

- (1) Spiral Creek and Kløftelv (Pre-Cambrian/Cambrian);
- (2) Kløftelv and lower Bastion (intra-Cambrian);
- (3) lower Bastion and upper Bastion (intra-Cambrian);
- (4) Dolomite Point and Cass Fjord (?Middle Cambrian/Lower Ordovician).

Résumé. L'auteur passe en revue la succession stratigraphique cambro-ordovicienne en mentionnant les fossiles caractéristiques. Il fait des observations sur les phénomènes de sédimentation et en tire des conclusions paléo climatiques. Il constate les indices de mouvements tectoniques pendant le Précambrien supérieur et le Paléozoïque inférieur et discute la question de l'âge de l'orogénie principale.

The Fossil Vertebrates from East Greenland and their Zoological Importance

By E. JARVIK*

The collections of fossil vertebrates brought together by the collaborators of Dr. LAUGE KOCH during the Danish expeditions to East Greenland in 1929–1957 include more than ten thousand specimens. Much of this enormous material has been or is being described, and since the beginning of the thirties the East Greenland material has played a prominent role in the discussions on the comparative anatomy and phylogeny of the vertebrates. However, the importance of these collections is due not only to the vast amount of material, to the excellent state of preservation of many of the specimens, and to the careful studies of the fossils. As a matter of fact, only a few of the numerous papers which have been published about East Greenland material deal exclusively with such material. Frequently specimens from other areas, too, have been used, sometimes to a large extent, and in many instances fossil vertebrates from East Greenland have been considered more or less in passing, in order to elucidate special problems. But to be able fully to understand the value of the East Greenland collections it is necessary to know, too, that studies of both fossil and recent vertebrates have often been made with the main aim to produce a safe basis for the subsequent treatment of Greenland material. And of course the successful collecting work in East Greenland which has been going on for many years has encouraged fossil hunting in other parts of the world as well.

For more than a quarter of a century the fossil vertebrates from East Greenland have thus in various ways stimulated the paleozoological research work, in particular that concerning the lower vertebrates, and the many elaborate studies have contributed much to the great advance in vertebrate paleontology during the last few decades. In this article it is of course impossible to account for even the most important results of these studies. Only a short and in many respects incomplete review of the collections from the various geological periods will be given and some interesting results,

which have recently been gained partly on the basis of studies of East Greenland material, will be presented.

The Devonian was an important epoch in the history of the vertebrates and certainly the large and partly unique Devonian collections from East Greenland have attracted considerable interest. In a recent article¹, most of the papers dealing with these collections were recorded and the zoological importance of the fossils was briefly considered. However, with reference to what has been said above, it may be added that as a preparatory work for his description of the ichthyostegid material discovered in 1931, SÄVE-SÖDERBERGH² made a detailed study of the dermal bones and sensory canals of the head in *Osteolepis*; and, in order to be able to determine the important osteolepid material found in East Greenland mainly in 1936, he began a thorough revision of the Middle Devonian osteolepids from Scotland. Because of ill health he was regrettably unable to finish this work, which, however, later developed into a comprehensive morphological and taxonomic account³ and led to revisions of other osteolepids as well. Finally, it may be worth mentioning that SÄVE-SÖDERBERGH's paper⁴ on *Rhynchodipterus* was a consequence of the discovery of peculiar dipnoans in East Greenland.

The Carboniferous vertebrates taken from East Greenland are few and only some paleoniscids have been described so far^{5,6}. A slab with distinct tetrapod tracks figured by WITZIG⁷ indicates the presence of stegocephalians in East Greenland in late Carboniferous times.

* Naturhistoriska Riksmuséet, Paleozoologiska Avdelningen, Stockholm (Sweden).

¹ E. JARVIK, *Devonian Vertebrates*, Geology of the Arctic (University of Toronto Press, 1961), p. 197.

² G. SÄVE-SÖDERBERGH, *Nov. Acta Reg. Soc. Sci. Ups.* 9, 1 (1933).

³ E. JARVIK, *K. Vet. Akad. Handl.* 25, 1 (1948).

⁴ G. SÄVE-SÖDERBERGH, *K. Vet. Akad. Ark. Zool.* 29 B, 1 (1937).

⁵ J. A. MOY-THOMAS, *Ann. Mag. nat. Hist.* 9, 737 (1942).

