypophysial opening on the dorsal side of the head. This and other features led STENSJÖ (1958) to conclude that, with regard to the anatomy of the anterior part of the head, they were very much like the myxinoids.

As is thus evident the cyclostomes are more specialized than the gnathostomes in the development of the naso-hypophysial complex. It is also obvious that these most remarkable specializations had occurred very early in phylogeny, probably in the Precambrian, and in a much different way in the petromyzontid and myxinoid stocks. These conditions demonstrate that the recent cyclostomes must be *diphyletic*. However, they also demonstrate that *the gnathostomes cannot be descendants of the Agnatha*. That this is so is evidenced, too, by the very great differences between the *Agnatha* (cyclostomes) and the gnathostomes in the development of the gills and the visceral arches (as regards the otoliths see CARLSTRÖM, 1963).

4. In the petromyzontids (figs. 4 A, 6 C, D) the gills are situated *inside* the visceral arches. Except most anteriorly and most posteriorly each arch carries a gill septum with an anterior and a posterior hemibranch, the septum and the hemibranchs being directed *inwards* towards the pharynx. The efferent artery runs in the pharyngeal margin of the septum. The visceral nerve is

situated inside its arch and gives off branches supplying the septum and the anterior and posterior hemibranchs of the arch. There are no (pretrematic) branches supplying the gills of the arch next in front (cf. JARVIK, 1954, footnote 2, p. 91). In the adult the gills form sac-like structures.

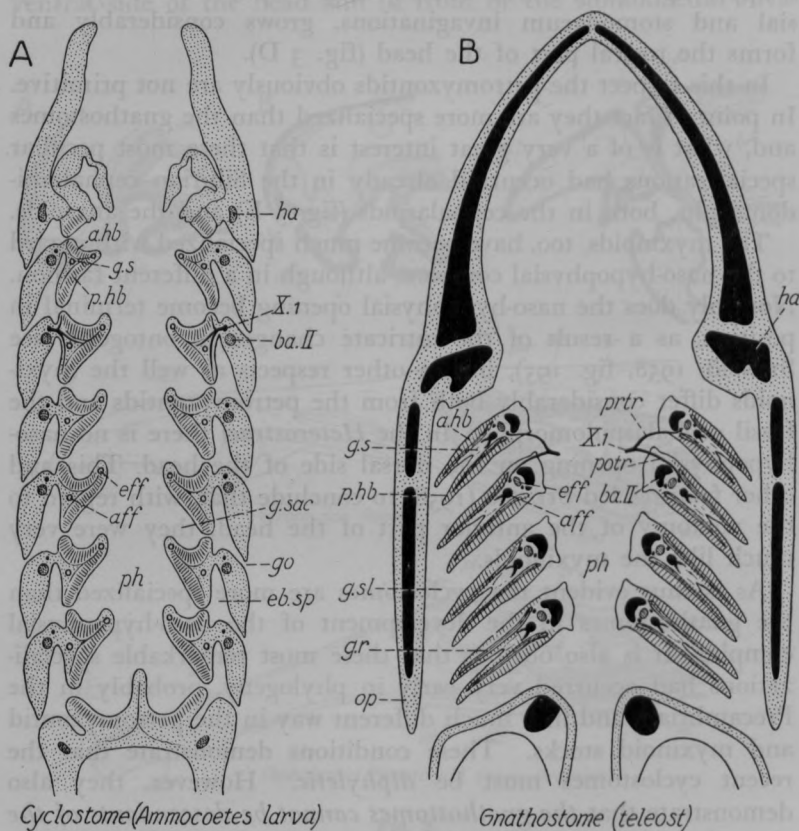


FIG. 4.

Diagrammatic horizontal sections through the head to show the fundamental differences between cyclostomes and gnathostomes in the position, innervation and vascular supply of the gills. A, *Ammocoetes* larva of *Petromyzon*. Mainly after Gaskell 1908 (fig. 74) and Daniel 1934. Nerves according to Johnston 1908. B, teleost. Combined from figures by Bertin (1958, fig. 944) and Goodrich (1909, fig. 57 E). Nerves according to Allis 1903 (pl. 11: 60).

aff, afferent branchial artery; *a.hb*, anterior hemibranch; *ba.II*, second branchial arch; *eb.sp*, extra-branchial space; *eff*, efferent branchial artery; *go*, gill opening; *g.r*, gill ray; *g.s*, gill septum; *g.sac*, gill sac; *g.sl*, gill slit; *ha*, hyoid arch; *op*, gill cover; *potr*, posttrematic branch of visceral nerve; *prtr*, pretrematic branch of visceral nerve; *ph*, pharynx; *p.hb*, posterior hemibranch; *X.1*, first visceral trunk of n. vagus.

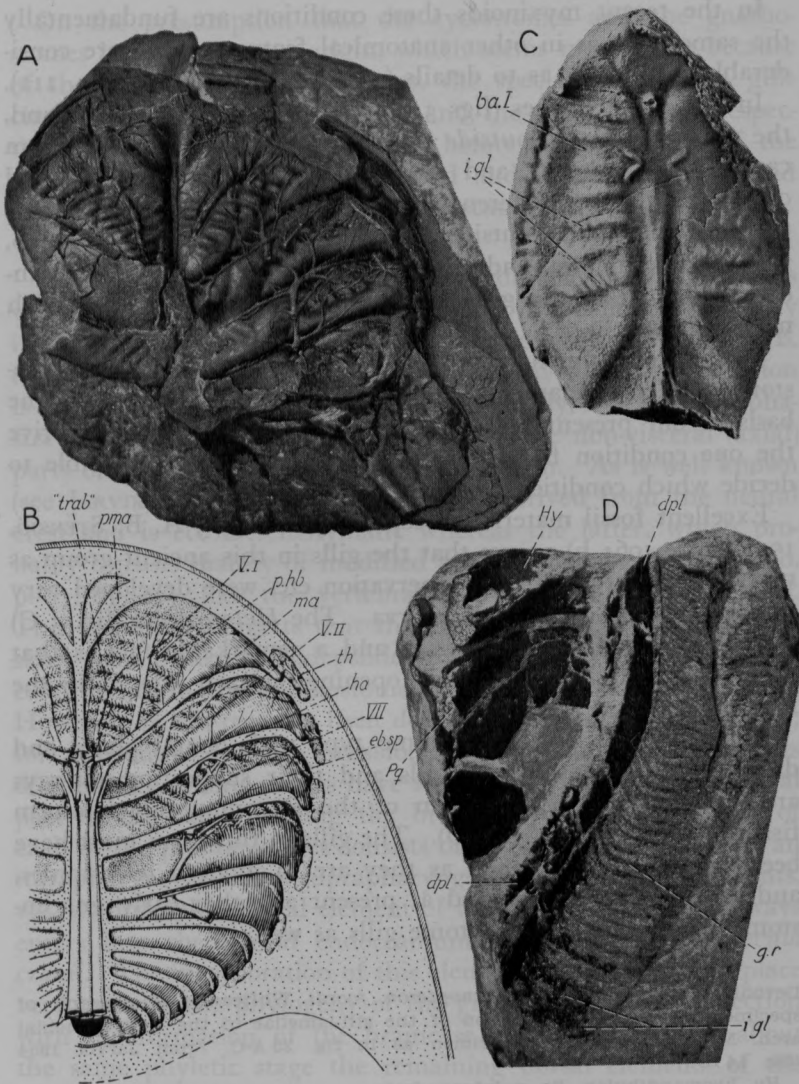


FIG. 5.

A-C, Lower Devonian cyclostomes (ostracoderms). A, B, *Zenaspis signata* (Wängsjö). A, photograph of imperfect natural cast of the orobranchial chamber of oligobranchiat cephalaspid. Dorsal view. The photograph has been retouched under the supervision of E. Stensiö and has been used by him as basis for textfigures (Stensiö 1958, fig. 114 A, D; see also Jarvik 1954, fig. 45 B). Specimen in the possession of the Palaeontological Museum, Oslo. B, restoration of the gills and branchial nerves, vessels, etc. on the basis mainly of the specimen shown in fig. 5 A. Dorsal aspect. From Stensiö (1964 b). C, *Simopteraspis primaeva* (Kiaer). Photograph of specimen of a cythaspid (*Heterostraci*) showing an impression of the inner (ventral) side of the dorsal shield. From Stensiö 1958 (fig. 199 A). D, Upper

In the recent myxinoids these conditions are fundamentally the same, but, as in other anatomical features, there are considerable differences as to details (see e.g. RAUTHER, 1937, p. 212).

In the gnathostomes (figs 3 B, 5 D, 6 B), on the other hand, the gills are situated *outside* the visceral arches, the gill septum carrying the anterior and posterior hemibranchs are directed *outwards*, while the efferent and afferent arteries run close together and are situated outside their arch. The visceral nerve, too, runs outside its arch and gives off anterior or *pretrematic* branches which cross the gill-slit and supply the gills of the arch next in front.

In the development of the gills, therefore, the recent cyclostomes differ fundamentally from the gnathostomes. On the basis of our present knowledge it is quite impossible to derive the one condition from the other, and it is also impossible to decide which condition is the most primitive.

Excellent fossil material of cephalaspids (fig. 5 A, B; STENSIÖ, 1927, 1958, 1964 b) proves that the gills in this ancient group as regards structure, position, innervation etc. were developed very much as in the *Ammocoetes* larva. The *Heterostraci* (fig. 5 C) too, had inwardly directed gills and a remarkable fact is that there was a single common gill opening on each side, as in the myxinoids.

Gill arches of the gnathostome type with dental plates and distinct impressions of the gills and their supporting gill-rays are preserved in one specimen of the Devonian osteolepiform fish *Eusthenopteron* (fig. 5 D). The gills in this form must have been developed very much as they are in modern teleostomes, and as far as can be judged at present all other early gnathostomes had typical gnathostome gills as well.

Devonian gnathostome, *Eusthenopteron foordi* Whiteaves. Photograph of specimen showing an impression of the gill-lamellae of the first branchial arch. Medial view. Same specimen as in fig. 25 A-C. From Jarvik 1954 (fig. 14 B).

Hy, hyomandibular; *Pq*, palatoquadrate.

ba.I, first branchial arch; *dpl*, dental plates; *eb.sp.*, extra-branchial space; *g.r.*, gill-rays; *ha*, hyoid arch (second interbranchial ridge); *i.gl.*, impression of gill-lamella; *ma*, mandibular arch (first interbranchial ridge); *p.hb*; posterior hemibranch of premandibular arch; *p.ma*, premandibular arch; *th*, thymus; «*trab*», medial portion of first interbranchial ridge (dorsal part of mandibular arch), probably corresponding to infrapharyngo-mandibular (trabecula cranii) in gnathostomes; *V.I*, visceral trunk of n. trigeminus I (n. profundus), probably corresponding to r. maxillaris trigemini in gnathostomes (see Jarvik 1954); *V.II*, visceral trunk of n. trigeminus II; *V.II*, visceral trunk of n. facialis.

On the presumption that the cyclostomes and the gnathostomes have a common origin, which seems most likely because of their many common features, the specialized type of gills characteristic of the cyclostomes and the gnathostomes, respectively, must have been developed before the separation of the cyclostomes into the petromyzontid and myxinoid stocks had begun, i.e. probably well back in Precambrian times.

5. In the cyclostomes the visceral endoskeleton is continuous with the neural endocranium, and since this connection is very intimate in the early fossil cyclostomes (cephalaspids, figs. 5 B, 6 A), it has been assumed that it is primitive. This assumption is contradicted by the following facts. Firstly, it is to be emphasized that the visceral endoskeleton and the non-visceral (axial) parts of the braincase are of different origin. As is well known (see JARVIK, 1954, p. 76) the former is derived from the neural crest and is ectomesenchymatic whereas the latter, which probably consists mainly of modified arcual elements (JARVIK, 1960, p. 87, fig. 27), like the vertebral column, is endomesodermal. This condition suggests that the visceral and axial parts of the skull were primarily independent. Secondly, the posterior visceral arches in the gnathostomes are always separate (fig. 6 B). However, as has recently been demonstrated (JARVIK, 1954, 1960; for arthrodires see also STENSIÖ, 1963), certain dorsal elements of the three prootic arches have *secondarily* fused with the axial part of the skull forming the braincase. The dorsal part of each of the prootic arches consists of three elements, an epal, an infrapharyngeal, and a suprapharyngeal. One of these elements, viz. the infrapharyngeal element of the mandibular arch, always enters into the neural endocranium and forms the *trabecula cranii*. The incorporation of this element must have taken place very early in the phylogeny of the gnathostomes, in connection with the formation of the braincase and the jaws. At about the same phyletic stage the remaining dorsal elements of the prootic arches either became incorporated into the braincase or fused with each other forming the palatoquadrate. There is some variation in this respect but the palatoquadrate always includes at least the epal elements of the premandibular and mandibular arches. In autostylic forms the palatoquadrate, too, has fused with the neural cranium. This fusion must have happened at a much later phyletic stage, and it may therefore be of some interest to mention that in the dipnoans this fusion had

occurred already at the first appearance of the group in the early Devonian.

As discussed elsewhere (JARVIK, 1954, pp. 89-95), the conditions in the cephalaspids favour the belief that the dorsal parts of the visceral arches in the cyclostomes were originally divided into three dorsal elements (*Eb*, *Ib*, *Sb*, fig. 6 A), corresponding to those in the gnathostomes. However, these elements have fused with each other and with the axial part of the skull into a solid unit. In this respect the cyclostomes can be said to be more advanced than the gnathostomes. However, in the cephalaspids (and the heterostraceans, fig. 5 C) the visceral arches have retained their primitive transverse position or are directed obliquely forwards (not backwards as in the gnathostomes) and the medial portion of the dorsal part of the mandibular arch (« *trab* », fig. 5 B), which portion presumably corresponds to the infrapharyngo-mandibular or *trabecula cranii* of the gnathostomes, is still a transverse element resembling the medial portions of the other branchial arches. Provided this interpretation is correct *there is thus no true trabecula in the cephalaspids*. This is of considerable interest since a real *ectomesenchymatic trabecula* has hitherto not been identified with certainty in the recent cyclostomes (see JOHNELS, 1948, pp. 173-175, 256-260; JARVIK, 1954, pp. 76, 94, footnote 1). A possibility would be that the trabecula in the petromyzontids is represented by the so-called trabecle commissure (JOHNELS, 1948, pp. 174, 257-258) which is ectomesenchymatic and appears to occupy the same position as the medial portion (« *trab* », fig. 5 B) of the mandibular interbranchial ridge in the cephalaspids.

The incorporation of elements of the prootic arches into the neural endocranium obviously represents very ancient specializations which are of fundamental importance to the formation of both the neural endocranium and the jaw apparatus in the gnathostomes. In these respects, too, the cyclostomes differ widely from the gnathostomes.

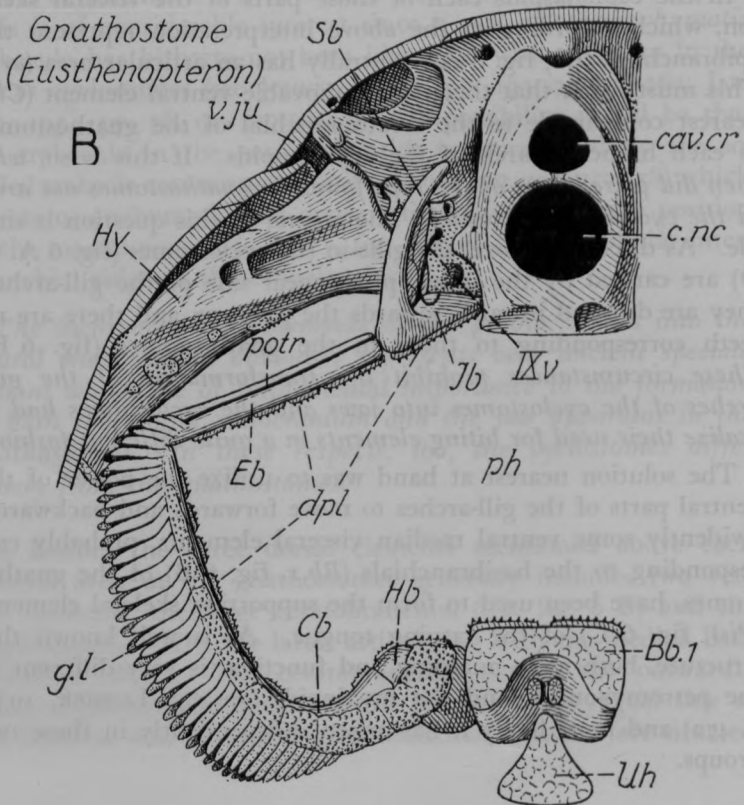
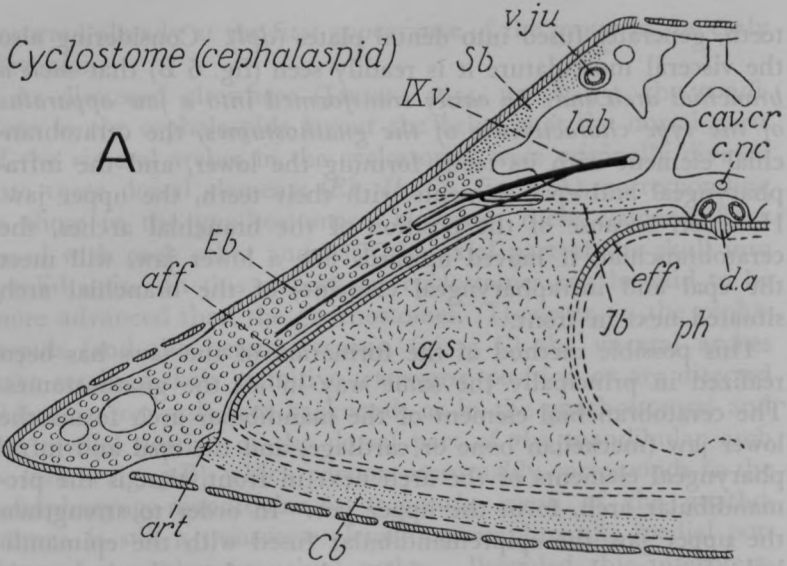
6. Besides the three dorsal elements mentioned above each visceral arch in the gnathostomes generally includes two ventral elements, the large ceratobranchial (*Cb*, fig. 6 B) and the hypobranchial (*Hb*), the latter articulating with the median basi-branchial (*Bb.1*). The ceratobranchial carries the outwardly directed gill-laminae (*g.l.*). On the inner or pharyngeal side of the latter as well as on the other branchial elements are situated

teeth, generally fused into dental plates (*dpl*). Considering also the visceral musculature it is readily seen (fig. 6 B) that *such a branchial arch may be easily transformed into a jaw apparatus of the type characteristic of the gnathostomes*, the ceratobranchial element with its teeth forming the lower, and the infra-pharyngeal and epal elements with their teeth, the upper jaw. However, because of the position of the branchial arches, the ceratobranchial, if moved upwards like a lower jaw, will meet the epal and infrapharyngeal elements of the branchial arch situated next in front.

This possible method of the formation of the jaws has been realized in principally the same way in all the gnathostomes. The ceratobranchial element of the mandibular arch forms the lower jaw (meckelian bone or cartilage) and the epal and infra-pharyngeal elements of the arch next in front, that is the pre-mandibular arch, form the upper jaw. In order to strengthen the upper jaw the epipremandibular fused with the epimandibular forming the main part of the palatoquadrate (JARVIK, 1954).

In the cephalaspids each of those parts of the visceral skeleton, which according to the above interpretation represent the epibranchials (*Eb*, fig. 6 A), ventrally has an articular area (*art*). This must mean that there was a movable ventral element (*Cb*), nearest comparable to the ceratobranchial of the gnathostomes in each branchial arch of the cephalaspids. If this is so, *why then did paired jaws of the type found in gnathostomes not arise in the cyclostomes as well?* The answer to this question is simple. As discussed above, the gills in the cyclostomes (fig. 6 A, C, D) are carried by the inner, pharyngeal side of the gill-arches, they are directed inwards towards the pharynx and there are no teeth corresponding to those in the gnathostomes (fig. 6 B). *These circumstances prohibit the transformation of the gill-arches of the cyclostomes into jaws and the cyclostomes had to realize their need for biting elements in a quite different fashion.*

The solution nearest at hand was to utilize the power of the ventral parts of the gill-arches to move forwards and backwards. Evidently some ventral median visceral elements, probably corresponding to the basibranchials (*Bb.1*, fig. 6 B) of the gnathostomes, have been used to form the supporting skeletal elements (*Pist*, fig. 6 C) of the rasping tongue. As is well known this structure, both as to anatomy and function, is very different in the petromyzontids and the myxinoids (see e.g. LUTHER, 1938, p. 472) and most likely it has arisen independently in these two groups.



The points so far presented demonstrate two basic facts viz. that :

a) The *Agnatha* (*Cyclostomata*) and the *Gnathostomata* are two equivalent stems of vertebrates which have been separate probably since Precambrian times. *The cyclostomes cannot be*

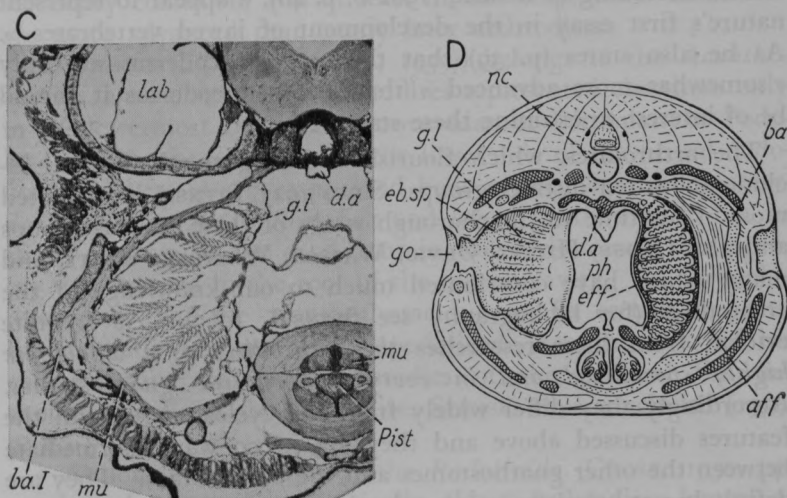


FIG. 6.

A, diagrammatic, almost transverse section through the left half of the skull of a cephalaspid. The section is thought to run along the third interbranchial ridge and accordingly the part of the visceral skeleton cut by the section corresponds to the first branchial arch in the gnathostomes. The ventral part of the gill arch, the visceral nerves and vessels in the gill-septum (interbranchial diaphragm) are restored. The presumed elements of the arch indicated by different dotting. Modified from Jarvik 1954 (fig. 46). B, the corresponding view of an early gnathostome, *Eustenopteron foordi*. Modified after Jarvik 1954 (fig. 47). The gill laminae restored after the specimen shown in fig. 5 D. C, *Lampetra* (*Petromyzon*) *planeri* Bloch, transverse section of *Ammocoetes* larva (metamorphic stage) in the region of the first branchial arch. From Johnels 1948, fig. 60. D, diagrammatic transverse section of the gill-region of an *Ammocoetes* larva. From Goodrich 1909, fig. 35.

