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ON THE FISH-LIKE TAIL IN
THE ICHTHYOSTEGID STEGOCEPHALIANS

WITH DESCRIPTIONS OF A
NEW STEGOCEPHALIAN AND A NEW CROSSOPTERYGIAN
FROM THE UPPER DEVONIAN OF
EAST GREENLAND

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WITH 36 TEXTFIGURES AND 21 PLATES

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I. INTRODUCTION

The first determinable ichthyostegid stegocephalians were collected by G. SÄVE-SÖDERBERGH and his assistants during the Danish East-Greenland expedition in 1931 under the leadership of Dr. LAUGE KOCH. The material, consisting of seven more or less complete skulls, was described in the following year by SÄVE-SÖDERBERGH, at that time a student only twenty-two years old, in a paper well-known to every vertebrate paleontologist (SÄVE-SÖDERBERGH 1932b). Two genera, *Ichthyostega* and *Ichthyostegopsis*, were erected and referred to the family *Ichthyostegidae* forming the order *Ichthyostegalia*.

The material had been collected on the northern slopes of Celsius Bjerg (Mt. Celsius) on Ymers Ø (Ymer Island) in Kejser Franz Josephs Fjord (fig. 1), and after a detailed comparison of the accompanying fish-fauna with similar fish-faunas in other parts of the world, SÄVE-SÖDERBERGH—in another paper (1932a)—arrived at the conclusion that the stegocephalian-bearing deposits in Celsius Bjerg are Upper Upper Devonian in age. This age determination has been doubted and it has been assumed that the deposits in question are somewhat younger, being lowermost Carboniferous. However, later investigations (JARVIK 1948b; 1950b) have fully confirmed SÄVE-SÖDERBERGH's opinion and it may now be considered definitely established that the ichthyostegid-bearing deposits in Celsius Bjerg and elsewhere in East Greenland, the Remigolepis Series, are Devonian. The ichthyostegids are thus the oldest known tetrapods.

The discovery of indisputable tetrapods in the Devonian and the abundance of other interesting fossil vertebrates (placoderms, dipnoans, crossopterygians) in the Greenland Upper Devonian naturally prompted further search for fossils, and on most of Dr. KOCH's scientific summer expeditions to East Greenland since 1931 one or two parties, each of 3—6 members, have been given the special task to continue the fossil-collecting in the Upper Devonian.

Thus in 1932 SÄVE-SÖDERBERGH (SÄVE-SÖDERBERGH 1933), assisted inter alia by the present writer, revisited the northern slope of Celsius Bjerg and discovered richly fossiliferous strata belonging to the Remigo-

lepis Series in the area from Smith Woodward's Bjerg to Nathorst's Bjerg along the northern coast of Kejser Franz Josephs Fjord in Gauss Halvø (Gauss Peninsula; fig. 1). Additional ichthyostegid material and the holotype of the new stegocephalian *Acanthostega* (see p. 69) are among the fine finds from that year. In 1933 SÄVE-SÖDERBERGH (SÄVE-SÖDERBERGH 1934), assisted by G. WÄNGSJÖ and others, made fine collections of fishes in the localities in Gauss Halvø discovered the year before and found richly fossiliferous sediments belonging to the Phyllolepis and Remigolepis Series in the Paralleldal (Parallel Valley) in Gauss Halvø (fig. 1). Only inconsiderable remains of stegocephalians were found that year, but a very good skull of a large dipnoan and a remarkable vertebrate column of another dipnoan were secured (see p. 41). In 1934 SÄVE-SÖDERBERGH made stratigraphical investigations in the area of Kejser Franz Josephs Fjord, and the present writer assisted by G. WÄNGSJÖ and others was given the task to collect fossils in the Paralleldal (JOHANSSON 1935). Besides fishes, several good skulls of ichthyostegids and important material of the postcranial skeleton were secured. In 1936 SÄVE-SÖDERBERGH again visited the Paralleldal. Among the material from that year is a small skull of the new crossopterygian *Eusthenodon* described below and good additional material of stegocephalians including one of the four nearly complete tails so far known. In 1947 the present writer searched for fossils on the southern slope of Celsius Bjerg, where inter alia a few ichthyostegids, another skull of *Acanthostega*, and further material of *Eusthenodon* were found. In 1948 the present writer together with G. WÄNGSJÖ revisited the northern slope of Celsius Bjerg—the excellent tail and hind foot shown in pl. 2 were found here—and made further collections in the area from Smith Woodward's Bjerg to the Agda Dal along Kejser Franz Josephs Fjord. Among the fossils obtained in the latter area is a very fine ichthyostegid specimen, showing besides the posterior part of the skull considerable parts of the postcranial skeleton with inter alia the shoulder girdles and the humerus of both sides extremely well preserved. In 1949 a fourth visit was paid to the Paralleldal, where Dr. WÄNGSJÖ and his assistants made very fine collections. Two additional ichthyostegid tails, a very good hind limb with remains of the pelvis and the other limb, other parts of the postcranial skeleton, several fine skulls together with a beautiful skull-material of *Eusthenodon* were collected at 1174 m. in the middle part of Sederholms Bjerg (fig. 1), a locality discovered in 1934 and the most