⁶ E. S. GOODRICH, *Quart. J. micr. Sci., London N.S.* 83, 459 (1942).

⁷ E. WITZIG, *Medd. om Grønland* 72, 1 (1954).

As may be gathered from STENSIÖ's recent review⁸, the Permian vertebrates are of interest mainly from a paleohistological point of view. In connection with his description of the Permian ganoids, ALDINGER thus made detailed studies of the scale structure of a large number of fossil ganoids, and as set forth by STENSIÖ⁸ the edestids are of fundamental importance for the understanding of the origin, composition, and evolution of the exoskeletal hard tissues in vertebrates in general. ØRVIG⁹, too, used East Greenland material for his paleohistological researches.

The East Greenland material of Triassic ganoids ranks among the best in the world, and hardly anywhere else have such well preserved fossil actinopterygians been found. In an important paper STENSIÖ¹⁰ described the material found in 1929-1931, and on the basis of this material he discussed the general principles of the evolution and classification of the actinopterygians. However, most of the Triassic material has been collected since 1932 by NIELSEN and his assistants. In 1936 NIELSEN published a preliminary report on the material found up to that time, and in two monographs^{11,12}, which have become standard works giving invaluable information on the structure of fossil ganoids, he carefully described four different forms. Another interesting Triassic fish from East Greenland is *Laugia*, remarkable for its well preserved postcranial skeleton¹⁰, but the fauna includes several other well preserved coelacanthids, too, together with elasmobranchs and various stegocephalians¹³⁻¹⁵. In connection with his description of the dermal bones of the head of the stegocephalians, SÄVE-SÖDERBERGH¹³ discussed at length the pattern of the dermal bones in lower tetrapods in general, and he advanced¹⁶ new and stimulating ideas about the classification of the vertebrates. Another consequence of the studies of the East Greenland stegocephalians was that the Triassic stegocephalians from Spitsbergen were thoroughly revised¹⁷, and in order to be able to interpret safely the many intricate structural details encountered in the Triassic stegocephalians, SÄVE-SÖDERBERGH made detailed anatomical studies of recent reptiles. These researches are being continued by H. C. BJERRING, who, partly on the basis of East Greenland material, is engaged in studies of the comparative anatomy and phylogeny of the parts of the skull surrounding the hypophysis.

The material of post-Triassic fossil vertebrates from East Greenland is inconsiderable. A well preserved head of a ganoid fish from the Upper Jurassic was described by ALDINGER¹⁸, but unfortunately all the material collected later, which included both fishes and reptiles (probably mainly plesiosaurs), was destroyed during the war.

The fruitful collecting work in East Greenland has now ceased but that does not mean that the vertebrate fossils have played out their role. Important parts of the material are still undescribed or have not been

fully utilized. This is true of the outstanding collections of Triassic fishes, and it is also true of those Devonian vertebrates which have bearing upon the problem of the origin of the tetrapods, that is in the first place the porolepiform crossopterygians and the ichthyostegals (ichthyostegids and acanthostegids).

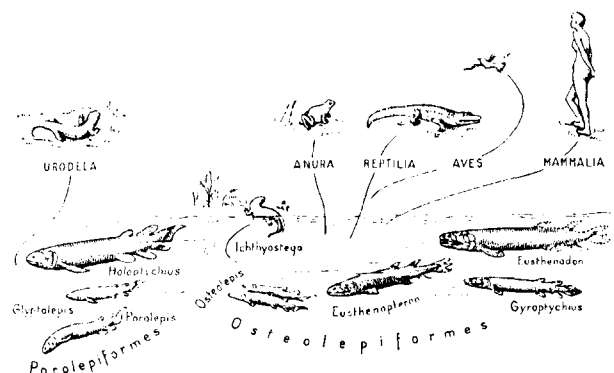


Fig. 1. Diagram of the phylogeny of the tetrapods. From JARVIK¹⁹. In addition to the ichthyostegals (ichthyostegids and acanthostegids), which are known only from the Upper Devonian of East Greenland, the genera *Glyptolepis* and *Holopterychius* among the porolepiforms, and the genera *Gyropterychius* and *Eusthenodon*, among the osteolepiforms, are represented in East Greenland.