Bb.I, basibranchial 1; *Cb*, *Eb*, *Hb*, ceratobranchial, epibranchial and hypobranchial of first branchial arch; *Hy*, hyomandibular; *Ib*, infrapharyngobranchial of first branchial arch; *Pist*, piston cartilage; *Sb*, suprapharyngobranchial of first branchial arch; *Uh*, urohyal.

aff, afferent branchial artery; *art*, articular area for ventral visceral element; *ba*, branchial arch; *ba.I*, first branchial arch; *da*, dorsal aorta; *dpl*, dental plates of first branchial arch; *cav.cr*, cranial cavity; *c.nc*, canal for notochord; *eb.sp*, extra-branchial space; *eff*, efferent branchial artery; *gl*, gill laminae; *go*, gill opening; *g.s*, gill septum; *lab*, labyrinth cavity; *mu*, visceral muscles; *nc*, notochord; *ph*, pharynx; *potr*, posttrematic branch of visceral trunk of n. glossopharyngeus; *v.jv*, jugular vein; *IXv*, visceral trunk of n. glossopharyngeus.

regarded as more primitive than the gnathostomes and the latter do not originate from any cyclostomes (STENSIÖ, 1958, p. 175).

b) The cyclostomes are diphyletic in origin.

7. The next stage in the evolution of the vertebrates should be represented by the placoderms or *Arthrodira* (see fig. 1), which, according to ROMER, (1962 b, p. 40), « appear to represent nature's first essay in the development of jawed vertebrates ». As he also states (p. 39) that the early placoderms are only « somewhat more advanced » than the ostracoderms it should be of interest to examine these statements.

The arthrodires, which flourished during the Devonian, include about ten distinct groups. Since 1925, STENSIÖ has devoted most of his time to the thorough study of these various groups and also GROSS, HEINTZ, ØRVIG, WATSON, WESTOLL, WHITE, and many others have contributed much to our knowledge of the arthrodires (for bibliography see STENSIÖ, 1963). As is quite evident from these researches *the arthrodires as a whole are highly specialized and in every respect true gnathostomes*. Accordingly they differ widely from the cyclostomes in all the features discussed above and they are in no way intermediate between the other gnathostomes and the cyclostomes. They are definitely not primitive « aphethochoideans », as stated in modern text-books (PARKER and HASWELL, 1962, p. 205), and no arthrodires are known from which the true teleostomes (crossopterygians, brachiopterygians, and actinopterygians) can be derived. Since it has been claimed that the early arthrodires are particularly primitive we may first turn to the oldest known forms.

8. Disregarding detached scales and other isolated skeletal remains of acanthodians, only two *Silurian placoderms*, *Radotina kosorensis* Gross 1950 and *Kosoraspis peckai* Gross 1959, have been described so far. Both these species originate from beds in the « Prager Mulde » hitherto considered to be Upper Ludlow in age (*).

GROSS (1958, 1959) refers *Radotina* (fig. 7 A, B), to the rhenanids but, as pointed out by him, it differs in several respects from the typical representatives of that group. STENSIÖ (1959) places it in a group of its own, the *Radotinida*. The neural

(*) The precise age of these deposits is now under debate and is held by some writers to be lowermost Lower Devonian.

endocranium (fig. 7 B) is clearly of the same type as that of other arthrodires and differs fundamentally from that in the cyclostomes. A remarkable fact is that the nasal opening (*fe.ex*), which, as in other gnathostomes, is paired, is situated on the dorsal side of the head between the eyes as is the case in the rhenanids (fig. 7 D). There is no doubt that this is a secondary condition, and at least in this respect the radotinids are more advanced than many later arthrodires.

Kosoraspis (fig. 7 C; GROSS, 1959) belongs to the *Acanthothoraci*, a small group of arthrodires represented elsewhere only in the lowermost Devonian (Downtonian or Dittonian) of Podolia (STENSIÖ, 1944, 1959). On the lower side of the neural endocranium there is a parasphenoid bone pierced by the hypophysial opening. As in *Radotina* and other gnathostomes, but in sharp contrast to the conditions in the cyclostomes, this opening was situated in the roof of the mouth cavity. Of particular interest is that the acanthothoracids, too, in certain respects, have already become highly specialized. On the basis of his comprehensive comparative studies of the pectoral fin and shoulder girdle of the arthrodires STENSIÖ thus concluded (1959, p. 201) :

« Although together with the *Radotinida* (GROSS, 1950, pp. 113-118) they are the geologically oldest Arthrodires known at the present, the *Acanthothoraci* had then reached a strikingly advanced stage of specialisation where their scapulo-coracoid and pectoral fin are concerned. This can only mean that the Arthrodires had already undergone a long evolution before the Lower Devonian and that they must be therefore a very ancient group of Lower Gnathostomes (STENSIÖ, 1944, p. 79) ».

Apparently the opinion that the oldest arthrodires are primitive cyclostome-like creatures is without any foundation.

9. Let us now turn to the jaw apparatus (fig. 8). As in other gnathostomes the endoskeleton of the jaw apparatus in *Arthrodira* is formed by two principal elements, the palatoquadrate in the upper jaw, and the meckelian bone or cartilage in the lower jaw. However, in contrast to conditions in all true teleostomes (crossopterygians, brachiopterygians and actinopterygians) there are no external toothbearing dermal bones (*De, Mx*, fig. 8 B) and there are considerable other differences with respect to the dentition. Certainly nobody intimately familiar with the jaws of the arthrodires will admit that these compli-

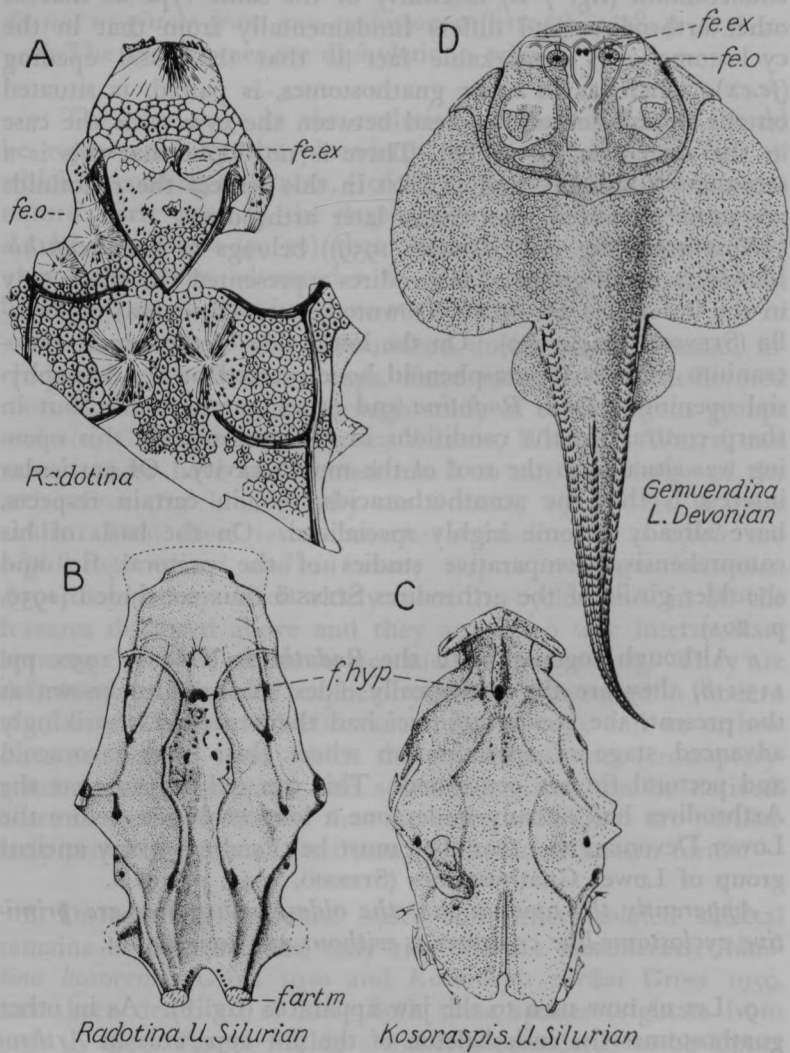


FIG. 7.

A-C, two arthrodires from the Upper Silurian of Bohemia. From Gross 1959, figs. 1A, 2A, 6A. A,B, radotinid, *Radotina kosorensis* Gross. A, imperfect dermal cranial roof in dorsal aspect. B, restoration of the neural endocranium in ventral aspect. C, acanthothoracid, *Kosoraspis peckai* Gross. Neural endocranium in ventral aspect. D, rhenanid, *Gemuendina stuertzi* Traquair. Dorsal aspect. From the Lower Devonian of the Rhineland. Modified from Broili, after Stensiö 1963, fig. 3C.

f.art.m, medial articular fossa of craniovertebral joint; *fe.ex*, fenestra exonarina, *fe.o*, orbital fenestra; *f.hyp*, hypophysial opening.

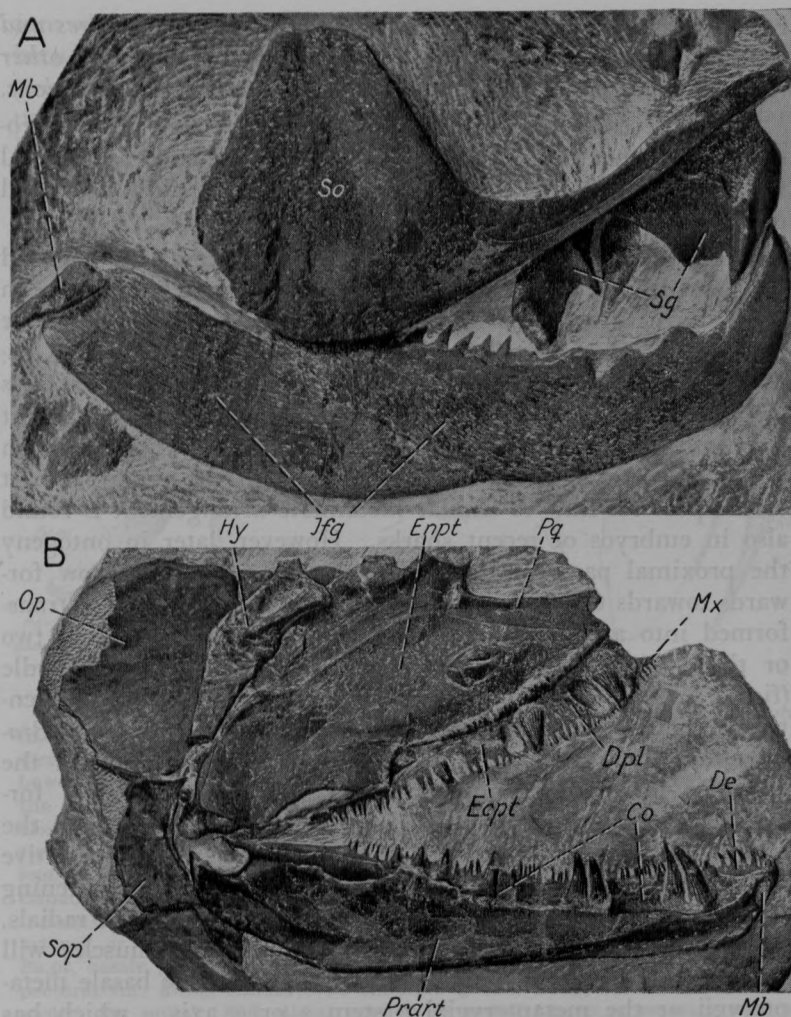


FIG. 8.

The jaw apparatus of two Devonian gnathostomes. A, arthrodire, *Hadrosteus rapax* Gross, from the Lowermost Upper Devonian of Wildungen, Germany. Photograph of specimen No. W.f.163 in the Geological-Paleontological Institute, Humboldt University, Berlin. Lateral aspect. Same specimen as figured by Stensiö 1963, pl. 21:3. B, teleostome, *Eusthenopteron foordi* Whiteaves, from the Lowermost Upper Devonian of Escuminac Bay, Canada. Photograph of specimen No. P.2197 in the Paleozoological Department of the Swedish Museum of Natural History.

Co, coronoids; De, dentary; Dpl, dermopalatine; Ecpt, ectopterygoid; Enpt, entopterygoid; Hy, hyomandibula; Ifg, inferognathal plate; Mb, meckelian bone; Mx, maxillary; Op, opercular; Pq, palatoquadrate; Prart, prearticular; Sg, superognathals; So, suborbital plate; Sop, subopercular.

cated structures are primitive and obviously *the arthrodires and the true teleostomes with regard to the jaws, as in many other respects, have become specialized in quite different directions.*

10. As recently demonstrated by STENSIÖ (1959) the arthrodires in the development of the shoulder girdle and the pectoral fin include both the most primitive and the most advanced types so far met with in fishes (fig. 9).

The most primitive shoulder girdle and pectoral fin is found in the Middle and Upper Devonian pachyosteomorphs. In these forms (fig. 9 A, B) the endoskeletal shoulder girdle (*En.sg*) extends far backwards in the body wall, it shows distinct impressions (*m.sc*) for the metameric radial muscles, it is pierced by canals for the metameric nerves and vessels, and it is provided with an elongated articular crest articulating with a row of metameric radials (*Ra*) situated in the proximal part of the pectoral fin. A similar metameric arrangement is found also in embryos of recent sharks. However, later in ontogeny the proximal parts of the radial muscles in sharks grow forwards towards the future shoulder joint (*jo*) and the fin is transformed into an internally short-based structure with only two or three basal elements articulating with the shoulder girdle (fig. 9 C, D). It is of great interest to find that this concentration had started already in the pachyosteomorphs. In *Brachyosteus* (fig. 9 A), as a beginning to the shortening of the shoulder joint, the hindmost radial has moved slightly forwards in its proximal part and has fused incompletely with the two radials following next in front. In this way a primitive basale metapterygii (*Ba.mt*) is formed and a further shortening of the shoulder joint, connected with the fusions of the radials, and a corresponding concentration of the radial muscles will lead to the conditions found in recent sharks. The basale metapterygii or the metapterygial « stem » or « axis » which has played such a dominant role in the discussions of the origin of the tetrapod limb (see also No. 29 below) is thus not, as hitherto generally has been assumed (see e.g. STEINER, 1935, fig. 3 A), formed by fusions of a row of metameric « basals » situated in the body wall. Like the basale metapterygii of sharks the axis of the typical biserial archipterygium has arisen by fusions of proximal parts of radials in connection with concentration of the proximal part of the fin and a shortening of the shoulder joint. *The metameric segmentation of the basale metapterygii or of the axis or stem of the « archipterygium » there-*

fore runs longitudinally and not transversely, as has hitherto been assumed. As I will demonstrate in a forthcoming paper (see also p. 77 below) this is of the greatest importance for the understanding of the origin and composition of the tetrapod limb.

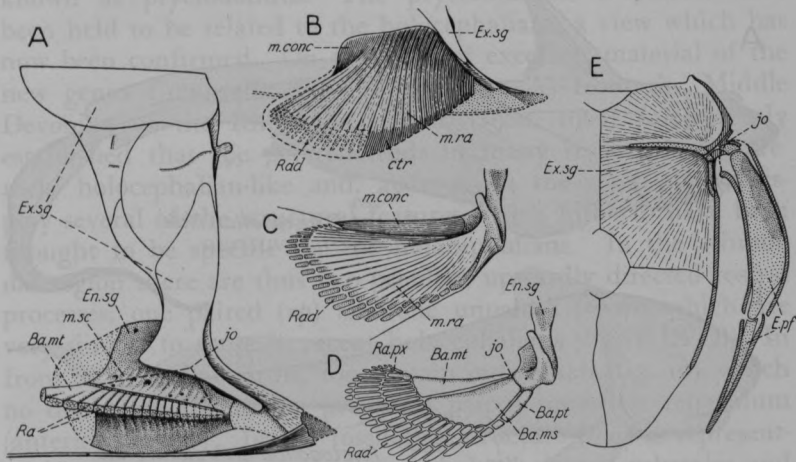


FIG. 9.

The shoulder girdle and the pectoral fin of certain elasmobranchiomorphs in, A-D, lateral and, E, dorsal aspects. A,B, two arthrodires, *Brachyosteus dietrichi* Gross and *Pachyosteus* sp., with holosomactidial pectoral fins. Lowermost Upper Devonian, Wildungen, Germany. In B the distal part of the radials, the radial muscles and the ceratotrichia restored. A, compilation from Stensiö 1959, figs. 6B, 49A, pls. 14, 15; B, from Stensiö 1959, fig. 7. C,D, recent shark, *Squalus acanthias* L. Original. E, antiarch, *Bothriolepis canadensis* (Whiteaves). Lowermost Upper Devonian, Escuminac Bay, Canada. From Stensiö 1959, fig. 22A

Ba.ms, basale mesopterygii; *Ba.mt*, basale metapterygii (metapterygial «stem» or «axis»), formed by fusions of proximal portions of radials; *Ba.pt*, basale propterygii; *E.pf*, jointed endoskeletal rod of monomesorhachic pectoral fin; *En.sg*, endoskeletal shoulder girdle; *Ex.sg*, exoskeletal shoulder girdle; *Ra*, radial; *Rad*, distal portion of radial; *Ra.px*, «preaxial» radials; *ctr*, ceratotrichia; *jo*, shoulder joint; *m.conc*, radial muscles, due to concentration fused into a muscle mass; *m.ra*, radial muscles; *m.sc*, impressions caused by radial muscles.

The most advanced types of shoulder girdle and pectoral fin in the arthrodires and in fishes in general is found in the antiarchs (fig. 9 E) in which the pectoral fin has become transformed into a peculiar arm-like structure (STENSIÖ, 1959). As the result of an excessive concentration the endoskeleton of the fin appears as a slender, sometimes jointed, rod (*E.pf*) enclosed in an exoskeletal armour formed by numerous dermal bones.

The mode of articulation with the shoulder girdle is very peculiar, quite unique among the gnathostomes, and obviously the muscles, nerves, vessels and other soft parts of the fin must have been much modified as well.

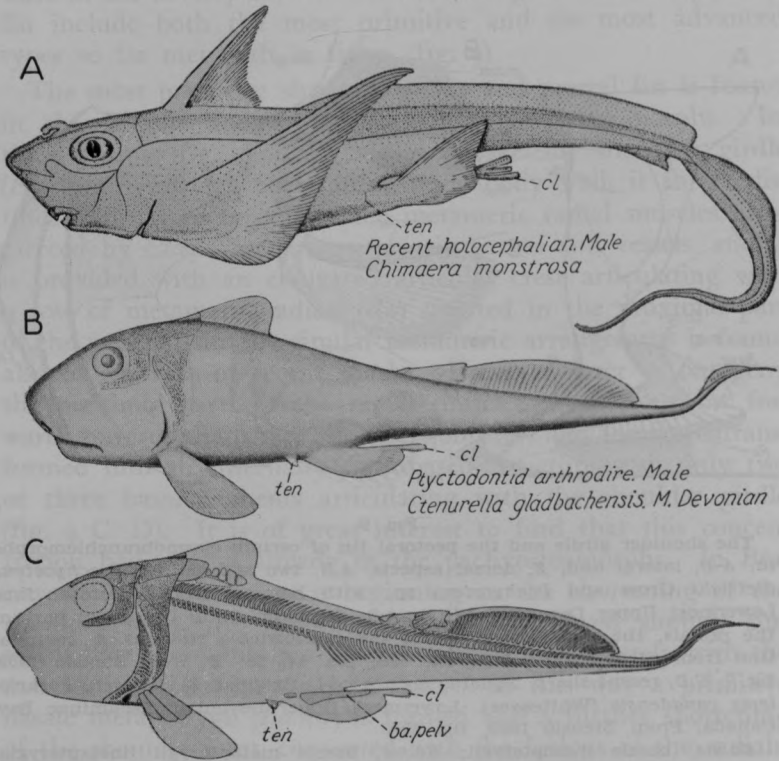


FIG. 10.

A, recent holocephalian, *Chimaera monstrosa* L. From Dean 1895, fig. 119 (modified after Garman 1888, pl. 2:1). B,C, restorations of Middle Devonian ptyctodontid, *Ctenurella gladbachensis* Ørving. Bergisch Gladbach, Germany. From Ørving 1960, fig. 5.

ba.pelv, basal plate of pelvic fin; *cl*, clasper; *ten*, pre-pelvic tenaculum (anterior clasper; in A only opening of pocket housing tenaculum is shown; cf. Goodrich 1909, fig. 139).

11. As claimed by STENSIÖ already in 1925, and as is now definitely established, the arthrodires are related to the recent elasmobranchs. The elasmobranchs today are represented by three distinct groups, the sharks, the rays and the holocephalians (chimaeras). These three groups differ considerably from each other and are therefore to be treated separately.

a) The *holocephalians* (fig. 10 A, 11 B, 12 A) constitute an aberrant group of fishes characterized by a great number of peculiar specific structural features. They have tooth-plates (*pl.tp*, *vo.tp*, fig. 12 A) of a distinct type and, as has long been known, similar tooth-plates occur in a group of Devonian fishes known as ptyctodontids. The ptyctodontids, therefore, have been held to be related to the holocephalians, a view which has now been confirmed. On the basis of excellent material of the new genus *Ctenurella* (figs. 10 B, C, 11 A) from the Middle Devonian of the Rhineland, ØRVIG (1960, 1962) has recently established that the ptyctodontids in many respects are extremely holocephalian-like and, apart from the tooth-plates, display several of the structural features which hitherto have been thought to be specific for the holocephalians. In the ethmoidal region there are thus two peculiar, upwardly directed rostral processes, one paired (*rp*) and one unpaired (*rp.m*) which are very similar to those in recent holocephalians (fig. 11 A, B). In front of the pelvic girdle, too, certain individuals (fig. 10), which no doubt are the males, present a paired pre-pelvic tenaculum (anterior clasper). In the fossil this structure (*ten*) is represented by a spine-like dermal plate with hook-shaped tubercles and behind that element there is in the same individual another, elongated paired bony element which similarly has hook-shaped tubercles (ØRVIG, 1962, p. 56). The latter is situated between the basipterygia of the pelvic fins and formed part of a posteriorly extending copulation organ (clasper) of the same type as is found in recent holocephalians.

On the basis of these most remarkable resemblances ØRVIG concluded that the ptyctodontids, which have been proved to be true arthrodires, either are in direct line of ancestry to the holocephalians or that both groups are derived from common ancestors among the early placoderms. However that may be, *the holocephalians are now to be regarded as surviving arthrodires.*

b) The rays (*Batoidea*) are generally classified together with the sharks as selachians, and because sharks are known since the Devonian and the rays do not appear until in the late Triassic, the rays are held to be descendants of shark-like ancestors (see ROMER, 1962 b, p. 43; PARKER and HASWELL, 1962; YOUNG, 1962). These views have been disputed by HOLMGREN (1940, 1941), who studied the ontogenetic development of the skull

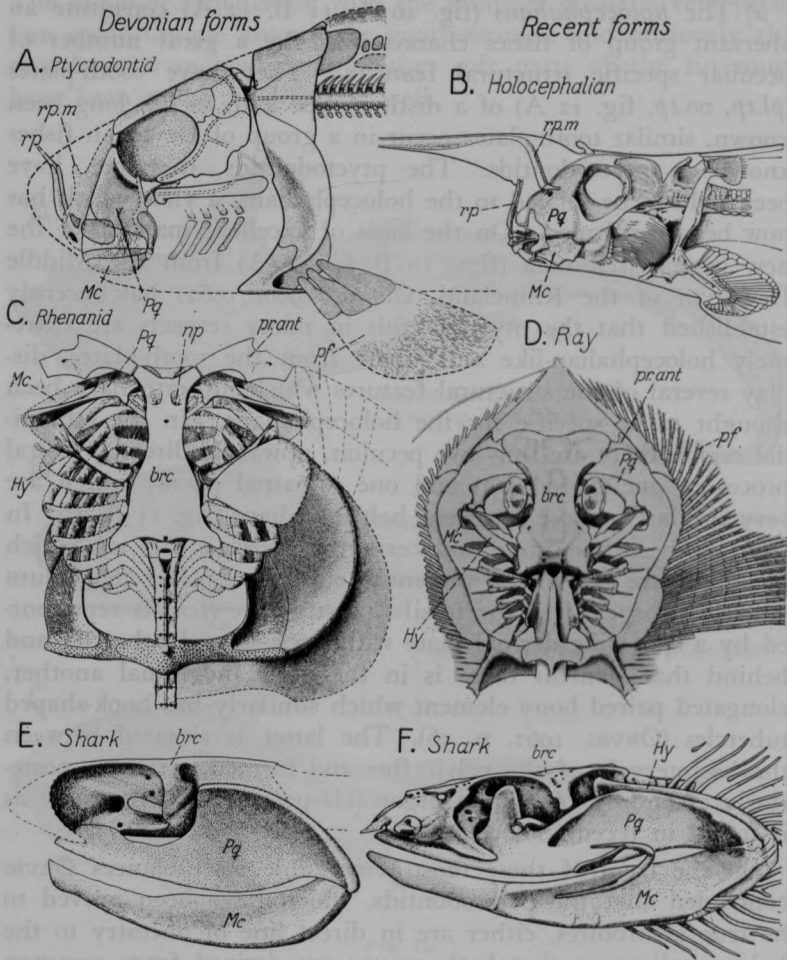


FIG. 11.