Fig. 1. Map of the western part of Gauss Halvø and the eastern part of Ymers Ø, East Greenland. From Sheet 73.6.2. Geodetic Institute, Copenhagen 1937. The Devonian stegocephalians originate from the southern slope of Sederholms Bjerg and the area to the south of the Paralleldal in Gauss Halvø and from the northern and southern slopes of Celsius Bjerg, Ymers Ø.

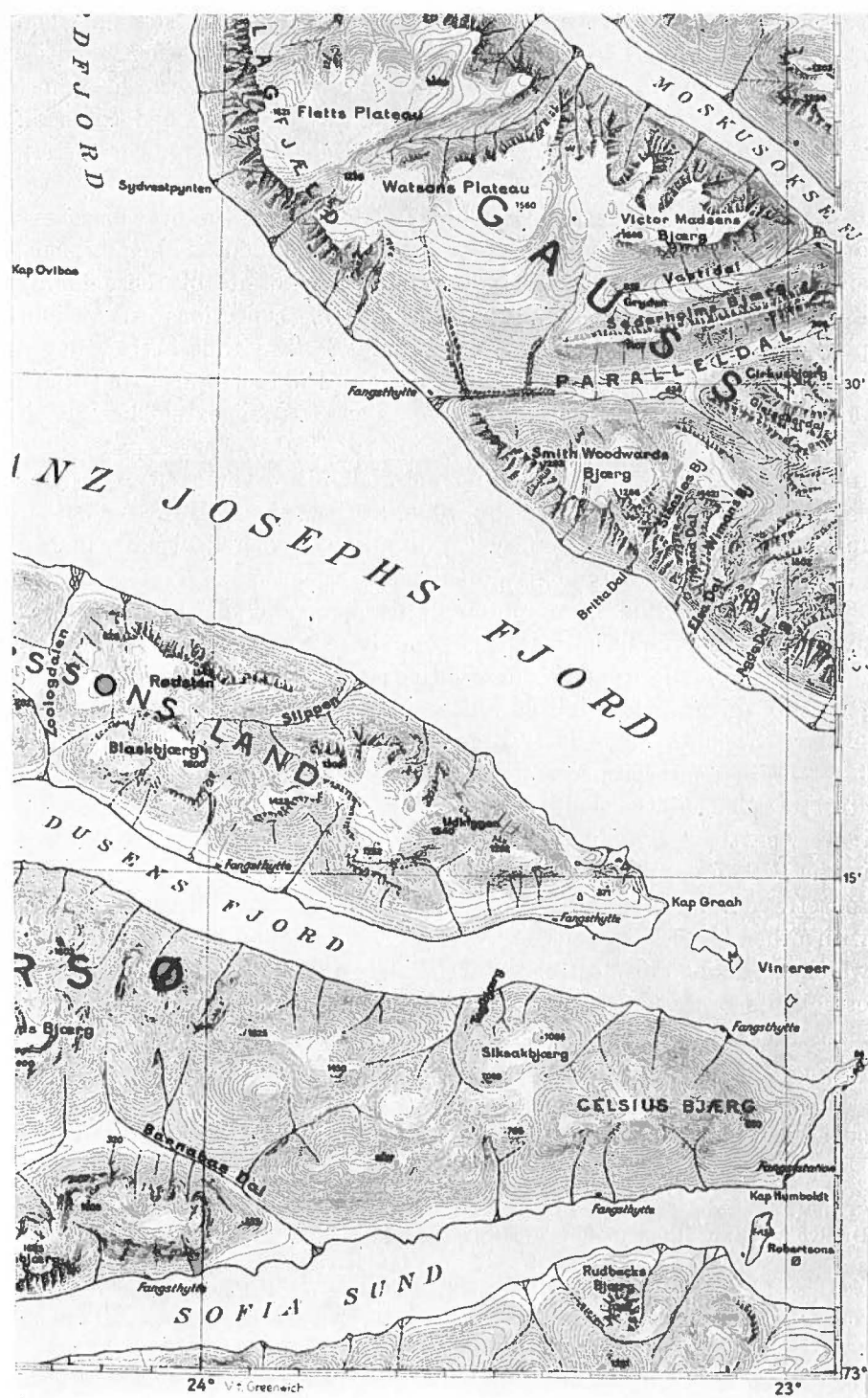


Fig. 1.

prolific stegocephalian locality hitherto known in the Devonian. Good material of ichthyostegids and *Eusthenodon* was found in other localities in the Paralleldal as well. In 1950 bad ice-conditions prevented almost all collecting in the Upper Devonian, and Dr. WÄNGSJÖ had to spend most of his time that summer in the Middle Devonian area in the eastern part of Gauss Halvø.

During the two decades that have elapsed since the first discovery of Devonian stegocephalians a great material (about 170 specimens, about 110 of them showing the skull or part of it) of these highly interesting forms, together with magnificent collections of various placoderms, dipnoans and crossopterygians¹⁾ have thus been brought home from the Greenland Upper Devonian. The crossopterygians have been entrusted to me for description and have to some extent been dealt with in previous papers (JARVIK 1942; 1948a; 1950a), whereas, according to the original plan, the outstanding material of Devonian stegocephalians should have been described by SÄVE-SÖDERBERGH. However, other tasks and a serious pulmonary consumption, which kept him in bed almost all the time from his appointment to professor in Uppsala in 1937, prevented him from fulfilling this plan, and after his death in June 1948 that material was also committed to me.