The discovery of the Devonian ichthyostegids²⁰ in 1931 is one of the great events in the history of vertebrate paleontology, comparable to the discovery of the famous Jurassic toothed bird *Archaeopteryx* sixty years earlier. The ichthyostegids are not only the oldest tetrapods known so far. In many respects they are fishlike and more primitive than any other tetrapods, and in a most illustrative way they bridge the gap between fish and tetrapod. Moreover, they are represented by a large and well preserved fossil material. Needless to say this unique material is of great scientific value and indispensable to unravel the changes which took place in one of the most important phases in the history of the vertebrates—the transition from fish to tetrapod. However, to understand what really happened when the fishes left the water and became land animals and to understand also the complicated type of organization we meet in the early tetrapods, it is necessary to

⁸ E. STENSIÖ, *Permian Vertebrates*. Geology of the Arctic (University of Toronto Press, 1961), p. 231.

⁹ T. ØRVIG, K. Vet. Akad. Ark. Zool. 2, 321 (1951).

¹⁰ E. STENSIÖ, Medd. om Grønland 83, 1 (1932).

¹¹ E. NIELSEN, Palaeozoologica Groenlandica 1, 1 (1942).

¹² E. NIELSEN, Palaeozoologica Groenlandica 3, 1 (1949).

¹³ G. SÄVE-SÖDERBERGH, Medd. om Grønland 98, 1 (1935).

¹⁴ G. SÄVE-SÖDERBERGH, K. Vet. Akad. Ark. Zool. 36 A, 1 (1944).

¹⁵ E. NIELSEN, Medd. om Grønland 72, 1 (1954).

¹⁶ G. SÄVE-SÖDERBERGH, K. Vet. Akad. Ark. Zool. 26 A, 1 (1934).

¹⁷ G. SÄVE-SÖDERBERGH, K. Vet. Akad. Handl. 16, 1 (1936).

¹⁸ H. ALDINGER, Medd. om Grønland 86, 1 (1932).

¹⁹ E. JARVIK, *Théories de l'évolution des Vertébrés inférieurs* (Masson & Cie, Paris 1960).

²⁰ G. SÄVE-SÖDERBERGH, Medd. om Grønland 94, 1 (1932).

know from which kind of fishes the tetrapods evolved, and we must be familiar, too, with the detailed structure of the ancestral fish. May be the greatest importance of the discovery of the ichthyostegids was, after all, that it increased the interest in the problem of the origin of the tetrapods.

In 1932, when the ichthyostegids were first described by SÄVE-SÖDERBERGH²⁰, the origin of the tetrapods was still obscure, but it was suspected that they were descendants of some Devonian fishes, either of rhipidistid crossopterygians or of dipnoans. SÄVE-SÖDERBERGH therefore had to pay attention to these two groups, which at that time were incompletely known, and it was for this reason that he made the study of *Osteolepis*² mentioned above. Later investigations^{21, 22} eliminated the dipnoans as possible ancestors of tetrapods, which are all descendants of rhipidistids. However, as was first established by my studies of the snout²¹ twenty years ago, the rhipidistids include two widely separate groups, the *Porolepiformes* and the *Osteolepiformes*. Both these groups independently gave rise to tetrapods: the porolepiforms to the urodeles, and the osteolepiforms to the ichthyostegals and most other stegocephalians, the anurans, and the amniotes (Figure 1).

Thanks to excellent *Eusthenopteron* material from Canada, we have a most detailed knowledge of the structure of one representative of the Devonian osteolepiforms^{21–26} and we have a good knowledge of the exoskeleton in several other forms³. We are thus in the fortunate position to be able to compare the ichthyostegids with their immediate ancestors among fishes. Such comparisons were made with respect to the dermal bones of the head, the vertebral column, and the skeleton of the median fins^{20–23}. However, studies of the paired fins and their transformation into the tetrapod limb are in progress, and comparative studies of the skull are planned. The material available thus enables us to make out in detail the changes occurring at the transition from fish to tetrapod in the osteolepiform-tetrapod stock. However, the researches on the osteolepiforms and the ichthyostegids now going on have also other, and for us as human beings most interesting, aspects. Man and other mammals are descendants of the osteolepiforms, too, and by studying these ancient fossil vertebrates, we also throw light upon a remote but significant phase in our own prehistory, and, as will be exemplified below, we can now better than before understand many structural details in human anatomy and embryology.