The skulls of representatives of the three groups of recent elasmobranchs (B,D,F) and of three Devonian elasmobranchiomorphs (A,C,E) to illustrate similarities in structure between, A,B, ptyctodontid arthrodires and holocephalians, between, C,D, rhenanid arthrodires and rays and between, E,F, Devonian and recent sharks. A, *Ctenurella gladbachensis* Ørvig. Middle Devonian, Bergisch Gladbach, Germany. From Ørvig 1962, fig. 2A. B, *Rhinochimaera pacifica* (Mitsukuri). From Garman 1904, pl. 1:2. C, *Jagorina pandora* Jaekel. Lowermost Upper Devonian, Wildungen, Germany. From Stensiö 1959, fig. 63. D, *Malacorhina mira* Garman. From Garman 1913, pl. 69:1. E, *Cladodus wildungensis* Jaekel. Lowermost Upper Devonian, Wildungen, Germany. From Gross 1938, fig. 1. F, *Chlamydoselachus anguineus* Garman. From Allis 1923, pl. 7.

Hy, hyomandibula; Mc, meckelian bone or cartilage; Pq, palatoquadrate; brc, braincase; np, nasal pit; pf, pectoral fin; prant, process supporting pectoral fin (processus antorbitalis); rp, paired rostral process; rp.m, unpaired (median) rostral process.

of both sharks and rays in great detail and made a thorough comparative anatomical analysis of the adult selachian skull. He found profound differences between the two groups and demonstrated that the alleged transition forms between sharks and rays (*Pristiophorus*, *Squatina*, *Rhinobatis*) are not intermediate at all. HOLMGREN concluded (1940, p. 259) that « the disagreement is really so great that one is bound to assume a diphyletic origin of sharks and rays, (for instance from two already strongly differentiated groups of arthrodires or allied, yet still unknown groups of Elasmobranchii) ».

Whether true rays are represented among the Paleozoic vertebrates is difficult to say, but possibly *Tamiobatis* (EASTMAN, 1897) from the Upper Devonian of the United States may be an early representative of the group. A remarkable fact is, however, that one group of the arthrodires, viz. the *Rhenanida*, in many respects is strikingly ray-like (see figs. 8 D, 11 C, D; see also STENSIÖ, 1950, 1959; as regards the *Stensiöellida* see GROSS, 1962). The rhenanids may very well be related to the rays but since the nasal opening (figs. 8 D, 11 D) secondarily has moved to the dorsal side of the head, in the same way as in the radotinids (fig. 8 A), they cannot possibly be on the direct ancestral line. The rhenanids are now being studied both by GROSS and STENSIÖ and for the moment we can only say that *the rays and the rhenanids are probably related and descendants of some unknown common ancestor among the pre-Devonian arthrodires.*

c) Whereas the holocephalians, as we have now seen, are almost certainly and the rays are probably descendants of early arthrodires, we cannot at present associate the *sharks* with any known group of arthrodires. The first sharks to appear in the fossil record are already typical sharks. As demonstrated by STENSIÖ (1937 a) and GROSS (1937, 1938) *Cladodus* (fig. 11 E) from the Lower Upper Devonian of Wildungen in many respects resembles the recent *Chlamydoselachus* (fig. 11 F) in the structure of the skull. The sharks apparently form an ancient group of fishes which has undergone but few structural changes during the last 300 to 400 million years. The view often elaborated in scientific papers and text-books, even today, that the sharks are primitive is a survival of the time when the presence of a cartilaginous endoskeleton was thought to be indicative of primitiveness.

12. The consideration of the elasmobranchs leads us to the *Dipnoi*, which, as is well known, agree in many respects with the elasmobranchs and previously (e.g. by GOODRICH, 1909) were classified together with the arthrodires. In particular the dipnoans agree with the holocephalians (see e.g. PARKER 1892), which, as we have seen, are surviving arthrodires. Figure 12 shows some of the apparent similarities in the structure of the palate. In dipnoans, as in holocephalians, the posterior (excurrent) external nostril has secondarily moved into the roof of the mouth cavity forming a pseudochoana; the dentition consists of paired anterior « vomerine » and posterior « palatine » tooth-plates which are similar not only as to their position and shape, but also in their histological structure (tubular dentine; see ØRVIG, 1951, p. 342); there are no external toothbearing dermal bones corresponding to the premaxillary and maxillary of the true teleostomes; the cranium is autostylic and the jaw articulation is far forwards. Whether these and other similarities (e.g. in the structure of the auditory organ, RETZIUS, 1881, p. 146; PARKER, 1892, p. 129; the musculature and cranial structures, EDGEWORTH, 1935, p. 230) imply a close relationship between dipnoans and holocephalians I would not venture to decide, but to me it seems unwise to disregard these resemblances altogether. The systematic position of the *Dipnoi* is still obscure (*) and I agree with PARKER who, seventy years

(*) In modern text-books (see e.g. Parker & Haswell 1962; Romer 1962b; Young 1962) the dipnoans are generally classified together with the crossopterygians, which in my opinion is incorrect. As I have repeatedly emphasized (1942, 1952, 1955a, 1959, 1960; see also Stensiö 1964a) the dipnoans differ from the crossopterygians in many important respects. Romer now agrees that there are considerable differences in dipnoans and crossopterygians, but according to him (1955, 1962a, p.225, 1962b, p. 47) they have at least one character in common which is not «superficial or unessential». They have «fleshy, lobate fins, covered with scales and with a well-developed internal skeleton of archipterygial type» and on this basis he suggests the new term *Sarcopterygii*, which means fleshy-finned fishes, to receive the *Dipnoi* and the *Crossopterygii*. However, fleshy lobed paired fins covered with scales were certainly developed in the arthrodires (fig. 9B; Stensiö 1959; Jarvik 1959) and early actinopterygians, and moreover many recent fishes, the elasmobranchs (fig. 9C; Jarvik 1959) and *Polypterus*, for instance, are good «sarcopterygians» as well. It may further be emphasized that a «biserial archipterygium», similar more to that of recent *Neoceratodus* than the endoskeleton of the fins in crossopterygians, is found in fossil elasmobranchs (e.g. *Pleuracanthus* and *Chondrenchelys*), and there are indications of such a structure in many recent sharks (e.g. in *Squalus*, *Ra.p.x*, fig. 9D), and in holocephalians (fig. 10B). If we add that the fin scales in elasmobranchs and dipnoans, in contrast to crossopterygians, almost completely cover the fins and that the dermal fin rays in recent dipnoans, as in elas-

ago, wrote (1892, p. 222) : « all that can be said with anything like certainty until we know something of the development of the *Dipnoi*, is, that they are the isolated survivors of an exceedingly ancient group, which was probably nearly allied to the ancestors of the existing Amphibians and Fishes — more particularly Elasmobranchs, though the Ganoid stock most likely arose not far off ».

13. That the *Dipnoi* are an ancient, early specialized group was emphasized already by GÜNTHER (1871, pp. 560, 561) who showed that several of the specializations in the palate. e.g. the peculiar dental plates characteristic of dipnoans, were developed in the Devonian *Dipterus*. More recently it has been demonstrated that there exists a close agreement between the Devonian and the recent dipnoans in the anatomy of the skull (SÄVE-SÖDERBERGH, 1952), in the vertebral column (JARVIK, 1952), etc.

The *Dipnoi*, no doubt, are a most conservative group of fishes which has changed very little since the Devonian. That this is so is well illustrated by the following conditions.

Figures 13 A and 14 C feature photographs of the anterior part of the head of the two recent lung-fishes *Protopterus* and *Neoceratodus*. In both there is a paired notch (*inc*) in the upper lip (*ul*) leading to the anterior (incurrent) nostril (*an*, figs. 12 B, 13 B). Behind that notch there is a ridge, the subnasal ridge (*ri. sbn*), particularly well shown in *Neoceratodus*. This ridge lodges the endoskeletal subnasal process (the subnasal cartilage, see JARVIK, 1942, pp. 272-275, 1955 a, fig. 7) while behind the ridge the upper lip forms a flap (*fl.ul*) which is applied to the ventro-lateral side of the lower jaw. When the mouth is shut, the lower jaws, which are fused in the median line, occupy a position close inside the arch formed by the upper lip. As in many other fishes (sharks, *Polypterus*) and certain urodele larvae, the lower lip forms a strong fold (*fo.ll*). In *Neoceratodus* (fig. 14, C, D) this fold is well exposed, whereas in *Protopterus* (fig. 13 A-C) it is grasped from the outside by the upper lip

mobranchs, are developed as ceratotrichia (Jarvik 1959), it would seem to me that the fin structure indicates that the dipnoans are related to elasmobranchs rather than to crossopterygians. The term *Sarcopterygii* being both unnecessary and misleading is to be rejected. Since the presence of a muscular lobe is certainly a primitive feature of vertebrates it is evident that the lobe fins in crossopterygians cannot have arisen in the way suggested by Schmalhausen (see Szarski 1962, p. 212).

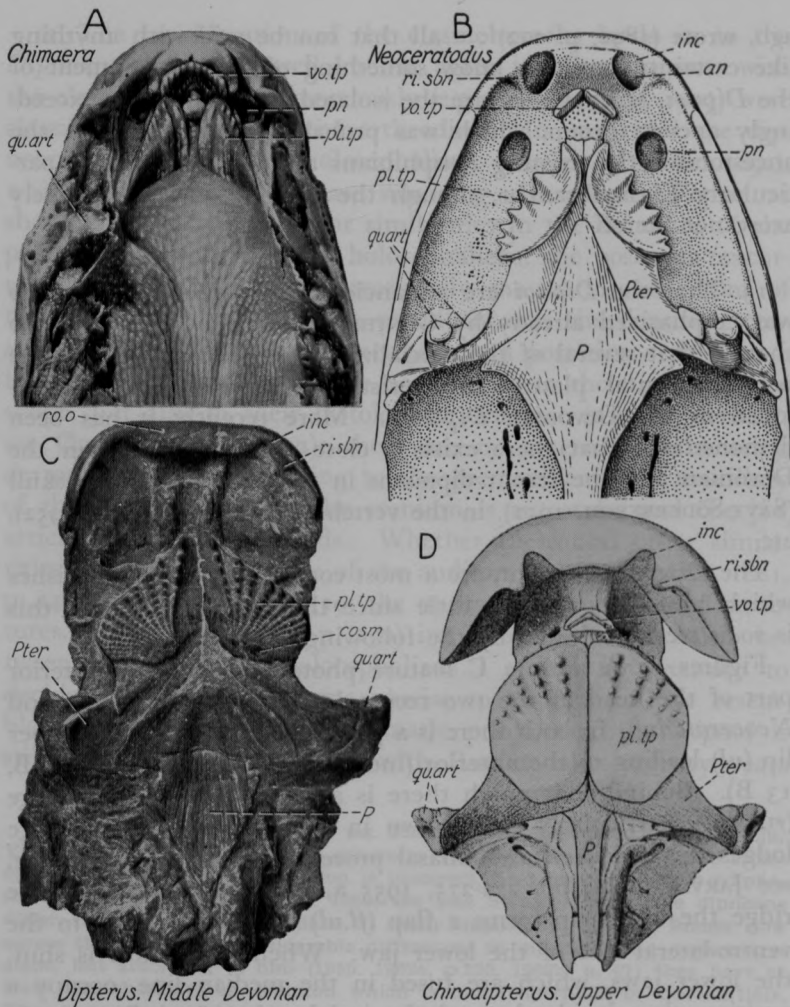


FIG. 12.

The palate in holocephalians and dipnoans in ventral aspect. A, *Chimaera monstrosa* L. Photograph of specimen in the Paleozoological Department of the Swedish Museum of Natural History. B, *Neoceratodus forsteri* (Günther). Compilation after Günther 1871, pl. 34:3, Holmgren and Stensiö 1936, fig 288A, and the specimen in figure 14C. C, *Dipterus* sp. Middle Devonian, Scotland. Specimen No. 53371, Geol. Surv., London. D, *Chirodipterus wildungensis* Gross. Lowermost Upper Devonian, Wildungen, Germany. From Säve-Söderbergh 1952, fig. 10.

P, parasphenoid; Pter, pterygoid.

an, anterior (incurrent) nostril; cosm, patches of «cosmine» (in some specimens the tooth plate is almost completely covered by «cosmine»); inc, notch in upper lip leading to anterior nostril; pl.tp, «palatine» tooth plate; pn, posterior (excurrent) nostril (pseudochoana); quart, position of quadrate articulation; ri.sbn, subnasal ridge; ro.o, opening of uncertain importance; vo.tp, «vomeric» tooth plate.

which is bent inwards and upwards around the lower lip. The fold of the lower lip occupies a large elongated pit (*p.lj*) in the lateral side of the lower jaw and the lower lip fold is attached to this pit anteriorly and along its dorso-medial margin (*a.at*,

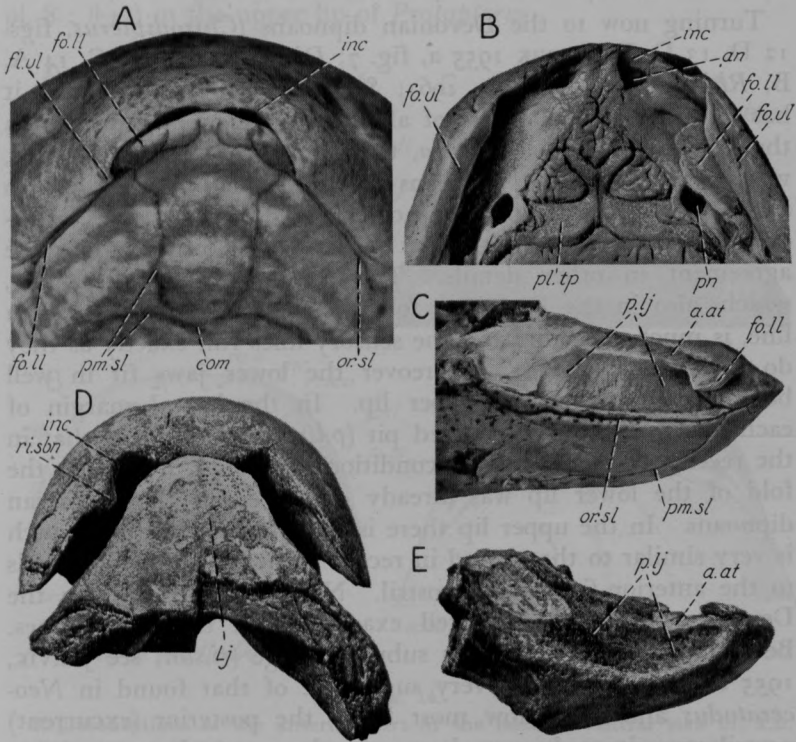


FIG. 13.

A-C, *Protopterus aethiopicus* Heckel. Photographs of a specimen in the Paleozool. Dept., Swedish Mus. Nat. Hist. A, anterior part of head in antero-ventral view. B, anterior part of palate in ventral view. The fold of the lower lip of the left side pulled out of the fold formed by the upper lip. C, right half of lower jaw in lateral aspect. The fold of the upper lip cut off. D, E, *Chirodipterus wildungensis* Gross. Lowermost Upper Devonian, Wildungen, Germany. Photographs of holotype, belonging to the Paleont. Inst. and Mus., Humboldt University, Berlin. Specimen figured by Säve-Söderbergh 1952. D, the anterior part of the skull and the lower jaws in ventral aspect. From Jarvik 1955a, fig. 7. E, right half of the lower jaw in lateral aspect.

fig. 13 C). The oral sensory line (*or.sl*) runs forward along the convex ventro-medial margin of the pit. A little behind its anterior end this sensory line lies close to or is joined to what is

considered to be the anterior end of the preoperculo-mandibular line (*pm.sl*). Further back, along the posterior margin of the symphyseal region of the jaws, the preoperculo-mandibular line is sometimes joined to the corresponding sensory line of the other side by a secondary anastomosis (*com.*).

Turning now to the Devonian dipnoans (*Chirodipterus*, figs. 12 D, 13 D, E; JARVIK 1955 a, fig. 7; *Dipterus*, figs. 12 C, 14 A, B; *Rhinodipterus*, ØRVIG, 1961; *Scaumenacia*, JARVIK, 1960) it has to be emphasized first of all that the lower jaw and, with the exception of *Scaumenacia*, the snout, are strongly ossified, whereas in the recent dipnoans the corresponding parts are to a considerable extent made up of cartilage or soft tissues. However, if we disregard this fact we will find amazingly close agreement in other details. The shape of the lower jaws, which, also in the Devonian forms, have fused in the median line, is much the same and the sensory lines run exactly as they do in recent dipnoans. Moreover the lower jaws fit in well behind the arch of the upper lip. In the lateral margin of each jaw there is an elongated pit (*p.lj*) very similar to that in the recent dipnoans. These conditions can only mean that the fold of the lower lip was already developed in the Devonian dipnoans. In the upper lip there is a distinct notch (*inc*) which is very similar to that found in recent dipnoans and which leads to the anterior (incurrent) nostril. No doubt the latter in the Devonian forms was situated exactly as in the recent ones. Behind the notch there is a subnasal ridge (*ri.sbn*; see JARVIK, 1955 a, fig. 7) which is very suggestive of that found in *Neoceratodus* and as is now most likely the posterior (excurrent) nostril was situated somewhat as in the recent forms and not outside the margin of the lower jaw as I claimed in 1955.

Finally, it is to be mentioned that one of the specimens of *Dipterus* (fig. 14 A) shows a large dermal bone (*Ulb*), situated just behind the subnasal ridge and lateral to the pit in the lower jaw. This is the only plate of its kind discernible on the side of the specimen shown in figure 14 A, and it apparently belongs to the right side of the specimen. However, on the other side of the same specimen there are at least three such plates (see JARVIK, 1950, fig. 9 A, *Rbr?x*, *Rbr?y*) situated in a row along the ventral margin of the infraorbital dermal bones of the left side of the specimen. These plates puzzled me for a long time, but it is now clear that they form a support for the upper lip and simply by putting them into posi-

tion, as has tentatively been done in figure 14 B, the upper lip will assume the shape characteristic of *Neoceratodus*. No equivalent plates have been observed so far in any other fossil dipnoans but the possibility exists that they might be represented by the layer of fibrous tissues figured by Parker (1892, pl. 8 : 8-12) in the upper lip of *Protopterus*.

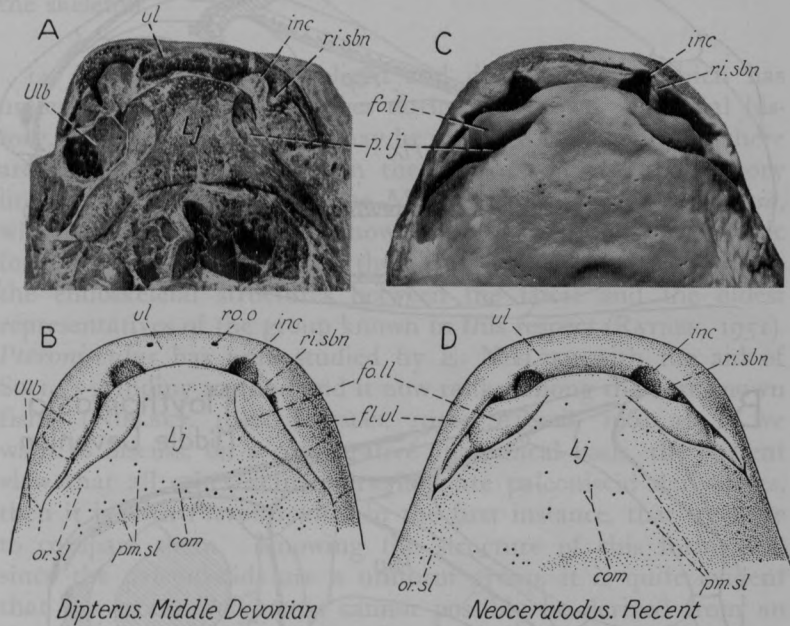


FIG. 14.

Representations of the anterior part of the head in ventral view, A,B, a Devonian and C,D, a recent dipnoan to show the striking similarities. A,B, *Dipterus valenciennesi* Sedgw. & Murch. A, photograph of specimen from the Middle Devonian of Scotland. Specimen No. 93, Royal Scottish Mus. Edinburgh. Same specimen as figured by Jarvik 1950, fig. 9A. B, restoration. C,D, *Neoceratodus forsteri* (Günther). C, photograph and, D, drawing of specimen in the Paleozool. Dept. Swedish Mus. Nat. Hist.

Explanations of index letters in figs. 13 and 14.

Lj, fused lower jaws; Ulb, supporting dermal bones of upper lip.

a.at, area of attachment of fold of lower lip; an, anterior (incurrent) nostril; com, secondary commissure between preoperculo-mandibular sensory lines; fl.ul, flap of upper lip; fo.ll, fold of lower lip; fo.ul, fold of upper lip; inc, notch in upper lip leading to anterior nostril; or.sl, oral sensory lines or pores of ditto; p.lj, pit in lateral side of lower jaw; pl.tp, «palatine» tooth plate; pm.sl, preoperculo-mandibular sensory line or pores of ditto; pn, posterior (excurrent) nostril; ri.sbn, subnasal ridge; ro.o, opening of uncertain importance; ul, upper lip.

All the peculiar specializations in the anterior part of the head, which have been considered here, were developed in the

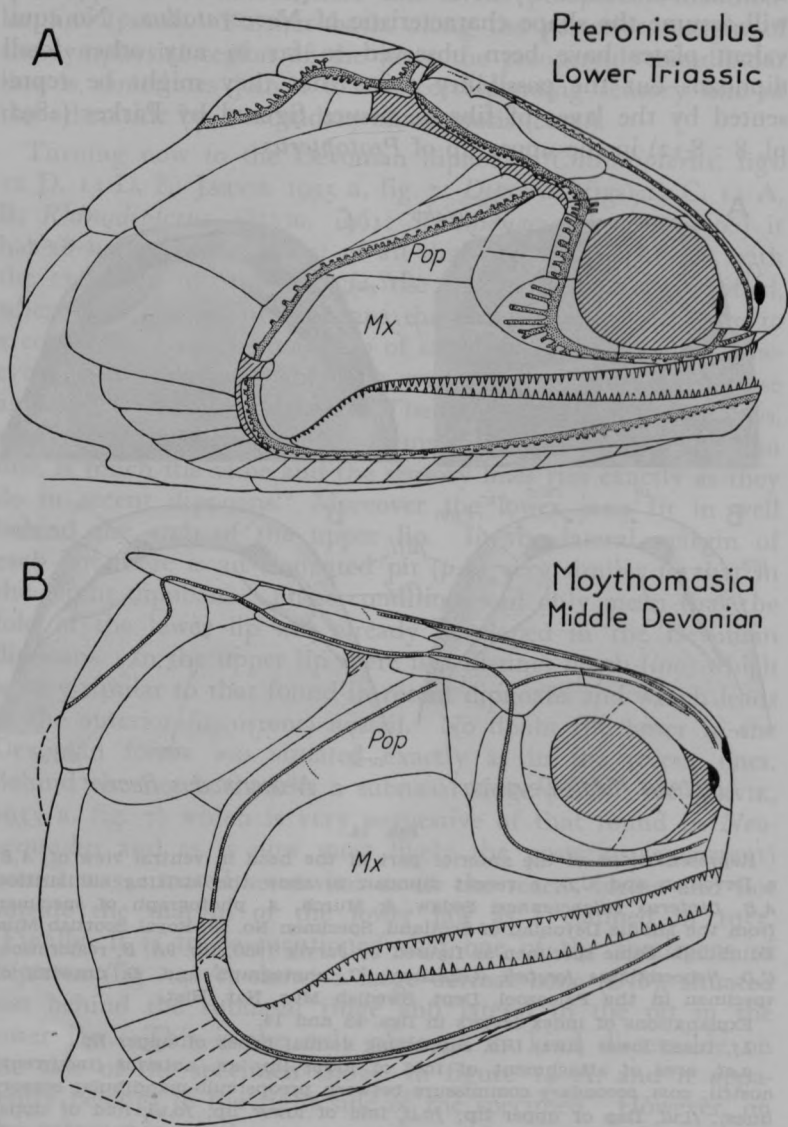


FIG. 15.