As is evident from the descriptions of the tail and certain other structures given below and as will be further elucidated in forthcoming papers, the ichthyostegids are unexpectedly fish-like in many respects. If we desire to interpret correctly the various and many times complicated structures both in the skull and in the postcranial skeleton, and especially if we want to make out and understand the changes which took place in the skeleton and associated structures during the transition from fish to tetrapod, it is necessary to make detailed comparisons not only with other lower tetrapods but also with fishes, first of all with those which no doubt are most closely related to the ichthyostegids, i. e. the osteolepiform crossopterygians. However, the osteolepiform crossopterygians are as yet imperfectly known and it will be necessary for me to go on with my investigations of the *Osteolepiformes*²⁾ alongside of my studies of the ichthyostegids. Besides, the development of the stegocephalian material, which generally is contained in a very hard and

¹⁾ Additional material of stegocephalians, crossopterygians, etc. was collected in the Paralleldal and in Celsius Bjerg by the present writer and assistants during Dr. KOCH's expedition to East Greenland in 1951.

²⁾ For that purpose I am fortunate enough to have at my disposal the extremely well preserved material of both the skull (including a grinding series of a nearly complete and almost uncrushed skull) and the postcranial skeleton of *Eusthenopteron foordi* in the possession of the Paleozoological Department of the Swedish Museum of Natural History, and other important material of this and other crossopterygians.

tough, fine-grained sandstone, is a difficult and time-consuming task¹). Accordingly, a complete description of the stegocephalians will require a considerable time and even if, as it is planned, my investigations be primarily concentrated upon the postcranial skeleton, it will certainly be a couple of years before a more comprehensive account can be published. Under these circumstances I have found it desirable already now to describe the tail: its structure is very remarkable and it should certainly attract general interest.