Up to quite recently, the other group of fishes giving rise to tetrapods, the porolepiforms, was incompletely known. The snout of an early representative (*Porolepis*) was described in detail in 1942²¹, and several years ago I started a description of the remainder of the porolepiform material at my disposal. However, this material, consisting mainly of specimens of *Porolepis*

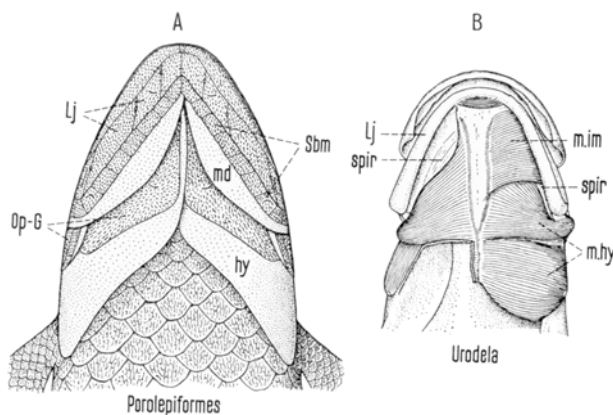


Fig. 2. A, restoration of the head of *Holoptychius* in ventral aspect to show the skin flaps of the mandibular (md) and hyoidean (hy) gill-covers, and the series of supporting dermal bones, the submandibular series (Sbm) along the lower jaw (Lj) and the operculo-gular series (Op-G) of the hyoidean gill-cover. Made mainly on the basis of material from East Greenland. B, head of larva of urodele (*Salamandra*) in ventral aspect. The skin removed to show the musculature of the mandibular (m.im, musculus intermandibularis) and hyoidean (m.hy) gill-covers. The m. intermandibularis of the right side removed to expose the persisting ventral portion (spir) of the spiracular gill-slit. From JARVIK²⁴.

lepis from the Lower Devonian of Spitsbergen and of *Holoptychius* from the Upper Devonian of East Greenland, is in many respects incomplete and important parts of the endoskeleton of the head and body are lacking. It was therefore most fortunate that in 1956, the last year Dr. KOCH had the opportunity to arrange collecting work in the Devonian of East Greenland, several excellent specimens of *Glyptolepis* were found in the Middle Devonian of Canning Land. This outstanding new material shows well the endoskeleton of both head and body, and an almost complete description of the structure of the porolepiforms, too, can now be given. Preparation of some of the specimens and a grinding series through one of the well preserved heads, which is now in progress, have revealed numerous new interesting structural details^{24, 25}. New urodele-like characters in the snout have thus been discovered, and it is of particular importance to note that the ventral part of the branchial basket (the hyobranchial skeleton) and the underlying subbranchial series are developed very much as in urodele larvae (see Figure 4). These and many other new facts prove definitively that the urodeles are closely related to, and descendants of, the porolepiforms, and that accordingly the tetrapods are diphyletic in origin (Figure 1). Quite in accordance with these conclusions, too, are the surprising results which were recently gained²⁴ concerning the

²¹ E. JARVIK, Zool. Bidr. Uppsala 21, 235 (1942).

²² E. JARVIK, Medd. om Grönland 114, 1 (1952).

²³ E. JARVIK, K. Vet. Akad. Handl. 6, 1 (1959).

²⁴ E. JARVIK, K. Vet. Akad. Handl. 9 (will be published in 1963).

²⁵ E. JARVIK, Les Porolepiformes et l'origine des Urodèles. Colloque International du C.N.R.S. 104 (Paris 1961). 'Problèmes actuels de Paléontologie' (1962).

²⁶ E. JARVIK, K. Vet. Akad. Handl. 5, 1 (1954).

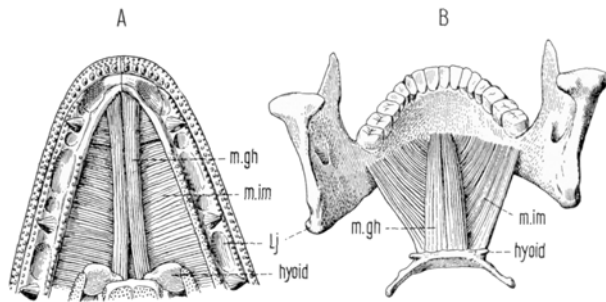


Fig. 3. The muscles of the floor of the mouth cavity of, *A*, Devonian osteolepiform (*Eusthenopteron*; attempted restoration) and, *B*, *Homo* (after SPALTEHOLZ). *m.im*, musculus intermandibularis (mylohyoideus in man) of the mandibular gill-cover; *m.gh*, musculus geniohyoideus.

composition of the floor of the mouth cavity and the origin of the tetrapod tongue. Since these results in essential respects rest upon the Devonian porolepiform material from East Greenland, and since they may be of a general interest, a brief review will be given.