Restorations of the skull in lateral aspect of, A, Triassic and B, Devonian paleoniscid. A, *Pteronisculus stensiöi* (Nielsen). Lower Triassic, East Greenland. From Nielsen 1942, fig. 27. B, *Moythomasia* sp. Middle Devonian, Bergisch Gladbach, Germany. Made by H. Jessen for the *Traité de Paléontologie*.

Mx, maxillary; *Pop*, preopercular.

Devonian forms, both in those forms which have been found in fresh water deposits (*Dipterus*, *Scaumenacia*) and in those which have been found in marine strata (*Chirodipterus*, *Rhino-dipterus*). The changes that have occurred during the phylogeny of the dipnoans are obviously mainly such changes as are due to the well-known trend of a retrogressive development of the skeleton.

14. Another early specialized and distinct group which has undergone only slight changes during its known geological history, is the paleoniscids. As may be gathered from figure 15 there are hardly any differences in the exoskeleton and the sensory lines of the head between the Middle Devonian *Moythomasia*, which is one of the oldest known paleoniscids, and the Triassic form *Pteronisculus*, nor are there any important differences in the endoskeletal structures between the latest and the oldest representatives of the group known in this respect (RAYNER, 1951). *Pteronisculus* has been studied by E. NIELSEN with the aid of SOLLA's grinding method and it now ranks among the best known fishes (NIELSEN, 1942; LEHMAN, 1952; STENSIÖ, 1964 a). If we want to discuss, on a comparative anatomical basis, the current view that all other actinopterygians are paleoniscid derivatives, then it is with *Pteronisculus*, in the first instance, that we have to compare them. Knowing the structure of this form, and since the paleoniscids are a uniform group, it is quite evident that the recent *Polypterus* cannot possibly be derived from an ancestral form specialized in the way characteristic of the paleoniscids. Since *Polypterus* differs widely in important respects from the actinopterygians it is most convenient to place it in a separate systematic unit, the *Brachiopterygii*. No doubt the sturgeons (STENSIÖ, 1932) are more typical actinopterygians but that does not necessarily mean that they are descendants of any paleoniscids either. This still remains to be proved as also the generally accepted view that the recent ganoids (*Amia*, *Lepisosteus*) and the teleosts are paleoniscid derivatives. What we do know is that the actinopterygians include a great number of independent evolutionary lines (see STENSIÖ, 1932, 1964 a; GARDINER, 1960; NYBELIN, 1961) but the origin of most of these lines is still obscure.

15. More than thirty years ago STENSIÖ made a grinding series and elaborate wax models of the neural endocranium, the uro-

hyal, and parts of the visceral endoskeleton of one of the oldest known *Coelacanthiformes*, *Nesides schmidti*, from the lowermost Upper Devonian of Germany (see STENSIÖ, 1932, pp. 17-39, figs. 6, 11, 14; 1937 b; HOLMGREN and STENSIÖ, 1936). On the basis of this series and excellent material of other Devonian coelacanthids (STENSIÖ, 1937 b; JARVIK, 1942, 1954) as well as the description of the skeleton and the muscles of *Latimeria*, given by MILLOT and ANTHONY (1958) detailed comparisons can now be made between the earliest coelacanthiforms and the living representative of the group (see also pp. 83-84).

As in other groups of vertebrates the skeleton in the coelacanthids has undergone a retrogressive development; the basiptyergoid process (*pr.bp*, fig. 16 B) has become reduced while certain small changes have occurred which are connected with the remarkable reduction in size and withdrawal of the brain (STENSIÖ, 1964 a), etc. However, in most respects *Latimeria* agrees closely with the Devonian forms even to the development of the peculiar rostral organ with its three paired external openings which was already developed in the oldest known coelacanthid (*Dictyonosteus*, JARVIK, 1942, p. 581). As may be gathered from figure 16 the shape of the two units of the braincase is very similar, the construction of the intracranial joint is much the same, the position of the openings for the nerves (*c.II*, *c.III*, etc.) and vessels (*c.a.ci*, *c.v.pit*, etc.) is very similar, and even the peculiar long passage for the r. ophthalmicus lateralis is developed as in *Latimeria*. This passage consists of anterior and posterior canals connected by a groove (*gr.o.lat*) in the lateral side of the ethmosphenoid. The canal for the n. trochlearis pierces the medial wall of the hindmost of these canals, a condition which proves that the n. trochlearis, in the fossil forms too, went to the orbit through the anterior part of the posterior canal. These and many other facts revealed by the grinding series of *Nesides* and other material of Devonian coelacanthiforms show that the nerves and vessels, already in the Devonian times, ran and branched very much as in *Latimeria* of the present days.

The interpretation of most of these canals and structures was correctly given by STENSIÖ in 1932, six years before the first specimen of *Latimeria* was captured and it is a rare event indeed for a paleontologist to see his interpretations confirmed in this way. However, the fact that the numerous structural details discovered by STENSIÖ more than thirty years ago in the Devonian coelacanthids, actually occur in the recent *Latimeria*, afford

indisputable proof of the accuracy and reliability of the methods employed by STENSIÖ for the study of fossils.

To illustrate this point two other examples can be given, which demonstrate at the same time the high degree of specialization in the earliest coelacanthiforms and the remarkable conservatism of that group of fishes.

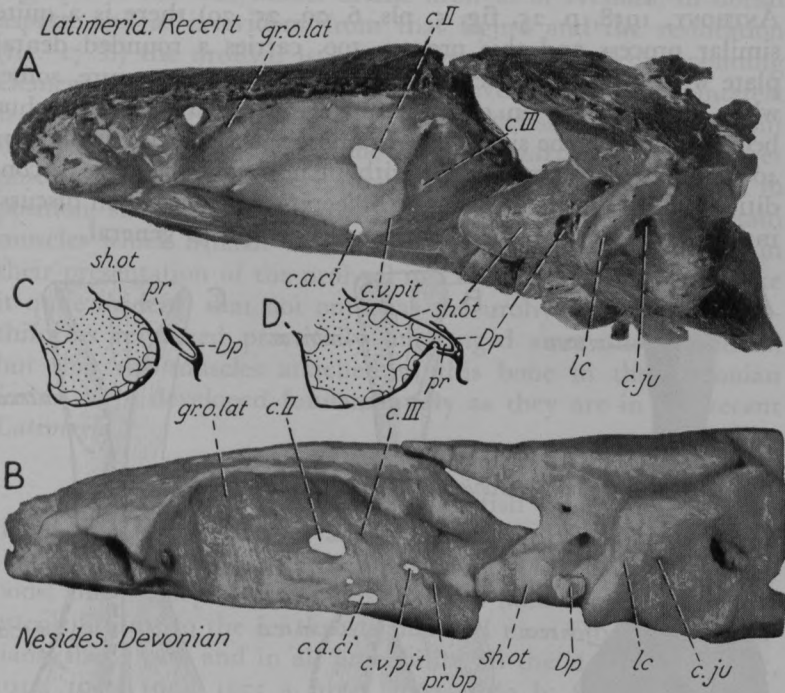


FIG. 16.

A, B, photographs of the neural endocranium (in A with certain dermal bones) in lateral aspect of recent and Devonian coelacanthiforms to demonstrate the similarities in structure. A, *Latimeria chalumnae* Smith. From Millot and Anthony 1958, pl. 20. B, *Nesides schmidtii* Stensiö. Model in wax made by E. Stensiö on the basis of a grinding series. Drawings of this model have been published by Stensiö 1932 (fig. 8), Holmgren and Stensiö 1936 (fig. 266) and Jarvik 1954 (fig. 4). C, D, parts of two consecutive transverse sections (Nos. 110a, 109a) of the grinding series of *Nesides* to show the collar-stud-like structure.

Dp, dental plate of collar-stud-like structure.

c.a.ci, canal for arteria carotis interna; c.ju, jugular canal; c.v.pit, canal for pituitary vein; c.II, canal for n. opticus; c.III, canal for n. oculomotorius; gro.o.lat, groove for r. ophthalmicus lateralis; lc, lateral commissure; pr, process of otical shelf supporting dental plate; pr.bp, basipterygoid process; sh.ot, otical shelf.

16. When making the serial sections of *Nesides*, STENSIÖ discovered a small pointed endoskeletal process on either side of the otic region of the neural endocranium (fig. 16 B-D). This process (*pr*) which is situated on the lateral side of the otical shelf (*sh.ot*), close in front of the lateral commissure (*lc*), carries a small rounded dental plate (*Dp*) with a few small denticles. In exactly the same place in *Latimeria* (fig. 16 A; see also MILLOT and ANTHONY, 1958, p. 25, fig. 5, pls. 6, 20, 25, 29) there is a quite similar process and this process, too, carries a rounded dental plate with a few denticles. This inconsiderable structure, somewhat suggestive of an old-fashioned front collar-stud, has thus been situated on the side of the braincase of the coelacanthids for 400 millions of years or more without noticeable changes, a condition which I think is well worth keeping in mind when discussing the evolution of vertebrates and evolution in general.

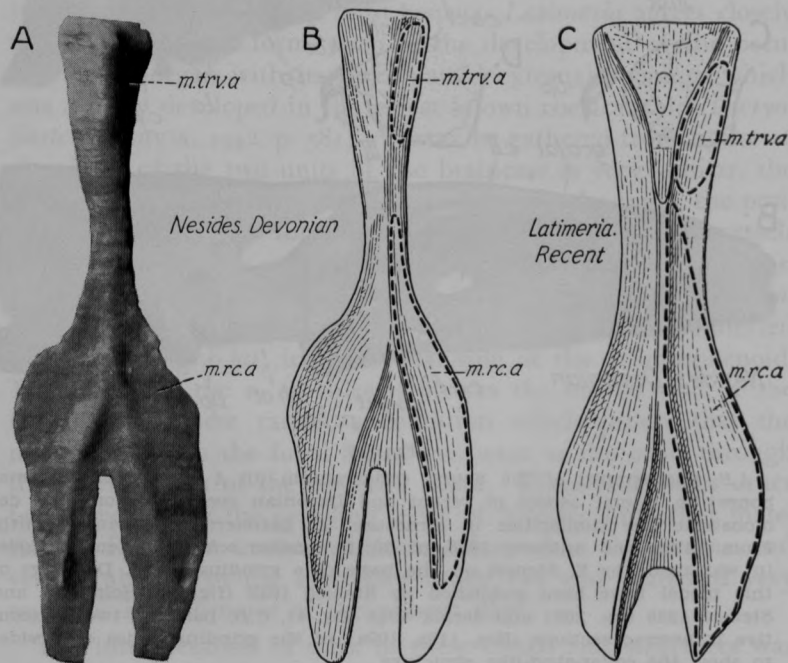


FIG. 17.

The urohyal in dorsal aspect of Devonian and recent coelacanthiforms to show similarities in the general shape and in the position and extent of the areas of attachment of muscles. *A, B*, *Nesides schmidtii* Stensiö. Lowermost Upper Devonian, Wildungen, Germany. *A*, photograph of model in wax made by E. Stensiö. *B*, restoration. From Jarvik 1963b, fig. 17B. *C*, *Latimeria chalumnae* Smith. From Millot and Anthony 1958, fig. 15.

m.rc.a, area of attachment of musculus rectus cervicis; *m.trv.a*, area of attachment of transversus ventralis muscles.

17. The other example of this remarkable unchangeability is provided by the urohyal. As is now well known (see JARVIK, 1963 b) this element, which is situated in the median line between the lower jaws, belongs to the subbranchial series which is endomesodermal in origin and forms a support for the hypobranchial muscles. The figure 17 A shows an unretouched photograph of the wax model of the urohyal of *Nesides*, in dorsal aspect, and as is evident from that figure and the restoration (fig. 17 B) the urohyal is very suggestive of the corresponding element in *Latimeria* (fig. 17 C). However, of particular interest is the fact that the dorsal side of the model shows two faint, but distinct, paired impressions, one anterior (*m.trv.a*) and one larger posterior (*m.rc.a*). These impressions agree extremely well as to position, shape and size with the areas of attachment of certain muscles which MILLOT and ANTHONY have shown, in outline, in their presentation of the urohyal in *Latimeria*. These facts make it quite evident, that not only has the urohyal in the coelacanthiforms remained practically unchanged since the Devonian, but that the muscles attached to this bone in the Devonian forms, were developed fundamentally as they are in the recent *Latimeria*.

18. The remaining two Devonian fish groups to be considered, the *Porolepiformes* and the *Osteolepiformes*, are of particular interest since both, independently, gave rise to tetrapods; the porolepiforms to the *Urodeles* (and *Apoda*?) and the osteolepiforms to the *Ichthyostegalia* and most other stegocephalians, the *Anura* and in all probability all the *Amniota* (JARVIK, 1942, 1952, 1954, 1955 a, 1960, 1962, 1963 b; STENSIÖ, 1964 a). Thus, like the cyclostomes, the tetrapods are diphyletic in origin and we may distinguish a *Porolepiform-Tetrapod* and an *Osteolepiform-Tetrapod stock*. These two stocks have been separate since pre-Devonian times.

The porolepiforms and the osteolepiforms have several characters in common (see JARVIK, 1942, pp. 488-489, 493-494; 1954, pp. 7-12; 1955 a, p. 149; 1960, pp. 47-48) and, as is to be expected, the recent amphibians often agree in the corresponding respects. Thus, for example, the premaxillary in the urodeles and the anurans is composed of three parts (*pars dentalis*, *pars palatina* and *pars facialis*) as is the corresponding element both in the osteolepiforms and the porolepiforms. That there is similarity in the structure of the skin in recent groups of the amphi-

bians (SZARSKI, 1962, pp. 233-234) is not surprising if we consider the similar mode of life and the well-known fact that the microstructure of the scales and dermal bones in the earliest porolepiforms (the porolepids) and earliest osteolepiforms (the osteolepids) too, is similar (see e.g. GROSS, 1935; ØRVIG, 1957).

These resemblances, surely, can not be disregarded in any discussion on the origin of the *Amphibia* and of the tetrapods in general, but of greater importance are the numerous specializations which characterize and clearly distinguish the Porolepiform-Tetrapod and the Osteolepiform-Tetrapod stocks. The fact that the porolepiforms agree closely with the urodeles in all aspects of the structure of the head which have been analysed (the snout and the intermandibular division, JARVIK, 1942, 1962, 1963 a, 1963 b), and that practically all the many intricate specific structures found in the Devonian porolepiforms have been encountered *only* in urodeles among recent vertebrates, can only mean that the urodeles are closely related to, and descendants of, the porolepiforms. The osteolepiforms, on the other hand, differ fundamentally from the porolepiforms and the urodeles both as regards the snout and the floor of the mouth cavity and agree with the anurans. Of particular interest is that the amniotes, in the structure of the floor of the mouth cavity, agree with the osteolepiforms and the anurans, a fact supporting the view that they belong to the Osteolepiform-Tetrapod stock.

The view that the tetrapods are diphyletic thus rests on a strong basis and it becomes more and more difficult to uphold the conception of a mysterious prototetrapod as a common ancestor of all the tetrapods. Arguing for a monophyletic origin of the *Amphibia*, ROMER (1962 a, p. 225), SCHMALHAUSEN and SZARSKI (see SZARSKI, 1962, p. 231; see also PARSONS and WILLIAMS, 1963), claim that the remarkable differences in almost every important respect, in the structure of the snout between the porolepiforms and osteolepiforms are due simply to differences in the breadth of the snout. It may be pointed out firstly that these writers ignore the fact, established by a great number of distinguished anatomists (for bibliography see JARVIK, 1942, pp. 284-333) that the urodeles and the anurans differ widely in the anatomy of the snout. That these differences, which on the whole are the same as those between the porolepiforms and the osteolepiforms, are due to variations in the breadth of the snout, remains to be proved. Moreover, it is to be strongly emphasized that the statement by these writers that the snout is broader in the porolepiforms than in the osteolepiforms is incorrect. In *Porolepis elongatus*, for example, the snout is distinctly narrower as compared with the length of the fronto-ethmoidal shield (the ratio d/b , JARVIK, 1948, table 1, p. 42; 1950,

p. 59) than it is in the osteolepiform *Gyroptychius* (see JARVIK, 1942, fig. 62 B, pl. 5 : 1) and there are considerable variations in this respect both in the porolepiforms and the osteolepiforms. This example illustrates how difficult it is to find reliable argument in favour of the view that the amphibians are monophyletic and the fact that arguments of this kind (see also pp. 51-52, 59-61, 63-65, 69, foot-notes pp. 57, 58, 66, addendum, p. 95) are used and are attributed great importance, shows plainly how weak the foundation of that view really is.

19. Among the many striking differences between the Porolepiform-Tetrapod and the Osteolepiform-Tetrapod stocks, those in the development of the hyobranchial skeleton and the subbranchial series are particularly clear (fig. 18; JARVIK, 1962, 1963 a, b). In the osteolepiforms the branchial arches, as in fishes in general (fig. 18 C, see also e.g. EDGEWORTH, 1935), all reach and articulate with the basibranchial series, and in the osteolepiforms and the anurans, at any rate, this series consists of two elements. In the porolepiforms and in larvae of urodeles, on the other hand, there is only one basibranchial, and due to a reduction of the hypobranchial elements, one (*Hb.IIIv*, *Hb.IVv*) or more of the posterior arches do not reach the basibranchial but articulate with the arches in front of it in a characteristic way. Moreover, the configuration of the external side of the ceratohyal in the porolepiforms proves that this side was occupied by muscles. These muscles (*m.sarI*, *m.bh.e*, *m.ih.a*) must have been developed very much as in urodele larvae and a most remarkable fact is that the strongest of these muscles, the *m. branchiohyoideus externus* (*m.bh.e*), among all the vertebrates, previously had been encountered only in larvae of urodeles. In the osteolepiforms again, the conditions are quite different and surprisingly primitive. In them the external side of the ceratohyal is occupied by dental plates (*chl*) which were situated in the medial wall of the spiracular gill-slit.

In the development of the subbranchial series, too, the porolepiforms and the osteolepiforms differ widely (fig. 18; JARVIK, 1963 a, b). In the osteolepiforms, as in the anurans and the amniotes, this series consists of two elements, the urohyal (*Uh*) and the sublingual rod (*Sl*). In the porolepiforms and the urodeles there is only one element, the urohyal. This element is a characteristic rod bifurcating posteriorly and quite different from the urohyal in the osteolepiforms. Finally it may be mentioned that the sublingual rod plays an important part in the development of the tongue in the Osteolepiform-Tetrapod stock.

In the Porolepiform-Tetrapod stock, where this rod is lacking and where there is instead a peculiar glandular field between the anterior parts of the jaws, the tongue is formed in a different way (see JARVIK, 1963, a, b).

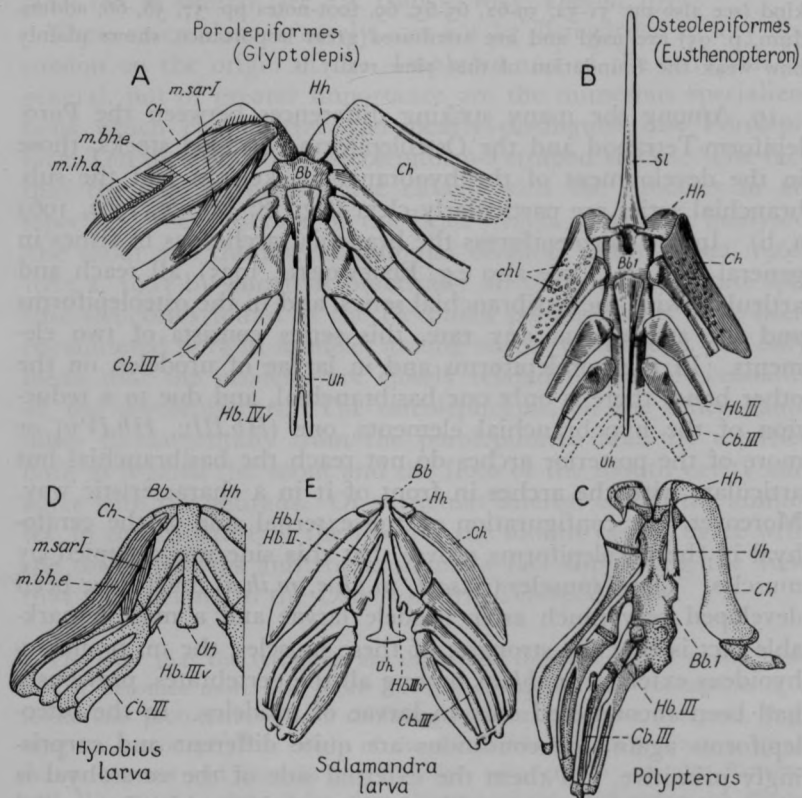


FIG. 18.

The hyobranchial skeleton and the subbranchial series in, A-D, ventral and, E, dorsal aspects. A, porolepiform, *Glyptolepis* sp. Middle Devonian, East Greenland. Certain muscles restored. After Jarvik 1963a, fig. 4. B, osteolepiform, *Eusthenopteron foordi* Whiteaves. Lowermost Upper Devonian, Escuminac Bay, Canada. From Jarvik 1963b, fig. 16. C, brachiopterygian, *Polypterus* sp. From Devillers 1958, fig. 432 A. D, urodele, *Hynobius nebulosus* (Schlegel). Larva 22 mm. Simplified after Fox 1959, fig. 32. E, urodele, *Salamandra salamandra* (L.). Larva 35 mm. From Stadtmüller 1936, fig. 493.

Bb, basibranchial; Bb.I, anterior basibranchial; Cb.III, ceratobranchial III; Ch, ceratohyal; Hb.I, Hb.II, Hb.III, hypobranchials I, II, and III; Hb.IIIv, Hb.IVv, vestigial parts of hypobranchials III and IV; Hh, hypohyal; Sl, sublingual rod; Uh, urohyal.

chl, lateral dental plates of ceratohyal in medial wall of spiracular gill-slit; m.bh.e, musculus branchiohyoideus externus; m.ih.a, musculus interhyoideus anterior; m. sarI, musculus subarcualis rectus I.