As pointed out above (foot-note 1), two different types of humerus are represented in the material and also other postcranial elements show a wide range of variation, indicating that the fauna includes stegocephalians of different types. It is then of interest to find that among the skulls there is one type, represented by two specimens only, which differs so strongly from the ichthyostegids that it cannot be referred to the family *Ichthyostegidae*, and only provisionally and with great hesitation may it be included in the *Ichthyostegalia*. Before I start my planned detailed description of the postcranial skeleton, it will be useful to have this interesting form named and it may therefore be justifiable to include a description of it in this paper. As already mentioned, it has been referred to the new genus *Acanthostega*. Partly for the same reason a brief description will be given of a large osteolepiform crossopterygian, *Eusthenodon wängsjöi* n.g. n.sp., which originates from the same strata as the stegocephalians. For comparative purposes a brief, new description of the vertebral column and the median fin-supports in *Eusthenopteron foordi* has been included, and in addition new data are given with regard to the structure of the vertebral column in early *Dipnoi*.

I am greatly indebted to Dr. LAUGE KOCH, Copenhagen, the leader of the Danish East Greenland expeditions during which this material has been collected, for the great honour to have been entrusted with the so valuable and unique materials of crossopterygians and stegocephalians from the Upper Devonian of East Greenland. My thanks are also due to Dr. KOCH for the great interest he has always taken in the paleontological collecting work and for the ready courtesy and generosity with which he has always granted our requests for assistants, special outfit, etc. It is Dr. KOCH's merit that the short time at our disposal during an arctic summer expedition—usually less than a month—could always be devoted entirely to the collecting work instead of being split

¹) Hitherto, only the best of the material of the postcranial skeleton has been prepared sufficiently well to allow a detailed description and several almost complete and uncrushed specimens of the exoskeletal and endoskeletal shoulder-girdle, the humerus (two quite different types), the radius and ulna, the pelvic girdle, the hind leg and foot and the tail have been disclosed. Most of the comprehensive skull-material remains untouched.

up on various tasks. The importance of this is evident if we consider that the Upper Devonian strata in East Greenland, which have yielded so much and important material of fossil vertebrates, are really comparatively poor in fossils.

The Greenland material belongs to the University of Copenhagen and I also wish to express my sincere gratitude to Professor R. SPÄRCK, Director of the Zoological Museum, where the material is to be stored. For the generous loan of material used for comparative purposes I am greatly indebted to the authorities of the Royal Scottish Museum, Edinburgh, and the Geological Survey and Museum of Great Britain, London.

This paper has been elaborated in the Paleozoological Department of the Swedish Museum of Natural History, Stockholm, and for technical assistance I am indebted to Miss A. BRASCH (preparation), Mr G. AHL (photography) and Mr S. EKBLOM (retouch work and drawings). I also wish to thank Dr. T. ØRVIG for the preparation of a section of the dermal fin-rays.

II. THE TAIL OF THE ICHTHYOSTEGIDS

Material and taxonomy.—The first find of an ichthyostegid tail, No. A. 69 (pl. 1), was made by SÄVE-SÖDERBERGH in the Paralleldal as early as 1936 but it was regarded as a fish-tail and it was not until 1948, when a similar tail, specimen No. A. 109 (pls. 2—4), with a beautiful hind foot and leg and remains of the pelvis almost in their natural position (fig. 5A), was found, that its true nature was revealed. Two additional good tails, specimens Nos. A. 156 (pl. 5), A. 157 (pl. 6), were found in 1949, one of them together with remains of the pelvic bone and hind leg of the left side (fig. 5B). These four tails are almost complete, and on the whole they are well preserved though the skeletal elements sometimes are somewhat displaced. Two of the tails, Nos. A. 69 and A. 156, present the skeleton from the sacral region to the tip of the tail, whereas in No. A. 109 the very tip and in No. A. 157 the most anterior part of the tail are missing. The rock has split along the tails and parts of the bones are found on the counterpart, which is more or less completely preserved in all specimens.