On the lower side of the head in the rhipidistids (Figure 2A) two series of dermal bones, the operculo-gular and the submandibular series, may be distinguished in the area between the lower jaws. The operculo-gular series, which is found in other teleostome fishes too, is composed of branchiostegal rays, proved to be the supporting elements of the main or hyoidean gill-cover. A most remarkable but previously overlooked fact is that in all gnathostomes this gill-cover has antero-laterally fused with another well developed gill-cover. The latter is carried by the lower jaw and is the persisting original gill-cover of the mandibular arch (Figure 5A). The submandibulars, which, as far as the teleostomes are concerned, are present only in porolepiforms and osteolepiforms, are the persisting supporting elements of the mandibular gill-cover, serially homologous to the branchiostegal rays of the hyoidean gill-cover. A remarkable fact is that in the porolepiforms (Figure 2A) even the skin flap (*md*) of the mandibular gill-cover was retained, which is to be considered as a very primitive condition. The mandibular gill-cover has always fused with that of the other side in the median line and usually it has become modified in various other ways, too. However, the musculature (Figures 2B, 3, 5) which is represented mainly by the *m. intermandibularis* or, as it is generally called in mammals, the *m. mylohyoideus*, has been retained with surprisingly small changes and is well developed even in man. The intermandibular muscles of both sides, which have fused in the median line or meet in a median raphe, generally form a thin muscular sheet stretched between the lower jaws. As may be gathered from Figure 3, there is no important difference in this respect between man and his Devonian forerunners, and in man, as in other gnathostomes, the mandibular gill-cover is an important constituent of the floor of the mouth cavity.

Inside the mandibular gill-cover, between the mandibular and hyoid arches, there is often a pocket, which, as proved by the conditions in *Eusthenopteron*, is a vestige of the ventral portion of the gill-slit between these arches. This gill-slit, the spiracular gill-slit (Figures 2B, 5A-C, 6), is generally well developed in embryos, but according to current views only a postero-dorsal portion persists in the adult (spiraculum in fishes, tympanic cavity in tetrapods). It was therefore surprising to find that also a ventral portion is often retained in the adult. This portion may be recognized even in man and is the pocket which contains the main portions of the salivary glands. These glands in the human embryo arise in the tissues lining the inner side of the *m. intermandibularis* (mylohyoideus). In other words they arise on the inner side of the mandibular gill-cover (see Figure 5B), and since the latter forms part of the outer wall of the spiracular gill-slit, they may be regarded as derivatives of that gill-slit.