20. Figure 19 A is a photograph of a wax-model made on the basis of grinding series 1 of *Eusthenopteron*. It shows the anterior part of the left nasal capsule with the prominent inwardly projecting processus intermedius (*pr.im*) from behind and slightly from above. The processus intermedius is bent in such a way that two crests, the lamina superior (*la.s*) and the lamina inferior (*la.i*) are formed. Medially to these crests, both of which are joined anteriorly to the anterior wall of the nasal cavity, there is another crest, the crista intermedia (*cr.im*), also projecting backwards from the anterior wall. The processus intermedius is covered by a strong exoskeletal process, the processus dermintermedius (*pr.dim*, figs. 18 C, F, 20 A) of the lateral rostral (*Rl*) which is shaped as, and intimately connected with, the underlying endoskeletal process. Ventrally to the lateral part of the crista intermedia lies the posterior opening of a wide canal (*c.nb*) leading forwards, and just dorsally to the medial end of the crista is the ventral opening of another, but smaller, ascending canal (*c.ext*). In all these obviously highly specialized structural features the osteolepiforms (fig. 18 A-C, F) agree in a most striking way with the recent anurans (*Rana*, fig. 18 D, *Calyptocephalus*, fig. 18 E; JARVIK, 1942), and no doubt the various crests and openings in the osteolepiforms are homologous to the correspondingly named structures in the recent anurans. It is also obvious that the processus dermintermedius of the lateral rostral is equivalent to the anuran septomaxillary (*Smx*, fig. 19 G).

In all these important respects the osteolepiforms and the anurans differ fundamentally from the porolepiforms (fig. 19 H) and the urodeles (fig. 19 J.).

As demonstrated by the well preserved fossil material of *Porolepis* described by me in 1942, and now definitely proved by the grinding series of *Glyptolepis* (see JARVIK, 1962), the inner faces of the walls of the anterior parts of the nasal cavity in the porolepiforms are smooth, as in urodeles. There are thus no equivalents to the peculiar crests which are characteristic of the osteolepiforms and the anurans, and there is no equivalent to the processus dermintermedius or the septomaxillary. However, in the postero-lateral part of the nasal cavity, behind the fenestra endonarina anterior (*fe.ena*), there is in the porolepiforms (fig. 19 H, 21 B) as well as in the urodeles (fig. 19 J; JARVIK, 1942, fig. 18), a distinct crest, the crista rostro-caudalis (*cr*), projecting inwards from the lateral wall of the nasal cavity. Dorsally to

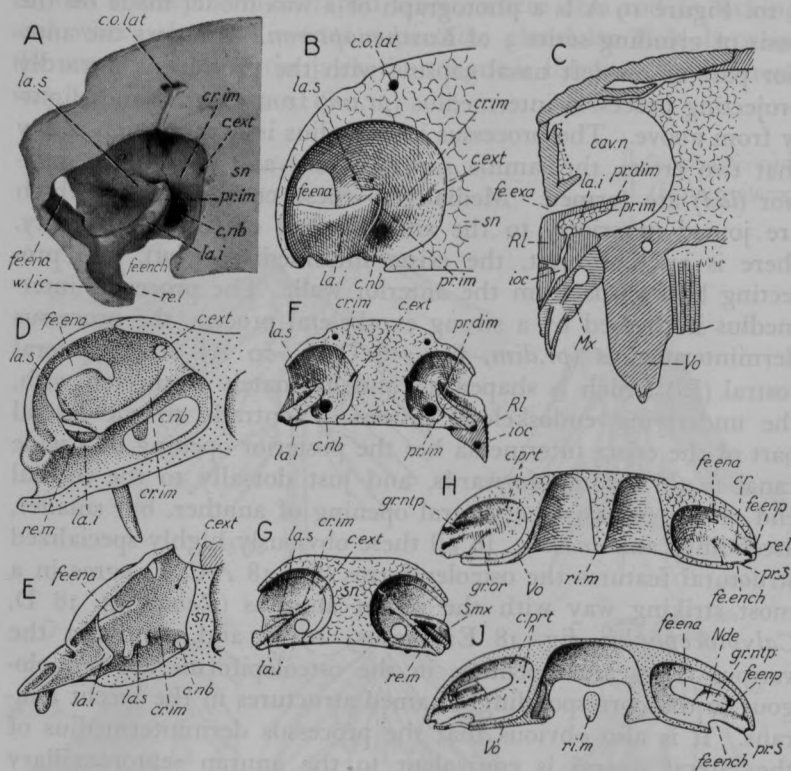


FIG. 19.

The anterior part of the snout in posterior aspects in, A,B,C,F, osteolepiforms, D,E,G, anurans, H, porolepiforms and, J, urodeles, to show some of the similarities between the osteolepiforms and the anurans and between the porolepiforms and the urodeles and the fundamental differences between the Osteolepiform-Tetrapod and the Porolepiform-Tetrapod stocks. A,B,C,F, osteolepiform, *Eusthenopteron foordi* Whiteaves. Lowermost Upper Devonian, Escuminac Bay, Canada. A, photograph of model in wax made on the basis of grinding series 1 (see Jarvik 1942, p. 426). B, restoration mainly on the basis of the wax model shown in A. C, diagrammatic transverse section made on the basis of grinding series 1. F, restoration made mainly on the basis of grinding series. The snout is cut transversely further forwards than in A and B. B,C,F, from Jarvik 1942, figs. 52 A, 71 A, 53. D, *Rana fusca* Rösel, larva. From Gaupp 1893, pl. 15:32. E, *Calyptocephalus gayi* Dum. & Bibr. From Reinbach 1939, fig. 9. F, diagram of hypothetical primitive anuran. From Jarvik 1942, fig. 71 B. H, *Porolepis spitsbergensis* Jarvik. Lower Devonian, Spitsbergen. From Jarvik 1942, figs. 39 A, 46 A. J, diagram on the basis of H, showing conditions actually found in primitive urodeles. From Jarvik 1942, fig. 46 B.

Mx, maxillary; Nde, nariodal (endoskeletal); RL, lateral rostral; Smx, septomaxillary; Vo, vomer.

cav.n, nasal cavity; c.o.lat, canal probably for cutaneous vessel; c.ext, canal or foramen for r. externus narium of n. profundus; c.nb, nasobasal canal or foramen; c.prt, canals or foramina for twigs of medial terminal profundus branch; cr, rostro-caudal crest; crim, crista intermedia; fe.ena,

that crest, which has no equivalent in the osteolepiforms or the anurans, there is a groove (*gr.ntp*) which in the urodeles conducts the anterior portion (*ntp*) of the nasolachrymal duct and in the porolepiforms the posterior external nasal tube (see No. 21, fig. 21). Below the crest there is a lateral recess (*re.l*) bounded ventrally by a postero-lateral portion of the solum nasi. Both in urodeles and porolepiforms this portion is produced backwards into a small process, Seydel's palatal process (*pr.S*), situated laterally or antero-laterally to the fenestra endochoanalis (*fe.ench*) and as evidenced by the conditions in the urodeles supporting the plica palatina. In the osteolepiforms and the anurans the conditions again are different (JARVIK, 1942, pp. 315, 441, 466, 518). In them the lateral recess of the nasal cavity is bounded by the medially curved ventral portion (*w.lic*, fig. 19 A) of the lateral nasal wall and there is no equivalent of Seydel's palatal process (¹).

21. The very great and obvious differences between the Porolepiform-Tetrapod and the Osteolepiform-Tetrapod stocks demonstrated above, refer to skeletal features, which in the grinding series, wax-models and excellently prepared specimens of porolepiforms and osteolepiforms can be studied just as well as in the recent urodeles and anurans. The data presented in the preceding paragraph thus rest on indisputable evidence, and indis-

fenestra endonarina anterior; *fe.ench*, fenestra endochoanalis; *fe.enp*, fenestra endonarina posterior; *fe.exa*, fenestra exonarina anterior; *gr.ntp*, groove for posterior external nasal tube (proximal portion of nasolachrymal duct); *gr.or*, groove forming part of orbito-rostral passage; *ioc*, infra-orbital sensory canal; *la.i*, lamina inferior; *la.s*, lamina superior; *pr.dim*, processus dermintermedius of lateral rostral (homologous to septomaxillary in anurans); *pr.im*, processus intermedius; *pr.S*, Seydel's palatal process; *re.l*, lateral recess of nasal cavity; *re.m*, recessus medius of nasal cavity; *ri.in*, internasal ridge; *sn*, septum nasi; *w.lic*, ventral medially curved part of lateral nasal wall.

1) Szarski (1962, p. 232) claims that this process may be present in the anurans, too, and that it is represented by the processus lingularis in *Liopelma* (Stephenson 1951). Szarski has apparently not observed that the true Seydel's process of the urodeles and porolepiforms is situated in, and supports, the plica palatina (Jarvik 1942, pp. 291, 301, 401-402; see also e.g. Theron 1952, figs. 6, 7), whereas the processus lingularis in *Liopelma* (Stephenson 1951, fig. 14) is found close to the nasolachrymal duct, that is, far above both the plica palatina and the sulcus maxillo-palatinus (see also *Rana*, Ecker-Wiedersheim-Gaupp 1904, fig. 145; Jarvik 1942, fig. 27 B). The processus lingularis thus has nothing to do with Seydel's palatal process, and as I explained already in 1942 (p. 513, fig. 67 B) it is clearly a vestige of the lateral wall of the nasal cavity of the osteolepiform ancestors.

putable, too, is the fact, that the canals and other passages for nerves and vessels in the porolepiforms are essentially as in the urodeles, whereas in the osteolepiforms they are as in the anurans (JARVIK, 1942, 1962).

In this connection I would like to stress the fact that the nerves and vessels in the porolepiforms and osteolepiforms, because of the high degree of ossification of the skeleton which is characteristic of the early vertebrates (see JARVIK, 1960, pp. 46, 57-61), for long stretches were enclosed in bony canals which may be easily followed in the serial sections, or ran in distinct grooves on the external faces of the skeleton. The restorations of cranial nerves in the porolepiforms and osteolepiforms and other early, well ossified, vertebrates are therefore not quite as haphazard as zoologists acquainted only with recent material may be inclined to believe.

As first recognized by COGHILL (1901, 1902) on the basis of careful comparison between *Ambystoma* and *Rana*, and later confirmed by a great number of writers (for bibliography and discussion see JARVIK, 1942, pp. 302-307, 328-333; 1962; see also Fox, 1954, 1959), there are considerable differences between the urodeles and the anurans in the innervation of the snout, and in certain respects the urodeles are unique among recent vertebrates (¹). The urodeles differ from the anurans mainly in the following respects (fig. 20) : the strong development of the r. ophthalmicus profundus, which in the snout has entirely or almost entirely substituted the r. maxillaris V; the corresponding weak development of the r. maxillaris V; the mode of branching of the r. ophthalmicus profundus; the different development of the profundus-palatine anastomoses (fig. 20 E, F; JARVIK, 1962, p. 92); the fact that a branch of the r. buccalis lateralis runs forwards ventrally to the nasal sac and medially to the choana to supply the foremost neuromasts of the infraorbital sensory line (see JARVIK, 1942, pp. 305, 344; 1962, pp. 91-92; Fox, 1954, p. 270; SCHMALHAUSEN, 1957, fig. 17).

1) According to Szarski (1962, pp. 231-232) it has been demonstrated by Schmalhausen that « the arrangement of the nerve branches in the snout, which according to Jarvik are traits common to all urodeles, in reality characterize only the Hynobiidae whereas in the Ambystomidae the nerve pattern has a type that, according to Jarvik, characterizes the Salienta ». Since the differences in the innervation of the snout between the urodeles and the anurans were first established by Coghill, after careful studies of just an ambystomid, *Ambystoma tigrinum*, and since *Salamandra*, which I used in 1942, and many other non-hynobiid urodeles have been proved to follow the typical urodele pattern by a great number of anatomists and neurologists (Fox, Francis, Herrick, Norris, and others) I prefer to rely on these scientists.

In the porolepiforms (*Porolepis*, *Glyptolepis*, JARVIK, 1942, 1962) the postnasal wall is pierced by a wide medial (*c.prm*, fig. 20 C) and some lateral canals while there are several canals or foramina piercing the roof of the nasal cavity (*c.prt*, fig. 19 H). All these canals and foramina are situated very much as the profundus foramina in urodeles. On the other hand, the grinding series of *Glyptolepis* (cf. JARVIK, 1962, p. 91) has shown that canals which could have transmitted the r. maxillaris trigemini are lacking in the postero-lateral parts of the snout. If we now put nerves into all the canals and other distinct passages found in the snout of *Porolepis* or *Glyptolepis*, taking into consideration the size and direction of the canals and grooves, it will be seen that the nerves run and branch almost exactly as those in a recent urodele like *Salamandra* (fig. 20 C, D). If we now do the same with *Eusthenopteron* we will find a most striking agreement with *Rana*, even as to details in the branching of the nerves (fig. 20 A, B). This can not be mere coincidence. The very great resemblances, too, between the porolepiforms and urodeles and between the osteolepiforms and anurans in many other respects force us to conclude that the different patterns of innervation, characteristic of the recent urodeles and anurans, were developed in their pre-Devonian porolepiform or osteolepiform ancestors.

22. As demonstrated in 1942 (pp. 467, 514-518, 537-539) the posterior external nasal tube in the osteolepiforms extended backwards to the orbit very much as does the naso-lachrymal duct in the anurans and most likely it functioned as such a duct (*dnl*, fig. 20 A, B, E, 21 A). The most anterior part of the tube was situated close to the dorsal face of the processus dermintermedius (*pr.dim*) of the lateral rostral. However, during the transformation of the latter process into the horse-shoe-shaped septomaxillary and the formation of the recessus medius in the phylogeny of the anurans, it migrated through the dermal bone, from dorsal to ventral. This migration, like so many other phyletic changes in the nasal region, is recapitulated in the ontogeny of the anurans.

In the urodeles the naso-lachrymal duct has a peculiar course, a condition which obviously has puzzled SCHMALHAUSEN (see SZARSKI, 1962, fig. 39, pp. 213-214). However, as explained in 1942 (pp. 403-411; 1962, p. 92) the course of the naso-lachrymal duct and the transformations of the postero-lateral parts of the snout in the ontogeny of the urodeles may be easily understood

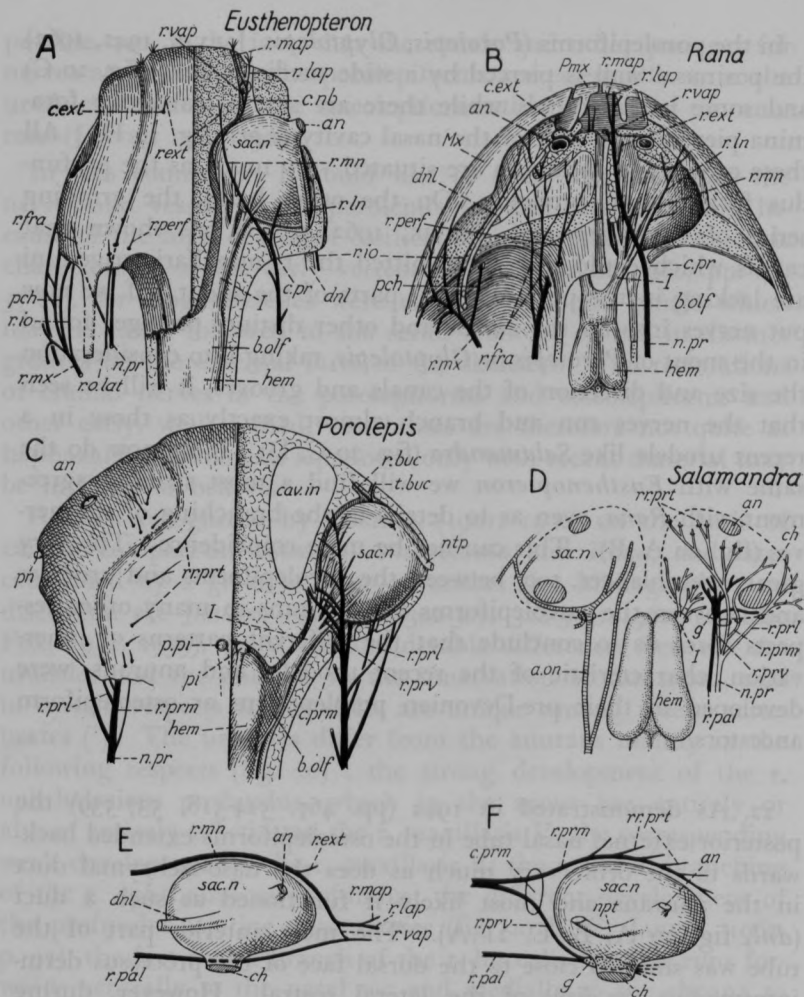


FIG. 20.

Representations to show the similarities between, A,E, the osteolepiforms and, B,E, the anurans and between, C,F, the porolepiforms and D,F, the urodeles in the innervation of the snout and the fundamental differences between the Osteolepiform-Tetrapod and the Porolepiform-Tetrapod stocks. A-D, dorsal aspects. A, osteolepiform, *Eusthenopteron foordi* Whiteaves. Lowermost Upper Devonian, Escuminac Bay, Canada. Restoration of the nasal sac, the anterior part of the brain and certain nerves in dorsal aspect. From Jarvik 1942, figs. 59-61. B, *Rana esculenta* L. From Jarvik 1942, fig. 30 (compilation after Ecker-Wiedersheim-Gaupp 1899, figs. 4, 35-37). C, porolepiform, *Porolepis* sp. Lower Devonian, Spitsbergen. From Jarvik 1942, fig. 43; modified with regard to the brain and in a few other respects according to observations on the grinding series of *Glyptolepis*. D, *Salamandra salamandra* (L). From Jarvik 1942, fig. 21. Compilation after the figures and descriptions given by Francis 1934. E,F, diagrams of the

on the basis of the conditions in the porolepiforms. As is clearly seen in hynobiids (fig. 21 F) the anterior part of the naso-lachrymal duct (*ntp*) runs from the area of the external nostril (*an*) in a postero-ventro-lateral direction, exactly as did the posterior external nasal tube in the porolepiforms (fig. 21 B-E). Moreover, this portion of the naso-lachrymal duct in the hynobiids is grasped from the outside by a sometimes gutter-shaped bone (*Nd*), the nariodal (JARVIK, 1942, « septomaxillary »), in exactly the same way as a gutter-shaped portion (*Nde*, figs. 19 J, 21 B) of the lateral nasal wall grasps the posterior nasal tube in the porolepids. If the so-called septomaxillary (nariodal) of the urodeles is an endoskeletal ossification, as was the current opinion in 1942, it is evident that it must be derived from that portion (*Nde*, fig. 21 B) of the lateral wall of the nasal capsule in the porolepiforms. But if, on the other hand, the so-called septomaxillary of the urodeles is a dermal bone, as is claimed by SCHMALHAUSEN (1958 a; see also SZARSKI, 1962, p. 231) and others it clearly corresponds to the small dermal bone, the dermonariodal (*Ndx*, fig. 21 E), situated outside that portion of the lateral nasal wall. In *Porolepis* and *Glyptolepis* this dermal bone has fused with the adjoining dermal bones of the fronto-ethmoidal

nasal sac and certain nerves in lateral aspect to show the differences in the development of the profundus-palatine anastomosis. *E*, the osteolepiform-anuran condition; *F*, the porolepiform-urodele condition. Compilation after the figures A-D and descriptions and figures given by Ecker-Wiedersheim-Gaupp 1899 and Francis 1934.

Mx, maxillary; *Pmx*, premaxillary.

an, anterior external nostril; *a.on*, arteria orbitonasalis; *b.olf*, bulbus olfactorius; *cav.in*, internasal cavity; *c.ext*, canal or foramen for r. externus narium of n. profundus; *ch*, choana; *c.nb*, nasobasal canal or foramen; *c.pr*, canal for n. profundus; *c.prm*, canal for medial terminal branch of n. profundus; *dnl*, nasolachrymal duct; *g*, ganglion; *hem*, hemisphere of fore-brain; *n.pr*, nervus profundus; *ntp*, posterior external nasal tube or proximal part of nasolachrymal duct; *pch*, postchoanal anastomosis; *pi*, pineal organ; *pn*, posterior external nostril; *p.pi*, parapineal (parietal) organ; *r.buc*, ramus buccalis lateralis; *r.ext*, ramus externus narium of n. profundus; *r.fra*, rami frontales anteriores of n. profundus; *r.io*, ramus infraorbitalis; *r.lap*, lateral terminal branch of r. medialis narium; *r.ln*, ramus lateralis narium of n. profundus; *r.map*, medial terminal branch of r. medialis narium; *r.mn*, ramus medialis narium of n. profundus; *r.mx*, ramus maxillaris trigemini (visceral trunk of n. trigeminus I); *r.o.lat*, ramus ophthalmicus lateralis; *r.pal*, ramus palatinus VII; *r.perf*, ramus frontalis perforans of n. profundus; *r.prl*, *r.prm*, lateral and medial terminal branches of n. profundus; *r.prv*, ventral terminal branch of n. profundus anastomosing with r. palatinus; *rr.prt*, terminal twigs of medial terminal profundus branch; *r.vap*, ventral terminal branch of r. medialis narium anastomosing with r. palatinus; *sac.n*, nasal sac; *t.buc*, twig of r. buccalis supplying neuromast of infraorbital sensory line; *I*, nervus olfactorius.

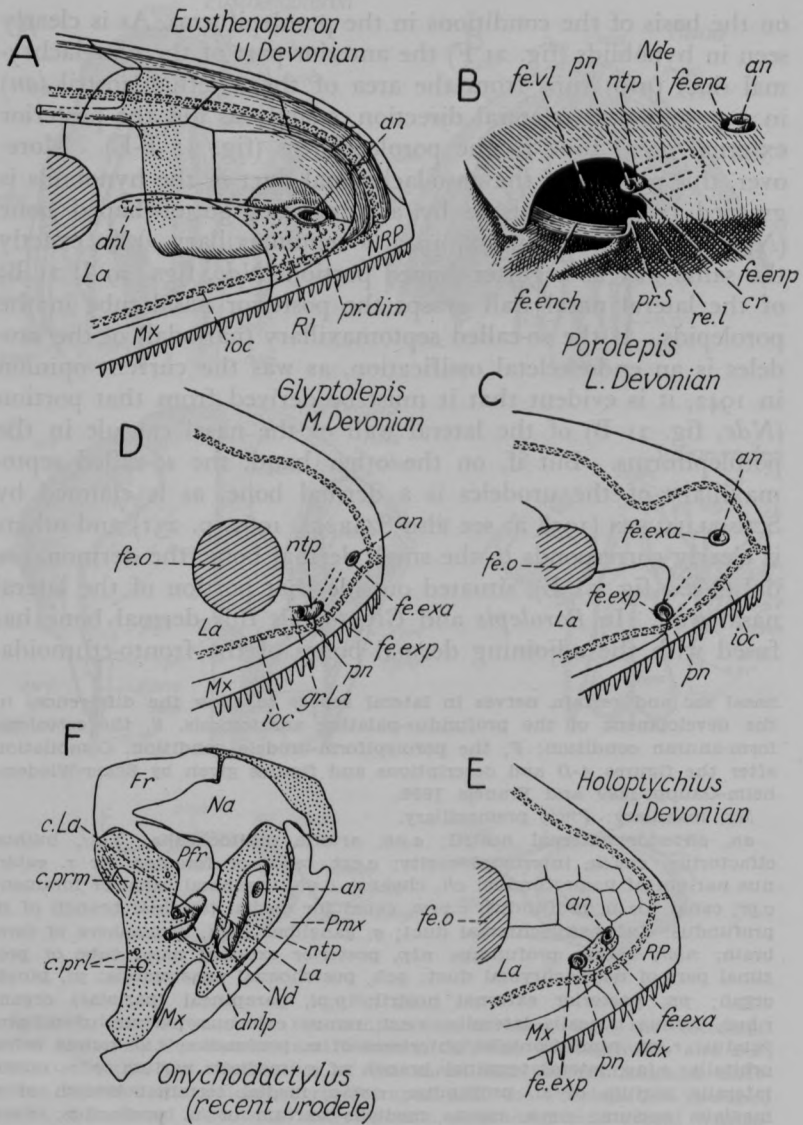


FIG. 21.