Specimen No. A. 69 is in a large block and the tail is continued forwards by imperfectly preserved remains of the vertebral column and abdominal ribs of the same type as in ichthyostegids in general. Together with these remains are detached shoulder girdles and lower jaws of at least two individuals and an incomplete skull. The latter no doubt belongs to the genus *Ichthyostega* and it may therefore be justifiable to conclude that the tail in No. A. 69 belongs to that genus, too. However, it is impossible to say whether it pertains to one of the species named by SÄVE-SÖDERBERGH or to a new species. The other three tails strongly resemble that in No. A. 69 and are mutually very similar. They no doubt originate from ichthyostegids, but unfortunately they are not connected with any skeletal elements allowing a generic determination. However, the two tails found in 1949 originate from the rich horizon at 1174 m. in the middle part of Sederholms Bjerg, where the fossils occur in a small lense-shaped part of the strata. Since the numerous skulls from this locality are very uniform and, as far as may be judged at present, they belong to a new species of *Ichthyostega*, it is reasonable to assume

that also the two tails belong to the same new species. The fourth tail, No. A. 109, finally, originates from the northern slope of Celsius Bjerg, where the original material and several other specimens of *Ichthyostega* have been found, and since in addition it strongly resembles the other tails it may be referred to that genus as well.

In addition to these four specimens, which thus—at least provisionally—may be referred to the genus *Ichthyostega*, inter alia the following specimens have been used: Nos. A. 54 (fig. 14A), A. 55, A. 132, A. 137, A. 138, A. 139, A. 140 (fig. 14B. C), A. 155, A. 160, A. 164 and A. 166 from the locality at 1174 m. in Sederholms Bjerg; Nos. A. 66 and A. 77 from other localities in Sederholms Bjerg; No. A. 64 from the Remigolepis-ryg; Nos. A. 115, A. 117, and A. 148 from Smith Woodward's Bjerg; Nos. A. 89 and A. 93 from Stensiös Bjerg; Nos. A. 94, A. 97, and A. 99 (fig. 32) from Celsius Bjerg.

All specimens originate from the Remigolepis Series (Upper Upper Devonian) in Gauss Halvø and Ymers Ø.

Description.

The tail of the ichthyostegids (figs. 2, 3, 5—7, 8D) has a very interesting structure in that it is provided with a long distinct median fin supported by skeletal elements of the same kind as in fishes. Besides the vertebral column and the postsacral ribs, the postsacral part of the skeleton—contrary to conditions in all other tetrapods—thus consists of both strong median fin-supports, radials, and dermal fin-rays, lepidotrichia. Small scales covering the tail are found in one specimen.

The pelvis and the hind limb, which are well preserved in the material available, will be described in detail in a forthcoming paper. The pelvis (fig. 5), shown inter alia in Nos. A. 109 (fig. 5A), A. 156 (fig. 5B), A. 54, A. 93, A. 97, A. 132, A. 155, A. 160, A. 164, A. 166, consists of a strong single ossification, the pelvic bone, on each side. Each pelvic bone is ventrally firmly connected with its fellow in a long median symphysis. Dorsally it is provided with a strong posterior process (*pr.Pb*) similar to that found in certain post-Devonian early tetrapods (see e. g. WATSON 1926, fig. 27). In front of this process, on the inner side of the dorsal part of the iliac portion of the bone, there is a very distinct articular area (*art.Sr*), conceivably for a sacral rib. The acetabulum (*ac*) is developed as usual. The hind leg and foot (fig. 5; pl. 2) on the whole agree well with those in *Trematops* (SCHAEFFER 1941) and other early tetrapods. The toes are five in number.

The vertebral column (figs. 2, 3, 6, 8D), from the sacral region backwards, first runs somewhat downwards forming a gentle curve