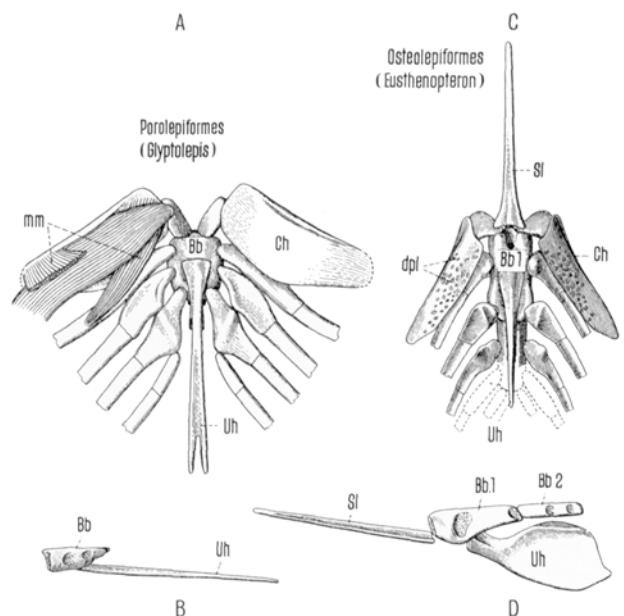


Fig. 4. *A, C*, the hyobranchial skeleton and the subbranchial series in ventral aspects, and, *B, D*, the basibranchial and subbranchial series in lateral aspects to show the differences between, *A, B*, the porolepiforms and, *C, D*, the osteolepiforms. In the osteolepiforms there are two basibranchials (*Bb1, Bb2*) and two elements in the subbranchial series: the sublingual rod (*SI*) and the urohyal (*Uh*). In the porolepiforms there is only one basibranchial (*Bb*), the sublingual rod is lacking, and in sharp contrast to conditions in the osteolepiforms, too, the urohyal is a narrow rod, bifurcating posteriorly. In all these respects the porolepiforms agree closely with the urodele larva. Moreover, the branchial arches articulate with each other in the way characteristic of urodeles, and the external side of the ceratohyal (*Ch*) carried muscles (*mm*) arranged exactly as in urodele larvae. In the osteolepiforms the external side of the ceratohyal is covered by dental plates (*dpl*), situated in the medial wall of the spiracular gill-slit.

From JARVÍK²⁴.

Close above the medial parts of the muscles of the mandibular gill-covers a strong paired muscle, the geniohyoideus, extends forwards to the symphysis of

the lower jaws, and in this respect, too, there is remarkable agreement between man and his piscine ancestors (Figures 3, 5A–D). The geniohyoideus belongs to the hypobranchial musculature. Other muscles of this category are the overlying hyoglossus and genioglossus, which constitute the main muscles of the tongue. As was recently proved²⁴, the hypobranchial muscles, both in fish and tetrapod, are supported by a special series of endoskeletal elements, the subbranchial series. This series (Figures 4, 5A–D) was first recognized and described in the osteolepiforms (*Eusthenopteron*²⁶), but, thanks to the new material of *Glyptolepis* from East Greenland, it is now well known in the porolepiforms, too. However, the series is differently developed in the

osteolepiforms and the porolepiforms, a condition which, as we shall now see, is of fundamental importance for the understanding of the origin of the tetrapod tongue.

In the osteolepiforms (*Eusthenopteron*; Figure 4C, D) the subbranchial series consists of two elements, the sublingual rod, which is of special interest in this connection, and the urohyal. The sublingual rod supported the anterior parts of the hypobranchial muscles and together with them it formed a distinct median elevation, the tuberculum impar, in the floor of the mouth cavity. The tuberculum impar (Figures 5B–D, 6A–C), which is situated in front of the site of the thyroid invagination (foramen caecum in man), is found in embryonic stages of all those tetrapods (anurans, reptiles, birds, mammals) which are descendants of the osteolepiforms, but not in the urodeles. In connection with the growth of the genioglossus and hyoglossus muscles in ontogeny, the tuberculum impar swells (Figure 5 D) and in the adult it forms the whole or, as in the amniotes, the main part of the tongue. In the amniotes the mucous membrane of the inner side of the mandibular gill-cover forms a kind of fold, the lateral lingual swelling (Figures 5B, 6A, C), which gradually grows over and replaces the original mucous membrane of the tuberculum impar. The mucous membrane of