Representations to illustrate the similarities between, B-E, the porolepiforms and, F, the urodeles in the development of the nasolachrymal duct and the nariodal («septomaxillary») and the differences in these respects between the Porolepiform-Tetrapod and, A, the Osteolepiform-Tetrapod stocks. A, *Eusthenopteron foordi* Whiteaves. Lowermost Upper Devonian, Escuminac Bay, Canada. The snout in lateral aspect to show the position of the lateral rostral in relation to the neural endocranium. Modified from

shield, whereas in *Holoptychius* it is independent and occupies the large opening in the exoskeleton which I described (1942) as the fenestra exonarina communis. Whichever of these alternatives is the correct one is of less importance. Of far greater importance is the fact that the nariodal of the urodeles differs from the true septomaxillary of the anurans both as to position and origin and so cannot possibly be homologous to that bone. The view held by SCHMALHAUSEN (1957, p. 513) and SZARSKI (1962, p. 231) that it corresponds to the lateral rostral of the osteolepiforms is incorrect. As a matter of fact, the lateral rostral of the porolepiforms, in contrast to the osteolepiforms, lacks the processus dermintermedius. Moreover it has fused with the premaxillary to form a compound rostro-premaxillary (*RP*, fig. 21 E).

As demonstrated in 1942 (p. 407) the posterior external nasal tube in *Porolepis* (fig. 21 B, C) and *Holoptychius* (fig. 21 E) opened outwards through a posterior nostril (*pn*) situated in the fenestra exonarina posterior (*fe.exp*). This opening in the exoskeleton is situated in the postero-ventro-lateral part of the snout, close above the infraorbital sensory canal (*ioc*), and is bounded, posteriorly, by a notch in the lachrymal (*La*) and, anteriorly, by

Jarvik 1942, fig. 68 A, B, C, *Porolepis brevis* Jarvik. Lower Devonian, Spitsbergen. B, right ventro-lateral corner of the ethmoidal region in postero-ventro-lateral aspect. C, the snout in lateral aspect. Modified from Jarvik 1942, figs. 40 A, 41. D, *Glyptolepis* sp. Middle Devonian, Canning Land, East Greenland. The snout in lateral aspect. Original. E, *Holoptychius* sp. Uppermost Upper Devonian, East Greenland. The dermonariodal after specimen from Escuminac Bay, Canada. The snout in lateral aspect. Original. F, *Onychodactylus japonicus* Houtt. The snout in dorso-lateral aspect. From Chung and Yatabe 1931, pl. 8:1.

Fr, frontal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *Nd*, nariodal; *Nde*, portion of lateral nasal wall corresponding to the nariodal of urodeles if this is an endoskeletal bone. *Ndx*, dermonariodal; *NRP*, naso-rostro-premaxillary; *Pfr*, prefrontal; *Pmx*, premaxillary; *Rl*, lateral rostral; *RP*, rostro-premaxillary (including the equivalent of the lateral rostral of the osteolepiforms).

an, anterior external nostril; *c.La*, canal in lachrymal for nasolachrymal duct; *c.prl.*, *c.prm*, lateral and medial profundus foramina; *cr*, rostro-caudal crest; *dnl*, ductus nasolachrymalis; *dnlp*, posterior portion of nasolachrymal duct; *fe.ena*, fenestra endonarina anterior; *fe.ench*, fenestra endochoanalis; *fe.enp*, fenestra endonarina posterior; *fe.exa*, fenestra exonarina anterior; *fe.exp*, fenestra exonarina posterior; *fe.o*, orbital fenestra; *fe.lv*, fenestra ventro-lateralis; *gr.La*, groove for posterior external nasal tube; *ioc*, infraorbital sensory canal; *ntp*, posterior external nasal tube in porolepiforms, anterior portion of nasolachrymal duct in urodeles; *pn*, posterior external nostril; *pr.dim*, processus dermintermedius of lateral rostral (homologous to septomaxillary in anurans and amniotes); *pr.S*, Seydel's palatal process; *re.l*, lateral recess of nasal cavity.

a corresponding notch in the fronto-ethmoidal shield, or, more precisely, in the posterior margin of the dermonariodal (*Ndx*). No doubt the posterior nasal tube (*ntp*) in the porolepiforms is homologous to the nasolachrymal duct in the urodeles. If we now imagine that this tube was produced backwards towards the eye during its transformation into a functioning nasolachrymal duct, then it is readily seen that it must take a sharp upward bend at the fenestra exonarina posterior in order to reach the eye, and that it is very likely that it will cause a groove on the outside of the lachrymal running in a postero-dorsal direction from the notch in the anterior end of the bone. This groove, the existence of which I postulated in 1942 (p. 408), has now been found in the grinding series of *Glyptolepis* (*gr.La*, fig. 21 D), and it is obvious that the posterior nasal tube in this form made a bend in the fenestra endonarina posterior and had begun to grow upwards towards the eye. With regard to these conditions it is of a very great interest to find that the nasolachrymal duct in primitive urodeles, after the passage through the gutter or canal formed by the nariodal, that is in the same place as in the porolepiforms, actually makes such an abrupt upward bend towards the eye (fig. 21 F; JARVIK, 1942, p. 406) and that in larval stages it runs in a groove on the outside of the lachrymal, a groove which later in ontogeny is overbridged and converted into a canal (*c.La*).

The peculiar fact that the nasolachrymal duct in primitive urodeles makes a sharp upward bend and runs in a groove on the outside of the lachrymal is thus in full accordance with, and strongly confirms, the view that the urodeles are descendants of the porolepiforms. This was explained in my paper on the snout (1942, pp. 403-412) in which also other remarkable similarities between the porolepiforms and primitive urodeles or urodele larvae in the postero-ventro-lateral parts of the snout were demonstrated.

In this connection it may be mentioned that there is never a communication between the nasal tubes and the infraorbital sensory canal of the kind postulated by SCHMALHAUSEN (1958 b, pp. 1717-1718, fig. 5; SZARSKI, 1962, pp. 212-215, fig. 39), either in crossopterygians or any other fishes (as regards the fortuitous connection in *Amia*, SCHMALHAUSEN, 1958 b, fig. 3; see ALLIS, 1889, p. 529, figs. 4, 6, 8, 12-14), and knowing the conditions in the porolepiforms it is quite obvious that the proximal portion of the nasolachrymal duct in the urodeles cannot be a derivative of such a communication. As we have seen this portion (*ntp*) corres-

ponds to the posterior nasal tube of the porolepiforms. It may also be pointed out that the external nostrils in crossopterygians (figs. 19 C, 21 A-E, 22 A) were always situated well above the margin of the upper jaw formed by the maxillary and the premaxillary, and above the infra-orbital sensory canal which always passes forwards to the snout without interruption. SCHMALHAUSEN'S contention (1957, p. 112, figs. 13, 14) that there is an interruption of the canal below the anterior external nostril in *Osteolepis* and *Ichthyostega* is founded on earlier, incomplete restorations (see fig. 22 A, B and JARVIK, 1942, p. 334; 1948, p. 122, fig. 32; 1952, p. 80, foot-note 1, figs. 35, 36).

23. In the *Tetrapoda*, too, the various groups are generally highly specialized at their first appearance in the geological record. As in fishes, too, several groups (ichthyosaurians and chelonians, for instance) have changed very little during their known geological history. The earliest known tetrapods, the *Ichthyostegalia*, which are known only from the late Upper Devonian deposits of East Greenland are also specialized in many respects. Of interest is the fact that they include two distinct groups, the ichthyostegids and the acanthostegids, differing considerably from each other in the development of the posterior part of the skull (JARVIK, 1952, 1955 b, 1960).

The ichthyostegids, which are more completely known than the acanthostegids, agree closely in several respects with their osteolepiform ancestors and they have retained several piscine features (true median fins supported by endoskeletal radials and dermal fin rays, subopercular, preopercular, lateral rostral, etc.) not encountered in any later tetrapods. However, in several respects they have become more specialized than other tetrapods and no doubt they represent an early side-branch of the Osteolepiform-Tetrapod stock. The humerus is a most complicated structure representing a type of its own (see JARVIK, 1955 b, p. 61, fig. 1); the « tabular » is provided with peculiar strong, descending laminae unparallelled in other tetrapods (JARVIK, 1952, pp. 78-80); the entopterygoid (*Enpt*, fig. 22 D) has fused with that of the opposite of the skull, which has caused a reduction of the anterior part of the parasphenoid bone (see JARVIK, 1942, pp. 629-630). Moreover, the (anterior) external nostril (*fe.exa*, fig. 22 B, D) has migrated ventrally where it has caused a distinct inward bend of the infraorbital sensory canal exactly as in those sharks in which a similar secondary migration of the nostrils towards the mouth opening has occurred, and where it can be followed in the embryological development (see JARVIK, 1942, pp. 279-280).

However, the canal has not become interrupted (¹) as it has in the dipnoans in which, as is well known (see JARVIK, 1942, pp. 278-279), both nostrils have secondarily migrated into the mouth cavity. Moreover, the anterior part of the maxillary bone in the ichthyostegids (and the acanthostegids) has become bent inwards in a manner unparallelled in other tetrapods and there have been other secondary modifications as well.

Another interesting specialization found in the ichthyostegids (fig. 22 D) is that the prominent tusks of the vomer (*Vo*), the dermopalatine (*Dpl*), and the ectopterygoid of the osteolepiform ancestors (fig. 22 C) have disappeared, like the tusks of the coronoids, and that the strongest teeth are carried by the premaxillary and the maxillary, and by the dentary. This peculiar *change in the dentition from the inner to the outer dental arcade*, which hitherto has attracted but little attention in the literature (see JARVIK, 1942, p. 638), has occurred in almost all tetrapods (also in urodeles) and in most lines of evolution it leads ultimately to a complete loss of the dentition of the inner arcade. A remarkable fact, however, is that the tusks have been retained in the inner arcade of the upper jaw in *Mastodonsaurus* (fig. 22 E) and many other Triassic stegocephalians. Besides, in many other respects (the intervomerine canal, *iv.c.*, the intervomerine pit, *iv.p.*, etc.; see JARVIK, 1942, pp. 632-638, 1955 a, pp. 149-150), these late stegocephalians agree more closely with an osteolepiform like *Eusthenopteron* than with the ichthyostegids (fig. 22 C-E) or any other well-known Paleozoic labyrinthodont stegocephalians. These conditions show that the said Triassic labyrinthodonts cannot possibly be descendants of any of the well-known Paleozoic forms and that *current views on the classification and phylogeny of the Labyrinthodontia* (see e.g. ROMER, 1947, fig. 48) *are probably incorrect in fundamental respects.*

24. The origin of the tetrapod limb has been discussed by a great number of scientists since the days of Gegenbaur, but up to now no satisfactory solution has been presented. The discovery and studies of the ichthyostegids have opened up new ave-

1) Misled by earlier incomplete restorations of *Osteolepis* and *Ichthyostega* and on the basis of an alleged communication between sensory canals and nasal tubes (see pp. 64-65) and speculations about function (cf. p. 41) Schmalhausen (see Szarski 1962, pp. 212-215) has developed a theory which implies, inter alia, that the ventral position of the anterior nostril in the ichthyostegids is primitive and that the ichthyostegids in this respect are more primitive not only than all other tetrapods but also than their osteolepiform ancestors.

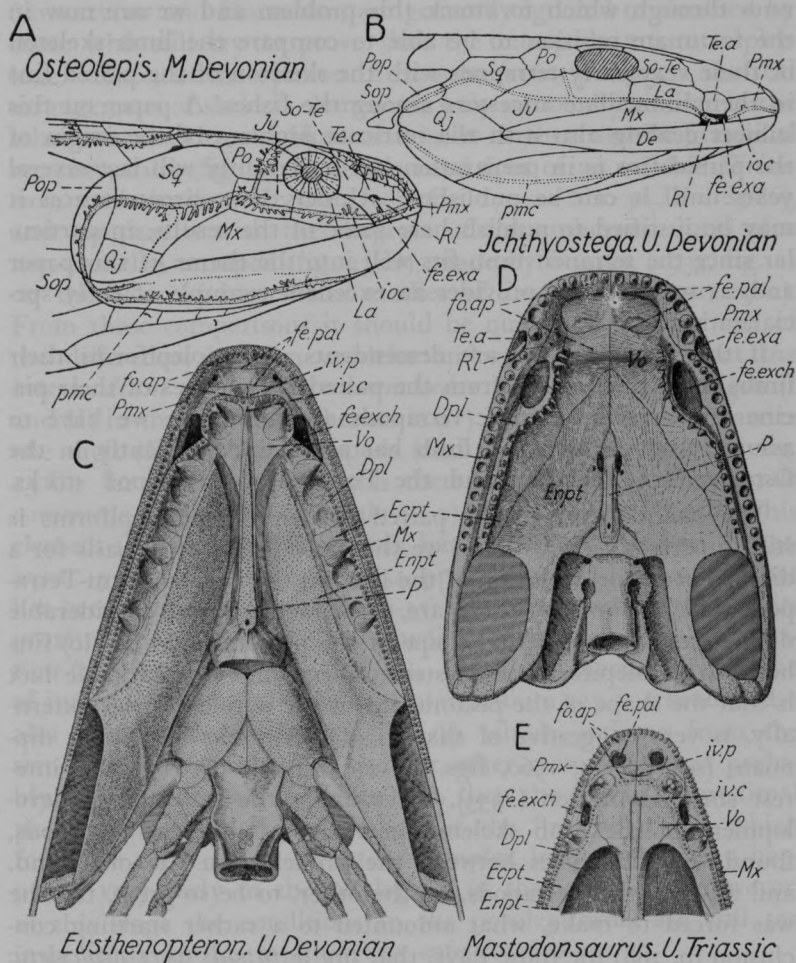


FIG. 22.

A, B, the skull in lateral aspect of, A, osteolepiform and, B, ichthyostegid. A, *Osteolepis macrolepidotus* Ag. Middle Devonian, Scotland. From Jarvik 1948, fig. 32 A. B, *Ichthyostega* sp. Uppermost Devonian, East Greenland. From Jarvik 1952, fig. 35 A. C-E, ventral views of the palate of, C, osteolepiform (*Eusthenopteron*), D, Devonian stegocephalian (*Ichthyostega* sp.) and E, Triassic stegocephalian (*Mastodonsaurus*). From Jarvik 1955 a, fig. 8.

De, dentary; Dpl, dermopalatine; Ecpt, ectopterygoid; Enpt, entopterygoid; Ju, jugal; La, lachrymal; Mx, maxillary; P, parasphenoid; Pmx, premaxillary; Po, postorbital; Pop, preopercular; Qj, quadratojugal; Ri, lateral rostral; Sop, subopercular; So-Te, supraorbito-tectal; Sq, squamosal; Te.a, anterior tectal; Vo, vomer.

fe.exa, fenestra exonarina anterior; fe.exch, fenestra exochoanalis; fe.pal, anterior palatal fenestra; fo.ap, fossa apicalis; ioc, infraorbital sensory canal; iv.c, iv.p, intervomerine canal and intervomerine pit for efferent ducts of intermaxillary gland; pmc, preoperculo-mandibular sensory canal.

nues through which to attack this problem and we are now in the fortunate position to be able to compare the limb skeleton of these very early tetrapods with the skeleton of the paired fins in their immediate ancestors among the fishes. A paper on this subject dealing also with the intricate problem of the origin of the paired fins is in preparation but it certainly will last several years until it can be published. Under these circumstances it may be justified to publish here some of the results, in particular since the tetrapod limb fits well into the theme of this paper and, as we shall see, provides an excellent example of early specialization.

If the ichthyostegids are descendants of osteolepiforms their limbs must have arisen from the paired appendages of their piscine ancestors, but if the tetrapods are diphyletic we have to assume that the tetrapod limb has arisen independently in the Osteolepiform-Tetrapod and the Porolepiform-Tetrapod stocks.

The endoskeleton of the paired fins in the porolepiforms is still imperfectly known, and we therefore lack a solid basis for a discussion of the evolution of the limb in the Porolepiform-Tetrapod stock. However, there are, as is well known, considerable differences in the external shape of the pectoral (and pelvic) fins between porolepiforms and osteolepiforms and a remarkable fact is that the shape of the pectoral fin of the porolepiforms, externally, is very suggestive of that in *Neoceratodus* and other dipnoans (see JARVIK, 1960, figs. 9, 12). This is of particular interest since Holmgren (1933), in studying the ontogenetic development of the limb skeleton in various fishes and tetrapods, found the differences between the urodeles, on the one hand, and all the other tetrapods, on the other, to be so great, that he was forced to make, what amounted to a rather startling conclusion (p. 288) for those days, that *the tetrapods were diphyletic* and that « *the urodeles must be considered to have originated from fish ancestors, (crossopterygian or) dipnoan, with a short biserially arranged archipterygium* ».

However, these ideas were not entirely new. As a matter of fact HOLMGREN arrived at fundamentally the same conclusions as SEWERTZOFF, who already in 1908 (p. 363) asked the question : « *Wir müssten also annehmen, dass die Extremitäten der Reptilien und der Anura einerseits, die der Urodela anderseits phylogenetisch vollkommen unabhängig von einander entwickelt haben?* ». The differences in the ontogenetic development of the limb between the urodeles and the other tetrapods, observed by

SEWERTZOFF and HOLMGREN, are generally ignored or doubted by those who still try to prove that the tetrapods are monophyletic. Since, in the opinion of SZARSKI (1962, p. 230), « the real arrangement of skeletal elements is only remotely similar to the schematic drawings of HOLMGREN », let us then use the graphical reconstruction (fig. 23 B) of the hind foot of an urodele (*Triturus*), made by SEWERTZOFF (1908, fig. 17; see also pl. V : 83-86), and compare it with the diagram of the embryonic limb of a non-urodelan tetrapod (fig. 23 D), made by STEINER (1935, fig. 2) on the basis of his careful studies of *Lacerta* (STEINER, 1922). From these comparisons it should be quite evident that one of the differences between urodeles and non-urodeles is that the *intermedium ray* (*Im*) is « branched » and carries two digits (I and II) in the urodeles, whereas it (*Ir*) is *unbranched* and carries one digit (*I*) in other tetrapods (and in the osteolepiforms, fig. 23 C). In accordance with this there is always a so-called *basale commune* (carpale 1+2, tarsale 1+2) in the urodelan limb. This element (*b.c.*, fig. 23 B) certainly has a double origin (see HOLMGREN, 1933, p. 215; FRANCIS, 1934, pp. 42-43), and in view of what has been set forth above (pp. 34-35) it can be assumed that, in its proximal parts, too, the intermedium ray is of double formation (cf. HOLMGREN, 1939, fig. 19). In this connection it may be of interest to point out that the intermedium ray is « branched » also in *Sauripterus* (*Im*, fig. 23 A), which, judging from the structure of the cleithrum and for other reasons is most probably a porolepiform. If this is true, then the fusion of proximal parts of the two original radials of the fin (see p. 76), which form the digits I and II, into a complex intermedium ray happened very early in the phylogeny of the urodeles. However, at this stage the conditions in the porolepiforms are still too imperfectly known to allow any safe conclusions.

25. We now turn to the Osteolepiform-Tetrapod stock, and will, in the first place, briefly consider the pelvic girdle. Like the pectoral fin, the pelvic fin in *Eusthenopteron* (fig. 25 A, B) and other osteolepiforms (JARVIK, 1948, pp. 19, 112-113, figs 1, 2, 3 G, J), is so situated that its « preaxial » (tibular) margin is ventro-lateral in position. The restoration by GREGORY and RAVEN (1941, fig. 33 A) is incorrect in this respect, and so, too, is the statement by SZARSKI (1962, p. 233) that the pelvis in tetrapods « is always formed by three bones on each side of the body ». In *Ichthyostega* (fig. 24 C, JARVIK, 1952, p. 12, fig. 5;

1955 b, p. 61, as regards the pelvis in the urodeles, see WIEDERSHEIM, 1892; NAUCK, 1938), there is a continuous ventral pubioischialic plate, on the inner side separated from the iliac portion by an indistinct line which possibly represents a suture. Seen in external view the pelvis in *Ichthyostega* appears as a single ossification, as it is in *Eusthenopteron* (fig. 24 A, B), and both in the ichthyostegids and in *Eusthenopteron* the bone is a triradiate structure with a well developed acetabulum (*acet*). Unfortunately the exact position of the bone is unknown in *Eusthenop-*

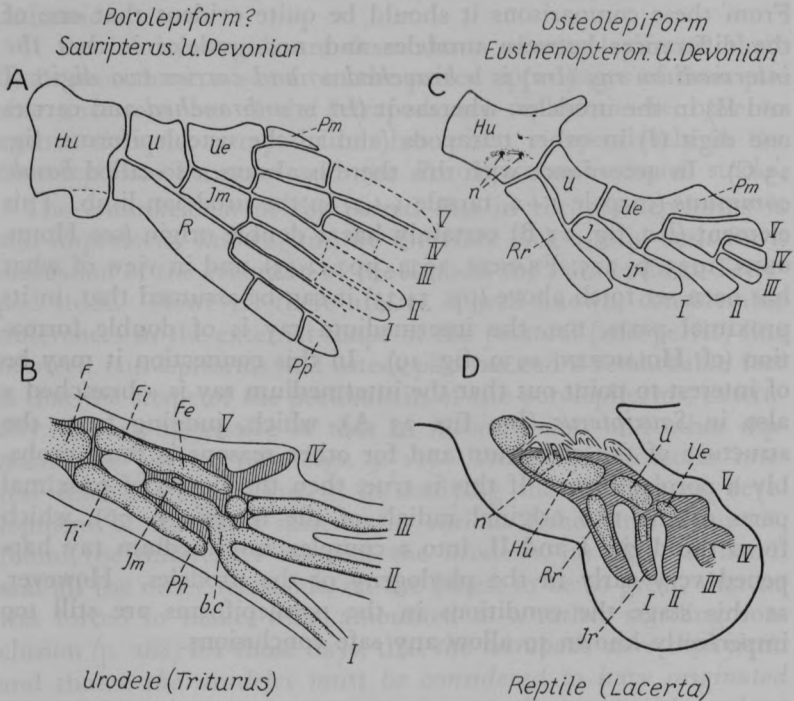


FIG. 23.

Diagrammatic representations of the left hand or, B, foot to demonstrate the differences in the basic pattern between, A, B, the Porolepiform-Tetrapod and, C, D, the Osteolepiform-Tetrapod stocks. A, probable porolepiform, *Sauripterus taylori* Hall. Upper Devonian, U.S.A. After plaster cast and Gregory and Raven 1941, fig. 19. B, *Triturus cristatus* Laurenti. From Severtzoff 1908, fig. 17. C, osteolepiform, *Eusthenopteron foordi* Whiteaves. After the specimen shown in fig. 25 A-C. D, *Lacerta*. Embryo. From Steiner 1935, fig. 2.