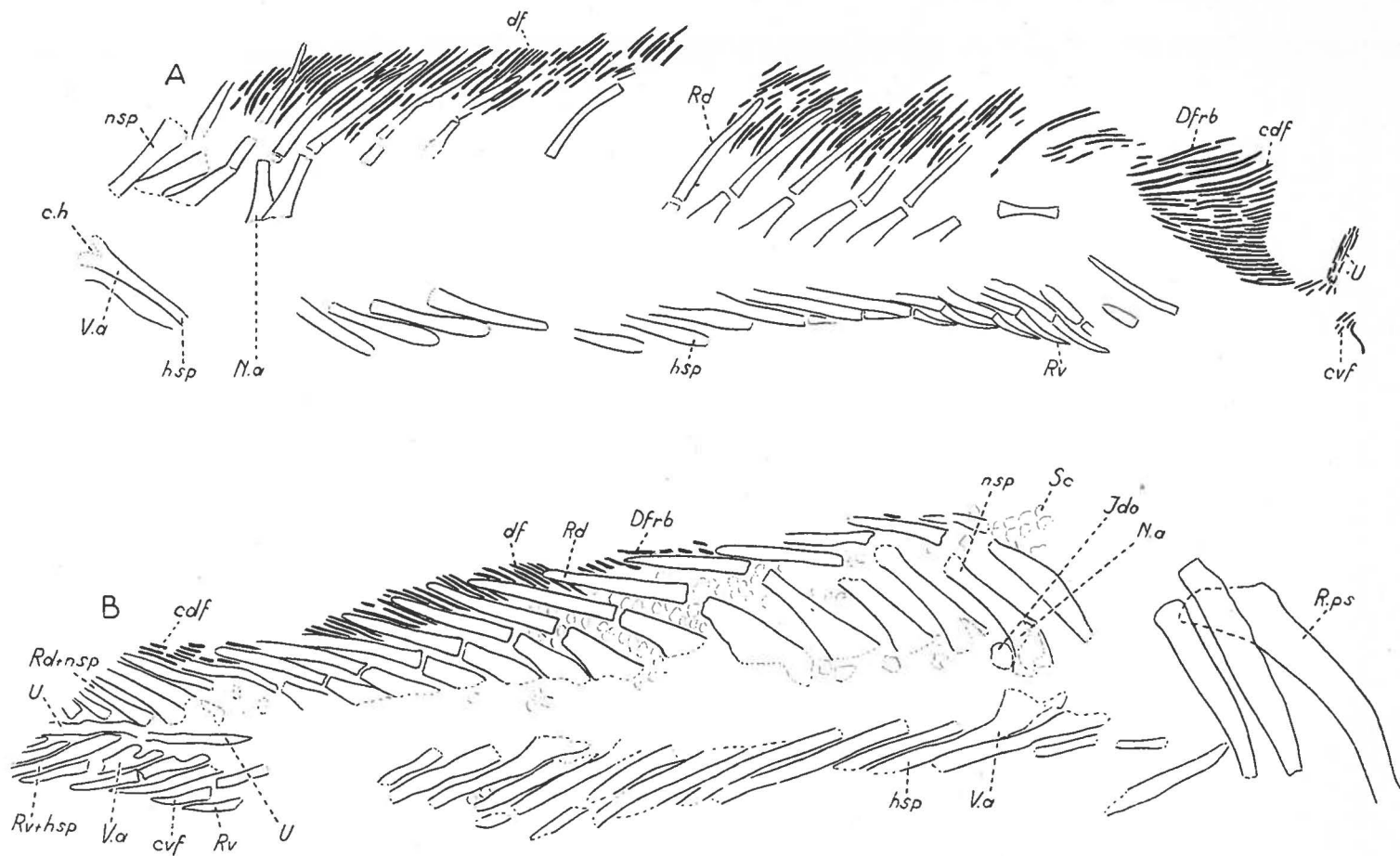


Fig. 2. *Ichthyostega* sp. Sketches of the skeleton of the tail. A, specimen No. A. 69 (pl. 1). 8/9. B, specimen No. A. 109 (pls. 2—4). Nat. size. *Dfrb*, dermal fin-rays; *Ido*, interdorsal; *N.a*, neural arch; *Rd*, dorsal radial; *R.ps*, postsacral rib; *Rd+nsp*, dorsal radial fused with neural spine; *Rv*, ventral radial; *Rv+hsp*, ventral radial fused with haemal spine; *Sc*, scale; *U*, urostyle; *V.a*, ventral vertebral (haemal) arch. *cdf*, dorsal lobe of caudal fin; *c.h*, haemal canal; *cvf*, ventral lobe of caudal fin; *df*, dorsal fin; *hsp*, haemal spine; *nsp*, neural spine.