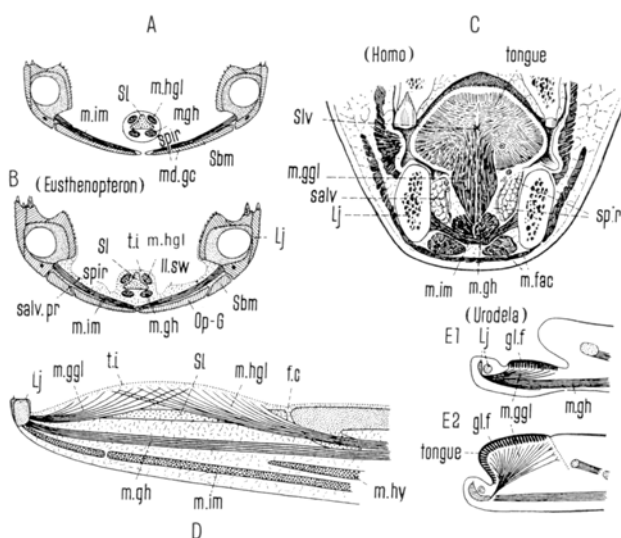


Fig. 5. A–C, three transverse sections through the floor of the mouth cavity to illustrate the general composition and the differences and resemblances between man and his Devonian forerunners. A, B, Devonian osteolepiform (*Eusthenopteron*). In order to show the composition the main constituents (the lower jaw with the mandibular gill-cover, and the hypobranchial muscles with the supporting sublingual rod) are drawn separate in A. In B the approximate position of the salivary glands and the lateral lingual swelling of the amniotes are indicated. In man (C) the musculature of the mandibular gill-cover (*m.im*) and the geniohyoid muscles (*m.gh*) have retained their original position (Figure 3); the tuberculum impar has grown to form the main part of the tongue and has got a new mucous membrane derived from the lateral lingual swelling; the sublingual rod has become reduced but often persists as a row of small cartilages (*Slv*); the salivary glands have increased in size and fill the spiracular gill-slit; and finally superficial facial muscles (*m.fac*; probably derivatives of the musculature of the hyoidean gill-cover) have developed. D, E, longitudinal sections to demonstrate some fundamental differences in the evolution of the tongue between, D, the osteolepiform-tetrapod and E 1, E 2, the porolepiform-tetrapod stocks. D, primitive tetrapod stage (based on conditions in *Eusthenopteron*), E 1, E 2, two stages in the ontogenetic development of the tongue in urodele larva (*Triturus*; after KALLIUS). A, B, D, E, from JARVIK²⁴, C, from SPALTENHOLZ. *Lj*, lower jaw; *Op-G*, operculo-gular series; *Sl*, sublingual rod; *Slv*, approximate position of vestiges of sublingual rod in human tongue (marked with x). *f.c.*, foramen caecum (site of thyroid invagination); *gl.f.*, glandular field of Kallius; *ll.sw*, lateral lingual swelling; *md.gc*, mandibular gill-cover; *m.fac*, facial muscles; *m.ggl*, musculus genioglossus; *m.hgl*, musculus hyoglossus; *m.hy*, musculature of hyoidean gill-cover; *m.im*, musculus intermandibularis (m. mylohyoideus in man); *salv*, salivary gland; *salv.pr*, presumed position of primordium of ditto; *spir*, prehyoid part of ventral portion of spiracular gill-slit; *t.i.*, tuberculum impar.

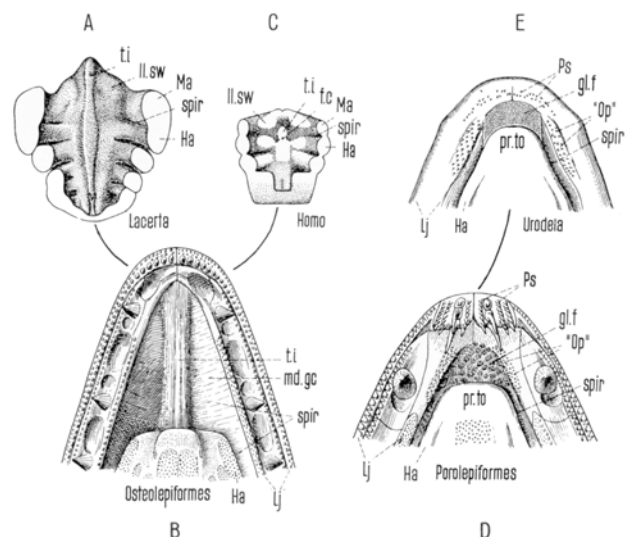


Fig. 6. Diagrams of the evolution of the tongue in, A–C, the osteolepiform-tetrapod stock and, D, E, the porolepiform-tetrapod stock. The floor of the mouth cavity in dorsal aspect of, A, embryo of reptile (*Lacerta*; after KALLIUS), B, Devonian osteolepiform (*Eusthenopteron*), C, *Homo* (embryo, fifth week; after NELSEN), D, Devonian porolepiform (after material of *Glyptolepis* and *Holoptychius* from East Greenland), and, E, urodele larva (*Triturus*). From JARVIK²⁴. *Ha*, hyoid arch; *Lj*, lower jaw (mandibula); *Ma*, mandibular arch; *Op*, the so-called opercular of urodele larvae and its equivalent in porolepiforms; *Ps*, teeth of parasymphysial dental plate of porolepiforms and their equivalents in urodele larva. *f.c.*, foramen caecum; *gl.f.*, glandular field of KALLIUS in urodele larva and its equivalent (prolingual field) in porolepiforms; *ll.sw*, lateral lingual swelling; *md.gc*, mandibular gill-cover; *pr.to*, primitive tongue (*Fischzunge* of KALLIUS); *spir*, ventral portion of spiracular gill-slit; *t.i.*, tuberculum impar.

the dorsal side of the tongue in amniotes and thus in man, too, is accordingly derived from the mandibular gill-cover, and this explains why this membrane is innervated by a branchial nerve (n. trigeminus). Another remarkable fact is that the sublingual rod is retained in all the descendants of the osteolepiforms. In man it is represented by a row of small cartilages, which is frequently found in embryos, and sometimes in the adult, in or just below the median septum of the tongue (*Shv*, Figure 5C).