F, femur; Fe, fibulare; Fi, fibula; Hu, humerus; I, intermedium; Im, complex intermedium; Ir, intermedium ray; Ph, prehallux; Pm, postminimus; Pp, prepollex; R, radius; Rr, radius ray; Ti, tibia; U, ulna; Ue, ulnare.

b.c, basale commune; n, nerves or foramina for ditto; I, II, III, IV, V, digits I-V.

teron but irrespective of whether it was situated as shown in figure 24 A or had the position (fig. 24 B) suggested by GREGORY and RAVEN (1941, figs. 10, 28 A), comparison with the ichthyostegids is still easy. We have only to imagine that during the transition from fish to tetrapod the bone had developed progressively in a ventral direction to meet its fellow of the other side in a median symphysis, and that the iliac portion (*p.il*) has grown a little upwards to gain contact with a sacral rib. On the presumption that the bone was situated as in figure 24 A the posterior process (*pr.il*, fig. 24 C) of the iliac portion must be a secondary formation. That this is so is supported by the conditions in ichthyostegids which show that this process is probably form-

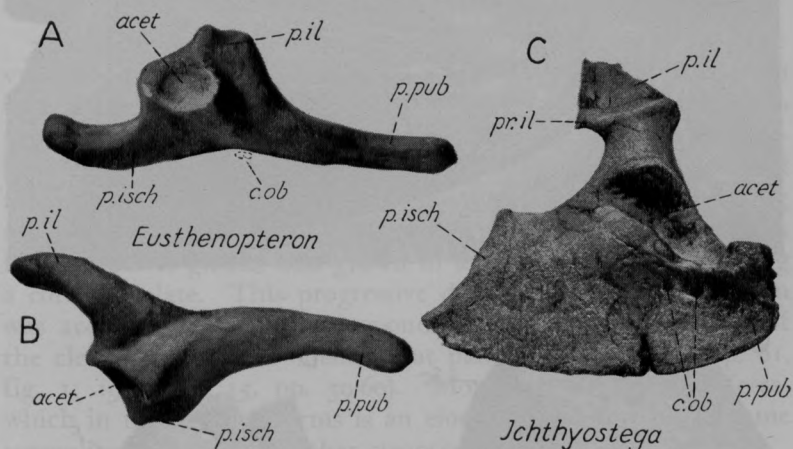
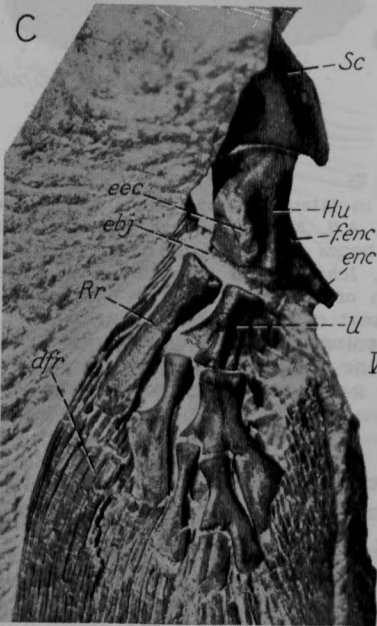


FIG. 24.

The pelvic bone of the right side in lateral aspect. A,B, osteolepiform fish and C, Devonian stegocephalian. A,B, *Eusthenopteron foordi*. Photograph of model of one of the pelvic bones of the specimen shown in fig. 25 A in two alternative positions. C, *Ichthyostega* sp. Uppermost Upper Devonian, East Greenland. Photograph of specimen No. A.93 belonging to the University of Copenhagen. Main part of iliac process missing.

acet, acetabulum; *c.ob*, external openings of branching obturator canal and presumed position of corresponding passage in *Eusthenopteron*; *p.il*, iliac portion; *p.isch*, ischiadic portion; *p.pub*, pubic portion; *pr.il*, posterior process of iliac portion.

ed by a postsacral rib which secondarily became incorporated into the pelvic bone (JARVIK, 1952, p. 14). In support of the alternative, illustrated in fig. 24 A, it may also be mentioned that in *Eusthenopteron* a groove leads downwards along the inner side of the pelvic bone to the notch in the ventro-medial margin of the bone where the presumed pubic (*p.pub*) and ischiadic (*p.isch*)



Eusthenopteron. U. Devonian

Ichthyostega. U. Devonian

portions meet. This groove has about the same course and position as the obturator canals in *Ichthyostega*, which run from the inner side of the bone, in a ventral direction, to open on the external side, either separately (*c.ob*, fig. 24 C) or in a common opening. The ventral notch in *Eusthenopteron* thus probably marks the position of the external opening of the future obturator canal (*c.ob*, fig. 24 A). The subdivision of the pelvic bone into three bones meeting in the acetabulum, which is characteristic of the post-Devonian representatives of the Osteolepiform-Tetrapod stock (see e.g. GREGORY and RAVEN, 1941, pp. 335-336, fig. 32; ROMER, 1962 b, figs. 126 A-C, 127, 128), should be regarded as a secondary condition.

26. The endoskeletal shoulder girdle of the ichthyostegids (JARVIK, 1955 b, p. 61, fig. 1) resembles and is easily derivable from that of the osteolepiforms (*Sc*, fig. 25 C). At the same time it is very suggestive of that in other early tetrapods. As in the osteolepiforms the scapular blade is lacking while the dorsal part of the cleithrum is well developed. What mainly happened during the transition from fish to tetrapod is that the shoulder girdle, like the pelvic girdle, had grown in a ventral direction forming a coracoid plate. This progressive development of the skeleton was accompanied by a corresponding reduction of the part of the cleithrum situated outside that plate (JARVIK, 1955 b, p. 61, fig. 1; 1960, fig. 15, pp. 59-60). Moreover, the glenoid fossa, which in the osteolepiforms is an elongated shallow pit, became screwshaped, as it is in other stegocephalians.

FIG. 25.

A-C, *Eusthenopteron foordi* Whiteaves. Lowermost Upper Devonian, Escuminac Bay, Canada. Specimen No. P.222 belonging to the Paleozoological Dept., Swedish Museum Nat. Hist. A, photograph of specimen before preparation in lateral aspect. Same specimen as figured by Jarvik 1948, fig. 2, 1955a, fig. 2, 1960, fig. 12 A. B, photograph to show the left pectoral fin in natural position. The fin scales of the lobate part removed. Lateral view. C, the pectoral fin and part of the endoskeletal shoulder girdle in external view. The same fin as figured by Holmgren 1933, fig. 18. D, *Ichthyostega* sp. Ventral side of the left hind limb. Uppermost Upper Devonian, East Greenland. Specimen No. A.109, belonging to the University of Copenhagen. Same specimen as figured by Jarvik 1952, pl. 2, 1955b, fig. 8.

Clm, cleithrum; *F*, femur; *Fe*, fibulare; *Fi*, fibula; *Hu*, humerus; *I*, intermedium; *Rr*, radius ray; *Sc*, endoskeletal shoulder girdle; *Ti*, tibia; *U*, ulna. *b.sc*, lateral basal scute of fin; *dfr*, dermal fin rays (lepidotrichia); *ebj*, elbow joint; *eec*, ectepicondylar process; *enc*, entepicondylar process; *f.enc*, entepicondylar foramen; *pf*, pectoral fin; *pvf*, pelvic fin; *I, V*, digits I and V.

27. As pointed out above the humerus of the ichthyostegids is a complicated structure and although it is of the same general type as in other early tetrapods it is not well suited for comparative purposes. Let us rather turn to the well-known humerus of *Eryops* (fig. 26 B; see also MINER, 1925) and compare it with the proximal element (*Hu*) of the pectoral fin in *Eusthenopteron*. As in *Eryops* the humerus in *Eusthenopteron* (*Hu*, figs. 23 C, 25 B, C, 26 A, D, 27 A) is a short massive bone, although more robust and less delicately modelled than in that form. The two extremities of the bone are flattened and set at angles but the « twisting » is less developed than in *Eryops*. The proximal articular area is oval-shaped and, as in *Eryops* (and *Ichthyostega*), broadest in its dorso-medial part. As in stegocephalians (see MINER, 1925, pp. 165-167), the shoulder joint was so constructed that it allowed the head of the humerus to slide in dorso-medial and ventro-lateral directions in the glenoid fossa, but apparently no or but little rotation of the bone took place on its long axis. At the distal end of the bone in *Eusthenopteron* there is a strong medial process (*enc*) which is very suggestive of, and no doubt homologous to, the *entepicondylar process* in *Eryops* and other tetrapods, and a lateral process which obviously includes the homologues of the *ectepicondylar* (*eec*) and *supinator* (*pr.sup*) processes in *Eryops*. A remarkable fact is that the base of the entepicondylar process is pierced by a canal (*f.enc*) obviously corresponding to the *entepicondylar foramen* in certain stegocephalians and reptiles (see e.g. ROMER, 1947, p. 78). Below the ectepicondylar process in *Eusthenopteron* and *Eryops*, there is a well developed rounded *radial condylus* (*c.R*). The articular area for the ulna (*art. U*) both in the fish and in the tetrapod is found at the distal margin of the bone, between the ectepicondylar and entepicondylar processes. Proximally to the entepicondylar process, on the ventro-medial side of the bone (not shown in the figures), there is an oblique crest running towards the narrow ventro-lateral end of the proximal articular area. This crest, which is notched and pierced by canals for nerves and vessels running to the flexor (ventro-medial) side of the fin, obviously corresponds to the so-called *deltoid crest* of *Eryops*. The nerves and vessels to the extensor side of the fin pass through similar notches and canals (*n*) in the ectepicondylar process. The position and course of these notches and canals demonstrate that the nerve and vascular supply of the pectoral fin in *Eusthenopteron* was in all essentials similar to that in the primitive tetrapod limb (see SEWERT-

ZOFF, 1908) and the presence of the various processes indicates that this was true of the musculature as well (cf. MINER, 1925).

The close resemblances between the proximal element of the pectoral fin in *Eusthenopteron* and the humerus in primitive tetrapods shows that this element was already a typical tetrapod

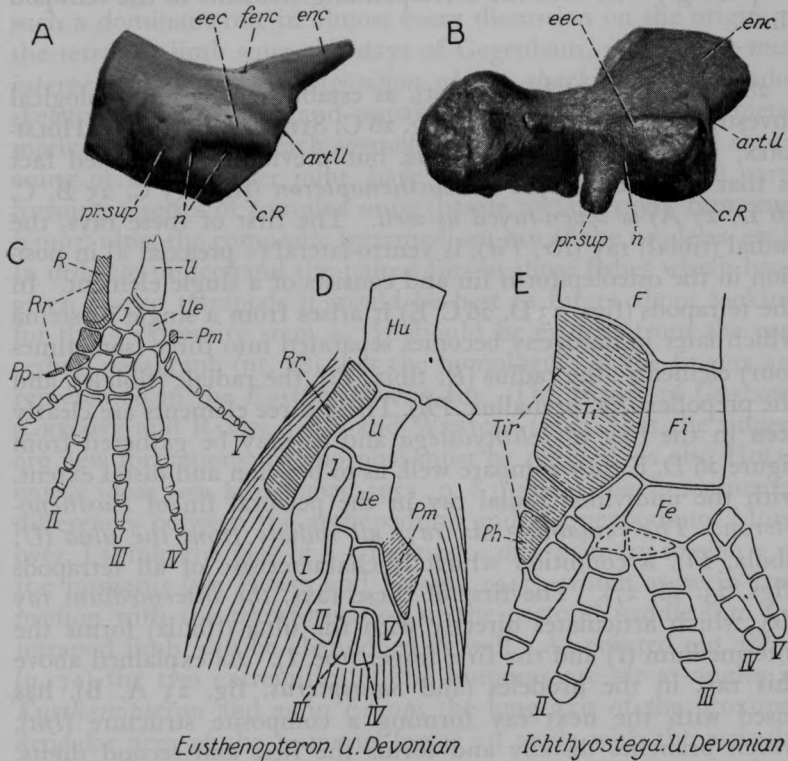


FIG. 26.

A, B, the humerus of osteolepiform fish and early tetrapod in lateral aspects. A, *Eusthenopteron joordi* Whiteaves. Photograph of model after the specimen shown in fig. 25 A-C. B, *Eryops megacephalus* Cope. Lower Permian, Texas, U.S.A. Photograph of model in plaster in the Swedish Mus. of Nat. Hist. C, diagram of the primitive tetrapod hand. From Steiner 1922, fig. 13. D, E, diagrammatic representations of the pectoral fin of a Devonian osteolepiform fish (*Eusthenopteron*) and the hind limb of a Devonian tetrapod (*Ichthyostega*). Original. Mainly after the specimens shown in fig. 25 C-D.

F, femur; Fe, fibulare; Fi, fibula; Hu, humerus; I, intermedium, Ph, prehallux; Pm, postminimus; Pp, prepollex; R, radius; Rr, radius ray; Ti, tibia; Tir, tibial ray; U, ulna; Ue, ulnare.

art.U, articulation area for ulna; *c.R*, radial condylus; *eec*, ectepicondylar process; *enc*, entepicondylar process; *f.enc*, entepicondylar foramen; *n*, passages for nerves and vessels; *pr.sup*, supinator process; I, II, III, IV, V, digits I-V.

humerus. The latter has thus arisen already in the fish stage, within the pectoral fin of the osteolepiform ancestors of the tetrapods, and obviously we are concerned here with a most remarkable case of early specialization. As we shall see the distal endoskeletal elements of the pectoral fin in Eusthenopteron, too, agree surprisingly well with the corresponding elements in the tetrapod limb.

28. The tetrapod hand (foot), as established by embryological investigations, is *seven-rayed* (fig. 26 C; STEINER, 1922, 1935; HOLMGREN, 1952, p. 94). An obvious, but previously overlooked fact is that the *pectoral fin in Eusthenopteron* (figs. 23 C, 25 B, C, 26 D, 27 A) is *seven-rayed as well*. The first of these rays, the radial (tibial) ray (*Rr, Tir*), is ventro-lateral (« preaxial ») in position in the osteolepiform fin and consists of a single element. In the tetrapods (figs. 23 D, 26 C, E) it arises from a single blastema which later in ontogeny becomes separated into three (sometimes four) elements: the radius (*R*; tibia, *Ti*), the radiale (tibiale), and the prepollex (*Pp*; prehallux, *Ph*). These three elements are clearly seen in the foot of *Ichthyostega* and as may be gathered from figure 26 D, E they compare well, as to position and distal extent, with the undivided radial ray in the pectoral fin of *Eusthenopteron*. *The remaining six rays all radiate from the ulna (U; fibula, Fi), a condition which is characteristic of all tetrapods (figs. 23, 26, 27). The first of these rays, the intermedium ray (Ir), which articulates directly with the ulna (fibula) forms the intermedium (I) and the first finger (toe, I). As explained above this ray, in the urodeles (and Sauripterus, fig. 23 A, B), has fused with the next ray forming a composite structure (Im), which branches distally and forms the first and second digits. The remaining five rays in the Osteolepiform-Tetrapod stock have a common proximal element, the ulnare (Ue; fibulare, Fe), and the first four of these rays form the second (II), third (III), fourth (IV), and fifth (V) digits (fig. 23 D). The last or seventh ray, which is unknown in the ichthyostegids, is the postminimumus (Pm) or pisiforme.*

29. As we have now seen *the fundamental structures characteristic of both the girdles and the limbs of the early tetrapods arose already in their piscine ancestors. Since a typical tetrapod limb occurred, in a practically final stage, within the paired paddles of the osteolepiforms it is evident that the transformations at*

the transition from fish to tetrapod were inconsiderable, and that these transformations may easily have occurred independently in the various lines of evolution that sprung from the osteolepiforms or related piscine ancestors. As shown above (pp. 34-35), and as will be further elucidated in a forthcoming paper, *the conception of a « metapterygial stem » or « axis »,* which has played such a dominant role in almost every discussion on the origin of the tetrapod limb since the days of Gegenbaur, *is due to a misinterpretation of the composition of the shark fin.* The endoskeleton of the paired (and unpaired) fins is composed of metameric radials (two in each segment) which, as a result of a shortening of the shoulder joint, have fused in their proximal parts forming a series of complex units (basale metapterygii, humerus, femur, ulna, the composite intermedium ray of the urodeles, etc.). In order to understand the paired fins in those fishes which have given rise to tetrapods it would be best to forget about looking for the « extremity stem ». It should be evident from the preceding paragraph (nr. 28) that the homologues of the fingers are represented in the *Eusthenopteron* fin. The theory of GREGORY (GREGORY and RAVEN, 1941) and WESTOLL (1943) that the fingers are new formations (neomorphs) must be rejected, as also HOLMGREN's ideas (see HOLMGREN, 1952, p. 83) about the fundamental differences between the archepodium and the neopodium. Moreover, I think, the idea of a « twisting » or « primary torsion » of the humerus (see EVANS and KRAHL, 1945), which arose in connection with the transformation of the pectoral paddle into the tetrapod limb, can be abandoned as well. As pointed out above (p. 74) the two extremities of the humerus are set at angles in *Eusthenopteron* and as in *Eryops* the long axis of the proximal articular area of the humerus forms an angle with the articulation of the elbow joint. The rotation of the bone on its long axis in *Eryops* and other early tetrapods is brought about by a sliding in the screw-shaped glenoid fossa (MINER, 1925). Finally, it is to be pointed out that the view of a peculiar swinging and bending of the pectoral paddle advanced by ROMER and illustrated in a well-known diagram (see ROMER, 1962 b, pp. 199-200, fig. 123; SZARSKI, 1962, fig. 46) is certainly erroneous. As demonstrated by GREGORY (GREGORY and RAVEN, 1941) and WESTOLL (1943) this view rests upon a misinterpretation of the position of the osteolepiform paddle.

As established from the excellent specimen of *Eusthenopteron* shown in fig. 25 A-C and other material of osteolepiforms at my

disposal (JARVIK, 1948), the pectoral fin of the osteolepiforms, when in trailing position, was so situated that its radial ray was ventro-lateral, its flexor side ventro-medial and its extensor side dorso-lateral. The pectoral fin was thus situated somewhat as the limb bud in the human embryo (HAMILTON, BOYD and MOSSMAN, 1952, figs. 104-107) and the embryos of other tetrapods, and no doubt the nerves, vessels and muscles were situated very much as in the embryonic primitive tetrapod limb (see SEWERTZOFF, 1908). If we now imagine that the pectoral fin in *Eusthenopteron* was spread out and lowered, the flexor side would touch the ground as it does in the tetrapod limb and by moving the fin slightly forwards and backwards the fish might conceivably have been capable of making short « steps ». These movements, which were accompanied by a backward and forward movement of the head of the humerus in the glenoid fossa, cannot have

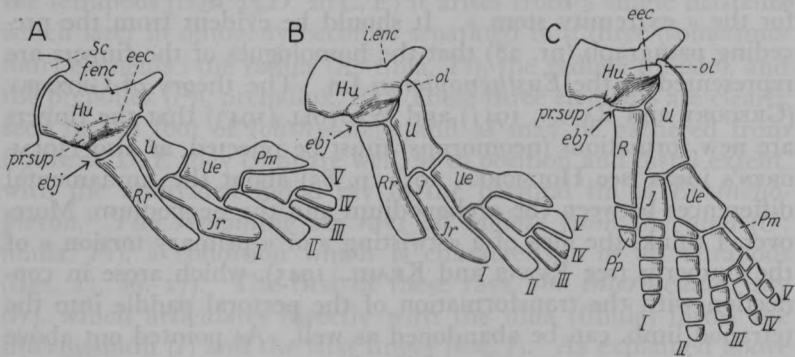


FIG. 27.

Diagrams to illustrate the main changes at the transformation of the osteolepiform pectoral fin into the tetrapod limb. *A*, *Eusthenopteron* stage. After fig. 25 C. *B*, intermediate stage. *C*, primitive tetrapod stage.

Hu, humerus; *I*, intermedium; *Ir*, intermedium ray, *Pm*, postminimus; *Pp*, prepollex; *Sc*, endoskeletal shoulder girdle; *U*, ulna, *Ue*, ulnare.

ebj, elbow joint; *eec*, ectepicondylar process; *f.enc*, entepicondylar foramen; *i.enc*, notch corresponding to ditto; *ol*, olecranon process of ulna; *pr.sup*, supinator process; *I*, *II*, *III*, *IV*, *V*, digits I-V.

been large in *Eusthenopteron* and other osteolepiforms where the pectoral fin is longbased externally and is anchored to the body wall by strong basal scutes (*b.sc*, fig. 25 A; JARVIK, 1948, pp. 19, 110; 1960, fig. 12 B; cf. the axillary scales in certain teleosts, NORMAN and GREENWOOD, 1963, pp. 65-66). As a first step towards the transformation of the osteolepiform pectoral fin into the tetrapod limb we must assume a reduction of the basal scutes. This reduction was certainly accompanied by a reduction of the

basal scales and adjoining parts of the squamation, the dermal fin rays, and the postero-ventral parts of the cleithrum. Contemporaneous with these retrogressive changes in the exoskeleton, the endoskeleton of the shoulder girdle and the pectoral fin underwent mainly the following changes. The endoskeletal shoulder girdle developed progressively in a ventral direction, forming the coracoid plate, while the glenoid fossa became screw-shaped. This condition is found in *Ichthyostega*. In more advanced forms the shoulder girdle also grew in a dorsal direction forming a scapular blade and this process has led to a more or less complete reduction of the dorsal part of the cleithrum as well. The main changes in the pectoral fin (fig. 27) concern the development of the elbow joint, and the subdivision of the various rays into segments (carpals, tarsals, phalanges). In the elbow joint (*ebj*), which is indicated already in *Eusthenopteron*, the position of the articular area of the radius has changed a little so as to be directed ventrally when the humerus is extended backwards (see also *Ichthyostega*, JARVIK, 1960, fig. 15), and in order to facilitate the movements of the forearm, the humerus has become hollowed out in front of the radial condylus. However, perhaps the most important modification is the formation of the olecranon (*ol*) of the ulna which is well developed even in *Ichthyostega*. Regarding the segmentation of the rays it may be sufficient to refer to the well-known fact (fig. 23 B, D; SEWERTZOFF, 1908, p. 115) that the digits, in early embryonic stages of tetrapods, are represented by undivided blastemas obviously corresponding to the undivided rays of the fin of the ancestral fish. The subdivisions of these blastemas, in ontogeny, into a varied number of segments, is clearly a recapitulation of the phyletic development.

CONCLUDING REMARKS.

It is generally taken for granted, even today, that the cyclostomes are the most primitive vertebrates, that the sharks, or at any rate the sharklike placoderms, are the most primitive gnathostomes and the discussions of the phylogeny of the tetrapods is stamped by the deep-rooted belief that the urodeles are the most primitive living tetrapods. However, if we reconsider the current conceptions about the phylogeny of the vertebrates in the light of the new evidence provided by the comparative anatomical studies of the early fossil vertebrates carried out during the last few decades, and try to keep strictly to well established

facts, it is readily seen that many of these conceptions are doubtful or erroneous (see also JARVIK, 1960).

As shown above (pp. 16-26, figs. 2-6) the cyclostomes and the gnathostomes are two early specialized equivalent stems of vertebrates differing fundamentally in the development of the nasohypophysial complex, in the position and structure of the gills, in the relations between the visceral and axial parts of the skull, in the jaw apparatus, the otoliths, etc. The cyclostomes cannot be considered as more primitive than the gnathostomes, and they do not include the ancestors of the latter. Nor the sharks, which belong to an ancient group which has changed very little since the Devonian (p. 39, fig. 11 E, F), are primitive, and the same applies to the placoderms (pp. 30-36, figs. 7-11). Even the oldest known placoderms from the late Silurian were highly specialized and neither these early forms nor any of the later appearing placoderms can include the ancestors of the teleostomes, which early had become modified in other directions. The urodeles are specialized descendants of the porolepiforms and they do not aid materially in elucidating problems concerning the development of the majority of tetrapods which have arisen from the osteolepiforms.