convex dorsally, and then continues straight backwards to turn slightly upwards in the tip of the tail, as is best seen in No. A. 157 (fig. 3B; pl. 6). The very strong upward bend of the whole tip of the tail found in Nos. A. 69 (fig. 2A; pl. 1) and A. 156 (fig. 3A; pl. 5: 1) is no doubt due to post-mortem deformations. The upturned posterior part of the tail is supported by a rather stout bony rod (*U*; pls. 2—6), which tapers distally and continues nearly to the very tip of the tail. This rod, the urostyle, certainly represents modified vertebral elements, and judging from No. A. 109 (pl. 4) it is pierced by a narrow longitudinal canal for the notochord. In front of the urostyle, which is longer, proportionately, in No. A. 109 than in the other three specimens, the vertebral column is poorly ossified in the central parts and is represented mainly by the neural and haemal spines and adjoining parts of the neural and ventral vertebral arches (as regards the structure of the vertebral column see p. 36). The neural spines (*nsp*) in the main posterior part of the tail are inclined backwards and articulate with a corresponding number of radials. They decrease in height posteriorly and disappear entirely at or a little in front of the anterior end of the urostyle. In the anterior part of the tail the neural spines are forwards gradually transformed into the neural spines of the trunk, which are almost vertical in position with somewhat expanded dorsal ends (fig. 14). The ventral vertebral arches (*V.a*) and haemal spines (*hsp*) in the posterior part of the tail, where they articulate with radials, resemble the corresponding neural arches and spines but seem to be developed also a little behind the anterior end of the urostyle. In the anterior part of the tail, where no ventral radials are developed, the haemal spines are somewhat different in that they are comparatively stout and about equal in length. Moreover, they lie close together and are more posteriorly directed, which causes the distinct shallow depression in the ventral margin of the tail clearly seen in all specimens and which no doubt is natural.

Three displaced postsacral ribs (*R.ps*) are shown in No. A. 109, but judging from another specimen (No. A. 54) they are at least five in number. In the latter specimen (fig. 14A) they are directed posterolaterally and the main distal part of the rib lies almost horizontally (fig. 6). The proximal end, which is expanded dorso-ventrally, articulates dorsally with the neural arch and ventrally with the haemal arch (fig. 13A, B). An interesting feature is that the postsacral ribs run about parallel with the posterior process of the iliac portion of the pelvic bone, and since they are of a corresponding size and somewhat resemble that process it is not impossible that the latter represents a modified postsacral rib, secondarily incorporated in the pelvic bone. No indisputable sacral ribs have been observed so far in the ichthyostegid material available, but, as already mentioned, a distinct articular area (*art.Sr*,