In the porolepiforms (*Glyptolepis*) the sublingual rod is lacking, as in the urodeles. The subbranchial series consists only of the urohyal and, as pointed out above, this element and the overlying hyobranchial skeleton are developed fundamentally as in urodele larvae (Figure 4A, B). In these respects, there are thus very great resemblances indeed between the urodeles and the porolepiforms, and other most striking similarities are found farther forwards in the floor of the mouth cavity (Figure 6D, E). The anterior part of each of the jaws of the porolepiforms thus carries peculiar tooth-bearing structures (*Ps*, '*Op*'), which can easily be identified in urodele larvae but are lacking in all other tetrapods, and between the jaws there is a crescent-shaped field (*gl.f*) of dental plates. This field, the prolingual field, no doubt contained glands and undoubtedly it corresponds to the similarly situated, also crescent-shaped glandular field of KALLIUS, which is characteristic of the urodele larva and plays an important part in the formation of the tongue in this group of tetrapods (Figure 5 E1, E2). Fibres of one of the hypobranchial muscles, the genioglossus (a true m. hyoglossus is lacking in the urodeles) grow up into the

glandular field and the floor of the mouth cavity in the area of that field rises and forms the tongue of the adult.

The tongue is thus formed in a different way in the urodeles, on the one hand, and in the anurans and the amniotes, on the other; and, as is now evident, this is due to the remarkable differences between the porolepiforms and the osteolepiforms in the structure of the floor of the mouth cavity (Figures 4, 6B, D). The fact that, in the detailed structure of this part of the head, the porolepiforms agree closely with larvae of urodeles — there are hardly any other differences than such as refer to the degree of ossification — whereas the osteolepiforms in all essentials are as anurans and amniotes, is in full accordance with the results gained by the studies of the snout^{21,25}, and that the tetrapods are diphyletic in origin (Figure 1) cannot be doubted any longer.

Zusammenfassung. Kurzer Bericht über die dänischen Expeditionen nach Ostgrönland (LAUGE KOCH) 1929–1957. Die zoologische Bedeutung des fossilen Vertebratenmaterials (über 10000 Exemplare) wird angedeutet. Neuere Ergebnisse über die Evolution der Tetrapoden zunge werden besonders im Zusammenhang mit Grönlandmaterial besprochen. Damit wird die Ansicht bestätigt, dass sich die Urodelen selbständig aus porolepiformen Crossopterygiern entwickelt haben, während Anuren, Sauropsiden und Säugetiere von Osteolepiformiern abzuleiten sind. Die Auswertung des umfangreichen Fossilmaterials ergibt eine diphyletische Herkunft der Tetrapoden.

The Jurassic Ammonite-Faunas of East Greenland

By J. H. CALLOMON*

To those geologists primarily interested in the grander aspects of the science such as the tectonics of mountain-building, or the petrology of igneous and metamorphic processes, the Mesozoic era has relatively little to offer, for it marked a period of comparative calm in movements of the earth's crust. This quiescence is one of three main factors which make Mesozoic rocks particularly suited for stratigraphical studies. The second is that in two of the three systems which make up the Mesozoic, namely the Jurassic and Cretaceous, relatively shallow seas covered a considerably greater proportion of the earth's surface than they do at present, leaving widely-spread sheets of usually little-disturbed sediments now readily accessible and well exposed. The third factor is that the Mesozoic period

marked the acme in development and abundance of the ammonites.

The stratigrapher classifies rocks according to the fossils they contain. In correlating beds found at different places, and generalizing his finding into a standard succession, or geological column applicable to a whole area, he makes use of what we may call the first principle of stratigraphy: *rocks containing the same fossils are of the same age*, with the more trivial extension that in undisturbed sediments, the higher beds are the younger. The evolution of fossils is made the basis of

* University College London (England).