These facts, gained by studies of the early fossil vertebrates, removes the very foundation of the accepted family tree (fig. 1). If we imagine that we cut off the trunk of a tree and then plant its branches well apart into the ground we will get a picture of the evolution of the vertebrates which agrees fairly well with the available facts (fig. 28; JARVIK, 1960, pp. 89-102). We know that *the vertebrates, when they begin to appear in the fossil record, in the Ordovician or, more commonly, in the late Silurian and early Devonian, were divided into a great number of distinct groups. Some of these groups display characters which may be regarded as primitive, e.g. the presence of teeth on the external side of the ceratohyal in the osteolepiforms, but on the whole these early groups were much advanced and the structural features characteristic of each group were already developed. None of these groups can be regarded as more primitive than the others. They are all equivalent and none of them may be derived from any of the others. Certainly some of these early groups are more closely related to each other than to the other groups.*

The cyclostomes and the gnathostomes form two natural units. The cyclostomes include two distinct stocks, the petromyzontids or cephalaspidomorphs and the myxinoids or pteraspidomorphs, each comprising several distinct groups (cephalaspids, anaspids,

astraspids, etc.). Among the gnathostomes the various groups of elasmobranchs and placoderms may be classified together as the *Elasmobranchiomorphi*, but the affinities of the *Acanthodii* are still uncertain. The systematic position of the *Dipnoi*, too, is obscure (p. 40), but generally they are included in the *Teleostomi* which, in the early Paleozoic, included not only the dipnoans, but also the paleoniscids, the coelacanthiforms, the porolepiforms and the osteolepiforms. The paleoniscids constitute an early specialized, uniform group and whether they include the ancestors of the recent actinopterygians remains uncertain (p. 47, fig. 15). The coelacanthiforms, the porolepiforms, and the osteolepiforms are

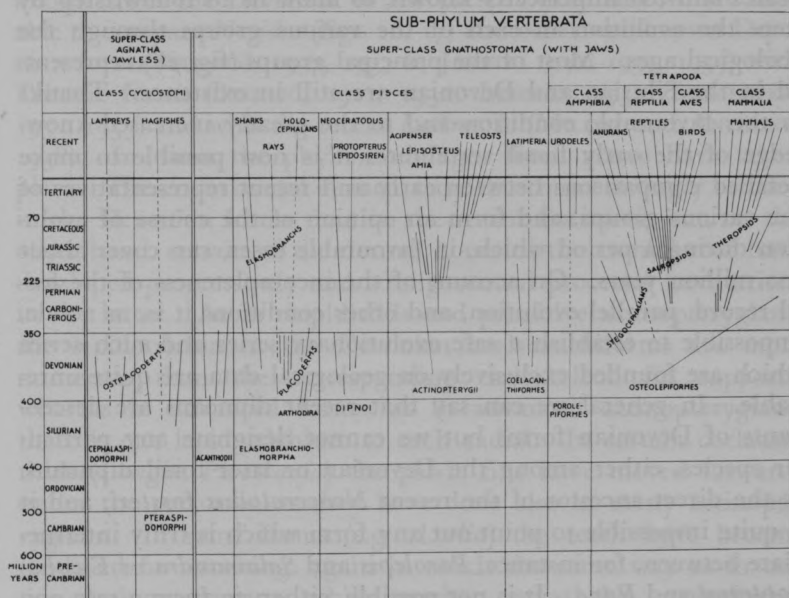


FIG. 28.

Diagrammatic representation of the phylogeny of the vertebrates in accordance with the results gained by the studies of the early fossil vertebrates. Modified from Jarvik 1960, fig. 28.

generally classified together as the *Crossopterygii* (cf. p. 40). New investigations of *Latimeria* and of fossil crossopterygians have revealed that the coelacanthiforms differ so widely, in many respects, from the other two groups that it is questionable whether this classification is justified. The porolepiforms and the osteolepiforms, on the other hand, have so many characters in common that they may be brought into a common systematic unit, the *Rhipidistia*. These similarities indicate a common ori-

gin, but since the porolepiforms and the osteolepiforms in many important respects differ considerably it is evident that they have become independent long before their first appearance as fossils in the early Devonian. As is now well established (pp. 51-79, cf. foot-note on p. 52) the osteolepiforms have given rise to the *Anura* and the *Amniota*, whereas the *Urodela* have arisen independently from the porolepiforms. This condition raises an intricate taxonomic problem, but, at any rate provisionally, an Osteolepiform-Tetrapod and a Porolepiform-Tetrapod stock may be distinguished.

The fossil record is far too incomplete and most fossil vertebrates still too imperfectly known, to allow us to follow, step by step, the evolution in each of the various groups through the geological ages. Most of the principal groups (fig. 28) represented in the Silurian and Devonian are still in existence. Thanks to this favourable condition and to the greatly increased knowledge of the early fossil vertebrates it is now possible to make detailed comparisons between early and recent representatives of the various groups, and form an opinion of the course of evolution during a period which, in favourable cases, can cover about 400 million years. On account of the incompleteness of the fossil record, parallel evolution, and other conditions it is, as a rule, impossible to establish a safe evolutionary series and such series which are founded exclusively on geological data are quite unreliable. In general we can say that recent dipnoans are descendants of Devonian forms but we cannot designate any particular species, either among the Devonian or later fossil dipnoans, as the direct ancestor of the recent *Neoceratodus forsteri*, and it is quite impossible to point out any form which is truly intermediate between, for instance, *Porolepis* and *Salamandra* or *Eusthenopteron* and *Rana*. It is not possible, either, to form a safe opinion of the tempo of structural change and we cannot say, with any degree of certainty, how long the various genera and species have existed. We have to admit that we do not know how old the recent species *Neoceratodus forsteri* is and we do not know when the characters distinctive of the genus *Latimeria* came into existence or when this genus will become extinct.

The detailed paleoanatomical investigations on the various groups of early vertebrates have, as pointed out above, invariably demonstrated that *each of these groups was highly specialized at its first appearance in the fossil record*. However, still more remarkable is the discovery that *these groups have, as a rule,*

changed very little or, in many respects, not at all during their known geological history. Moreover, it has been shown that these phyletic changes have been of much the same kind in the various groups. The most important of these parallel changes are (JARVIK, 1960, p. 92) :

Changes due to retrogressive or progressive development of the skeleton;

Changes of the locomotive organs (fins, vertebral column, etc.);

Changes of the jaw apparatus and the respiratory organs.

These conditions are well exemplified by the coelacanthiforms (see also pp. 47-51). The coelacanthiforms is one of the groups known from the Devonian to the present time and we are now able to compare *Nesides* (figs. 16, 17) and other well-known Devonian forms (STENSIÖ, 1932, 1937 b; JARVIK, 1942, 1954, 1959) with Triassic forms (STENSIÖ, 1921, 1932; LEHMAN, 1952; SCHAEFFER, 1952, 1953) and with the recent *Latimeria* (MILLOT and ANTHONY, 1958). In them the phyletic changes listed above have taken place. The endoskeletal elements are thus more strongly ossified in the Devonian forms than in the recent *Latimeria* but, on the other hand, certain of the dermal bones of the cranial roof have developed progressively and strong ventral processes have arisen in the latter. As in rhipidistids and primitive actinopterygians, the lepidotrichia in the Devonian coelacanthiforms are more numerous than the corresponding endoskeletal fin supports, whereas in advanced forms, as in advanced actinopterygians, there is one lepidotrichium to each radial. In certain coelacanthids (*Laugia*, *Piveteaunia*) the pelvic fins have moved forwards under the pectorals, as they have done also in many actinopterygians. In some forms (e.g. *Axelia*) the teeth have become modified for crushing, again in much the same way as in certain actinopterygians, while another remarkable evolutionary trend common to these two groups and met with also in the tetrapods is the loss of the basipterygoid process. It may be added that the coelacanthiforms show a considerable variation in size and a remarkable fact is that *Dictyonosteus* from the Middle Devonian of Spitsbergen, which is one of the oldest coelacanthids known so far, may be estimated to have attained a length of about two metres. It was thus larger even than the recent *Latimeria*, but certain of the Triassic forms were still larger (probably up to three metres).

Even at their first appearance in the fossil record in the middle of the Devonian period, the coelacanthiforms were divided into a

number of genera and species and new genera and species have successively arisen. Of great interest, too, in this connection is the fact that they during the course of their long geological history have invaded a great variety of aquatic environments both in freshwater and in the sea (SCHAEFFER, 1953, p. 175). *However, in spite of this repeated species and genus formation going on for about 400 million years and in spite of unusually strong variations in environments — and which is generally considered to promote evolutionary change — the coelacanthiforms have not undergone any changes of importance since the Devonian. Latimeria in many respects agrees most closely with its Devonian forerunners (pp. 47-50). During 400 million years or more the nerve impulses in the coelacanthiforms have travelled along the same paths, the blood, in generation after generation, has coursed through a vascular system the pattern of which was laid down in the unknown pre-Devonian ancestors, the peculiar rostral organ with its three outlets on each side has been retained without change, the urohyal has not changed its shape and the muscles are attached to it in Latimeria as they were in the Devonian forms (fig. 17), the inconsiderable collar-stud-like process (fig. 16) has been situated on the side of the neural endocranium all the time, etc.*

*This remarkable conservatism, so well demonstrated by the coelacanthids, is by no means an isolated phenomenon. A similar reluctance to change was discovered by STENSIÖ (1927) with regard to the late Silurian and early Devonian cephalaspids and the petromyzontids of today, and all the investigations of other groups carried out later have, without exception, given the same results. The Devonian sharks differ very little from the recent ones (p. 39, fig. 11 E, F). The peculiar rostral processes and clasper formations which distinguish the recent holocephalians were present already in their Devonian predecessors (the ptyctodontid arthrodires, p. 97, figs. 10, 11 A, B). Many of the characters distinguishing the recent rays are found in other Devonian arthrodires (rhenanids, pp. 37-39, fig. 11 C, D). The paleoniscids have apparently not changed from the Devonian until they became extinct in the Cretaceous (p. 47, fig. 15) and if we disregard the effect of the retrogressive development of the skeleton there are hardly any differences between the earliest fossil dipnoans and the recent *Neoceratodus* (pp. 40-47; figs. 12-14).*

With regard to the fact that all the groups of vertebrates which have remained aquatic have changed very little since their first

appearance in the fossil record it is not surprising to find that *a corresponding conservatism characterizes also those groups of fishes which left the water and became tetrapods*. As we have seen, many of the specific structural features characteristic of the recent urodeles were developed already in their porolepiform ancestors in the early Devonian (pp. 51-65, 68-69, fig. 18 A, D, E, 19 H, J, 20 C, D, F, 21 B-F). A corresponding most close agreement as to anatomical details has been demonstrated between the anurans and the Devonian Osteolepiforms (pp. 51-79, figs. 19 A-G, 20 A, B, E). As we have also seen, the tetrapod limb (pp. 66-79) and other pre-requisites for a life on land were in all essentials developed in these fishes.

Even the oldest porolepiforms and osteolepiforms possessed a choana and there was a posterior external nasal tube, developed, in all essentials, as a naso-lachrymal duct (fig. 21). It seems likely that these and other basic structures, such as lungs, common to all tetrapods, had arisen already in the primitive rhipidistids from which both the porolepiforms and osteolepiforms presumably derive their origin. From the moment when these structures, essential for a life on land, began to develop, we can say that the *history of the tetrapods began*. However, soon thereafter the primitive rhipidistids no doubt began to separate into the Porolepiform-Tetrapod and the Osteolepiform-Tetrapod stocks and in each of these stocks a great number of specific tetrapod characters developed independently. At the beginning of the Devonian, or earlier, the osteolepiforms and the porolepiforms had reached a stage in organisation where they could turn to a life on land without much further change. *In their internal structure the osteolepiforms and the porolepiforms were already tetrapods although they lived in the water and looked like fishes*. The transition from fish to tetrapod implies no radical transformations, and most likely took place gradually. The most remarkable preadaptation for terrestrial life found in the piscine forerunners of the tetrapods makes it inviting to assume that both the porolepiforms and osteolepiforms utilized their intrinsic possibilities for a life on land several times and that the tetrapods are polyphyletic. However, once in the new environments the descendants of the porolepiforms apparently were not very successful, for, as far as we know, the porolepiforms only gave rise to the urodeles (the origin of the *Apoda* is unknown). The osteolepiforms, on the other hand, became much diversified and the new living space was rapidly filled by a crowd of various

stegocephalians, anurans, reptiles, birds, mammals and, finally, human beings.

We may easily be dazzled by this strong expansion in the Osteolepiform-Tetrapod stock, but we must not forget that, without doubt, *the most important evolutionary changes in vertebrates have taken place in the water*. All the characters common to the vertebrates have, no doubt, arisen in water. The various groups of cyclostomes and gnathostomes developed in aquatic environments while contemporaneously with the radiation of the tetrapods on land, the actinopterygians underwent an equally fascinating expansion in the water. All the important tetrapod characters including the tetrapod limb, arose in the water. What we observe when studying the evolution of land animals are in fact only comparatively small modifications of the basic plan inherited from the osteolepiform ancestors.

The recognition of the osteolepiforms and the porolepiforms as the ancestors of the tetrapods and our much increased knowledge of these two groups, gained during the last few decades, have given us new possibilities of understanding the structure and the modifications of the tetrapods, and by studying the ontogeny of the living forms we can, in many cases, form an opinion of how these modifications have arisen. Knowing the osteolepiforms it is also easier to understand structural peculiarities in our own body. As I have recently demonstrated (1963 a, 1963 b), there are striking resemblances between man and his osteolepiform ancestors in the structure of the floor of the mouth cavity and the tongue. Also in the limbs man has retained primitive conditions, and the similarities with the osteolepiforms are obvious. The most prominent feature of man is no doubt his big and elaborate brain. However, this big brain would certainly never have arisen—and what purpose would it have served—if our arm and hand had become specialized as strongly as has, for instance, the fore leg of a horse or the wing of a bird. It is the remarkable fact that it is the primitive condition, inherited from our osteolepiform ancestors and retained with relatively small changes in our arm and hand, that has paved the way for the emergence of man. We can say, with some justification, that it was when the basic pattern of our five-fingered hand was laid down, for some unaccountable reason, in the ancestors of the osteolepiforms, in the Silurian or earlier, that the prerequisites for the origin of man and the human culture arose.

By the studies of the early fossil vertebrates it has thus been established that the vertebrates had passed the most important

stages in their evolution before they began to appear as fossils. *What has happened during the last 400 or 500 million years is inconsiderable, compared with what must have happened previously, when not only the qualities common to all vertebrates but also the distinctive characters of the various groups arose.* Unfortunately the fossils give us no information about these early and, by comparison, most important stages in the history of the vertebrates. However, as is now evident (p. 19) the separation of the cyclostomes into the petromyzontid and myxinoïd stocks must have taken place before the beginning of the Ordovician period, i.e. more than half a milliard years ago. Hence it follows that the structural features which are common to all the cyclostomes and which distinguish them from the gnathostomes must have arisen still earlier, conceivably already in the Precambrian. However, long before the cyclostomes divided into two stocks and before the vertebrates separated into cyclostomes and gnathostomes the many characters common to all the vertebrates (the differentiated brain, the cranial nerves, the lateral line system, the six eye-muscles, etc.) must have arisen. We are thus led to the conclusion that *the vertebrates must be a very ancient group* and that we do not know anything, with certainty, about their origin. We do not know if the vertebrates, or the *Chordata* as a whole, are related to any other of the phyla which constitute the animal kingdom. We do not know when they arose, but on the basis of the available facts (see also NURSALL, 1962) it seems likely that the specific vertebrate characters began to develop very early in the history of life and that the decisive division of the animal kingdom into phyla took place earlier and more contemporaneously than is generally assumed. *We do not know anything about the environmental conditions* in the remote past when vertebrates passed the most important stages in their evolution. Calculations about the percentage of fresh water forms in the late Silurian or early Devonian give no answer to the question if the vertebrates arose in fresh water or in the sea. We cannot say when or under what conditions the six eye-muscles, or the specialized hard tissues of the vertebrates arose. We do not know what factors caused and promoted the development of lobe fins, which are characteristic of practically all early fishes (pp. 40-41), and we cannot explain why the tetrapod limb, the choana and other pre-requisites for a terrestrial life arose in the piscine ancestors of the tetrapods. Theories about these things, often found in the literature, are purely guesswork. We cannot even say when or under what conditions the turtle

shell, for instance, arose. We can only state that it was present in the earliest chelonians known so far, and we can, on the basis of fossils, study the obviously very small changes which have occurred in this group from the Triassic to the present time. Like other groups of vertebrates the chelonians were highly specialized when they first appear in the fossil record and they have changed very little since that time. We may picture the evolution of the vertebrates as a tree or a bush, but if we want to discuss the evolutionary processes on the basis of fossils we have to remember that it is only the topmost twigs that are available for study. The earliest and most important phases in the history of the vertebrates and of the various groups are wrapped in obscurity.

RÉSUMÉ.

Dans cet article, qui fait suite à un autre (1960), consacré au même sujet, l'auteur critique quelques théories couramment admises concernant l'évolution des Vertébrés et aboutit à la conclusion que ces théories ne s'accordent pas avec des faits bien démontrés. Il présente une sélection de ces faits, tels qu'ils résultent notamment de travaux d'anatomie comparée des Vertébrés primitifs, réalisés par STENSIÖ et d'autres; ceci lui permet de préciser les conclusions de son travail de 1960 sur l'évolution des Vertébrés. L'ensemble des documents, anciens et nouveaux, permet les conclusions suivantes.

Les Cyclostomes (Agnathes) ne comprennent pas les ancêtres des Gnathostomes. Certaines des spécialisations les plus importantes (complexe naso-hypophysaire, branchies, arcs branchiaux et boîte crânienne) qui distinguent ces deux phylums de Vertébrés étaient complètement développées dans leurs représentants les plus anciens dont nous ayons une connaissance suffisante et, de certains points de vue, les Cyclostomes apparaissent plus évolués que les Gnathostomes. Le développement de branchies internes, très précoce dans la phylogénie des Cyclostomes, a empêché celui de mâchoires pareilles à celles des Gnathostomes.

Les premiers Arthrodires n'étaient pas des êtres primitifs proches des Cyclostomes mais, au contraire, des Gnathostomes typiques très spécialisés et l'idée suivant laquelle les Placodermes seraient les Gnathostomes les plus primitifs et les ancêtres des Téléostomes est sans fondement. Le schéma généralement admis de l'évolution des Vertébrés est donc fondamentalement incorrect.

Les Pétromyzontides récents diffèrent fort des Myxinoïdes par la structure et la fonction de la langue râpeuse et par beaucoup d'autres caractères. Beaucoup des caractéristiques anatomiques des Pétromyzontides se trouvaient dans les Céphalaspides du Silurien supérieur et les deux grands groupes de Cyclostomes étaient très probablement bien définis et distincts à la fin du Cambrien, il y a 500 millions d'années. Les caractéristiques

tères différentiels de ces groupes doivent s'être développés au Cambrien, voire plus tôt, et, avant même la scission des Vertébrés en Cyclostomes et Gnathostomes, les nombreux caractères communs à tous les Vertébrés doivent avoir apparus. Il semble donc que les Vertébrés soient un groupe d'animaux très anciens, sur l'origine et les relations desquels les fossiles, même les plus anciens, ne nous apprennent rien. Nous ignorons même quand, et dans quelles conditions les Vertébrés ont apparus.

Nous savons, par contre, que lorsque les Vertébrés apparaissent dans les documents paléontologiques, à l'Ordovicien ou, plus fréquemment, dans le Silurien supérieur et le Dévonien inférieur, ils sont déjà subdivisés en un certain nombre de groupes clairement définis. Aucun de ces groupes n'est plus primitif qu'un autre ni ne peut en être dérivé.

La plupart des principaux types de Vertébrés, représentés au Dévonien moyen ou même plus tôt, sont toujours actuels et la comparaison des représentants éteints et actuels permet de se représenter les modifications évolutives qui ont affecté chacun de ces groupes en 400 millions d'années. L'étude des formes primitives a ainsi considérablement étendu la compréhension que nous avons de l'évolution des Vertébrés.

De telles comparaisons, entreprises dès 1927, ont régulièrement montré que, de tous les points de vues étudiables, ces groupes de Vertébrés ont changé fort peu et quelquefois pas du tout au cours de leur histoire géologique connue. De nombreux exemples sont donnés de cette stabilité remarquable, qui s'étend même à des structures apparemment sans importance telles les « organes en bouton de col » des Coelacanthides.

Une autre constatation importante, soutenue par la paléontologie des Coelacanthides est que l'apparition successive de nouvelles espèces et de nouveaux genres, associée à des changements considérables de milieu, étendus sur de longues périodes, n'ont pas eu d'influence remarquable sur le processus évolutif. Si nous négligeons les conséquences spectaculaires de la régression du squelette et quelques autres tendances évolutives parallèles, encore inexplicables, le *Latimeria* actuel diffère à peine plus des genres du Dévonien que ces derniers ne diffèrent entre eux.

Cette remarquable inertie évolutive, s'étendant sur de vastes périodes géologiques, est caractéristique, non seulement de tous les groupes demeurés aquatiques, mais aussi des deux lignées qui ont donné naissance aux Tétrapodes. Du point de vue de leur anatomie interne, les Porolépipiformes et les Ostéolépipiformes avaient acquis indépendamment le niveau d'organisation des Tétrapodes dès le début du Dévonien. On a retrouvé, dans ces deux groupes de Vertébrés aquatiques — qui sont extérieurement des poissons typiques — de nombreuses structures spécialisées que leurs descendants Tétrapodes actuels ont maintenues avec peu ou pas de modifications.

La patte des Tétrapodes s'est développée dans leurs ancêtres Poissons et existait à peu près complète dans les membres pairs des Ostéolépipiformes du Dévonien. Bien que l'on puisse donc dire que le vieux pro-

blème de l'origine de la patte du Tétrapode soit maintenant résolu sur un certain plan, on pourrait dire aussi qu'il a été seulement repoussé dans le temps. Nous devons admettre que nous ignorons pourquoi, quand et dans quelles conditions la patte hautement spécialisée et d'autres préaptitudes complexes à la vie terrestre se sont développées.

Les phases les plus anciennes et, sans aucun doute, les plus importantes de l'histoire des Vertébrés sont donc enveloppées de ténèbres. Non seulement les nombreuses structures importantes communes à tous les Vertébrés — par exemple les six muscles de l'œil et leur innervation — mais même les spécialisations différenciant les Cyclostomes des Gnathostomes et les différents groupes entre eux se sont développées avant l'époque dont il nous reste des documents paléontologiques en nombre suffisant, soit il y a plus de 400 à 500 millions d'années.

Alors que, sur une base paléontologique, nous croyons étudier l'évolution, nous ne nous penchons guère que sur des modifications plus ou moins secondaires de structures déjà anciennes. Les événements évolutifs majeurs qui ont donné naissance à ces structures se sont déroulés dans un passé qui nous reste inconnu.

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Addendum: In an article in *Science Progress* (52, 1964, 451-459) and in three other papers T. S. THOMSON criticizes my views on rhipidistid classification and tetrapod origin. Besides on his own studies of the snout in an imperfectly ossified Permian form and arbitrary interpretations of fossil structures he relies on the descriptions of the snout by KULCZYCKI and VOROBEVA. KULCZYCKI's reinterpretation of *Porolepis*, which in important regards forms the basis of THOMSON's considerations, has been proved to be incorrect (JARVIK, 1962), and, disregarding the well-known form *Eusthenopteron wenzukowi*, VOROBEVA's descriptions rest on a much too fragmentary fossil material. Comparison with similar skull-fragments at my disposal indicates that important specimens, interpreted by her as parts of the snout, are more likely pieces of lower jaws.

THOMSON's views are inconsistent with safe information as to the structure to the rhipidistids, and are consequently unacceptable. The osteolepids and the rhizodontids, classified by THOMSON as separate orders, equal in rank with the *Porolepiformes*, are in fact very similar and it is doubtful even if they can be kept apart as separate families. The *Osteolepiformes* and the *Porolepiformes*, on the other hand, differ so widely that STENSIÖ recently (1964a, p. 83) found it necessary to rank them as two separate classes of the Vertebrata.