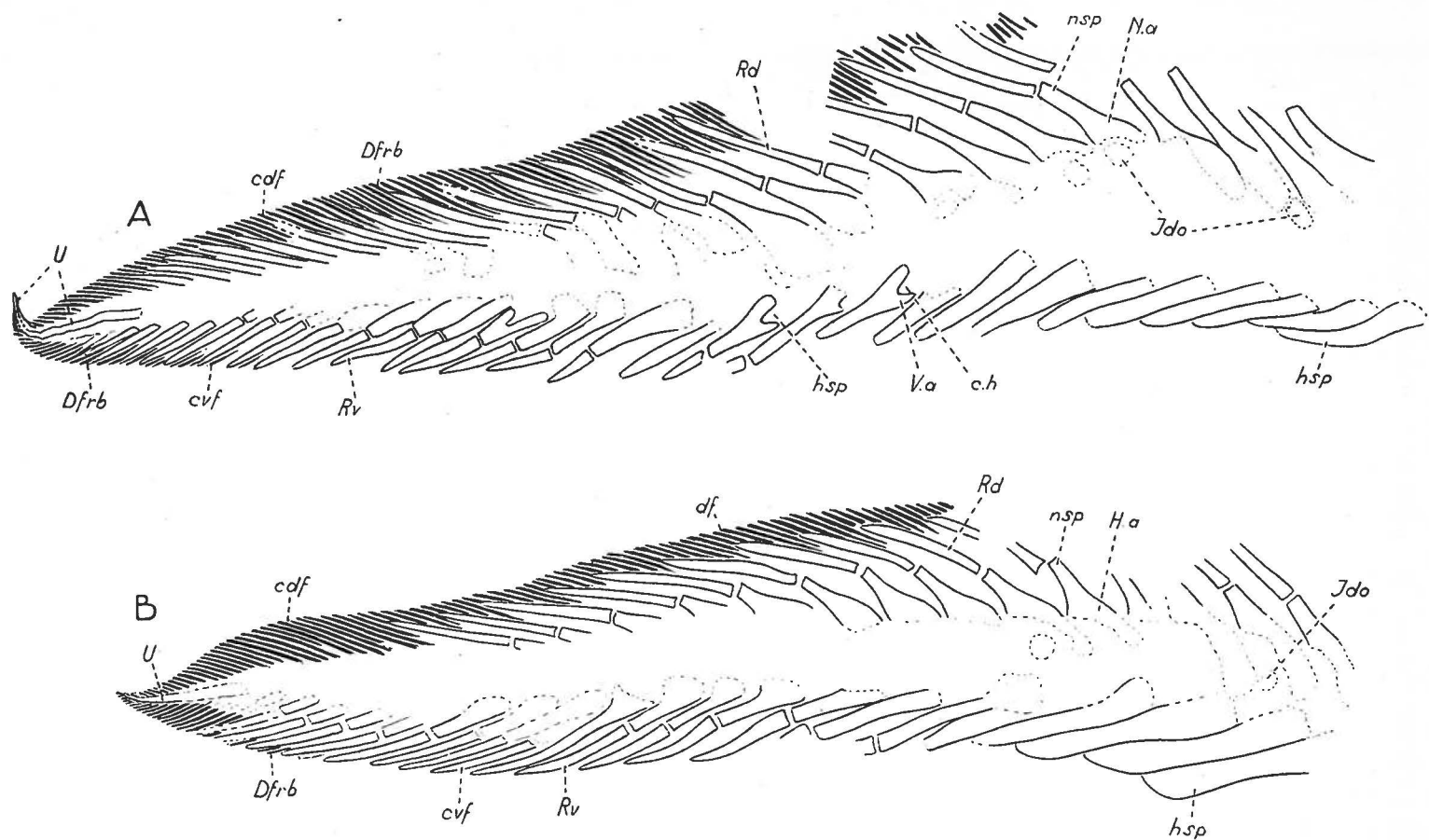


Fig. 3. *Ichthyostega* sp. Sketches of the skeleton of the tail. A, specimen No. A.156 (pl. 5). B, specimen No. A.157 (pl. 6). Nat. size. *Df-rb*, dermal fin-rays; *Ido*, interdorsal; *N.a*, neural arch; *Rd*, dorsal radial; *Rv*, ventral radial; *U*, urostyle; *V.a*, ventral vertebral (haemal) arch. *cdf*, dorsal lobe of caudal fin; *c.h*, haemal canal; *cvf*, ventral lobe of caudal fin; *df*, dorsal fin; *hsp*, haemal spine; *nsp*, neural spine.

fig. 5B) is found on the inner side of the broad dorsal process of the iliac portion of the pelvic bone.

The radials (*Rd*, *Rv*, figs. 2, 3, 5, 6, 8D; pls. 2—6) are long and slender rods pointed distally and arranged in two series, dorsal and ventral. The dorsal series, which consists of about 24 elements, extends farther forwards than the ventral one, which includes about 16 elements. The dorsal radials (*Rd*) run in the same directions as the neural spines, most of them articulating with the distal ends of the latter; the three or four hindmost elements seem to have been supported by the urostyle. All the dorsal radials support dermal fin-rays. In the ventral series (*Rv*), on the other hand, only the hindmost four to six radials are connected with such rays. These hindmost ventral radials resemble the dorsal radials and articulate with the distal ends of the haemal spines, whereas the anterior ventral radials, about ten in number, are slightly modified. Also these elements, which decrease in size forwards, articulate with, or are—in a few cases—continuous with, the distal ends of the haemal spines, but they are slightly bent backwards and lie comparatively close together, especially at their distal ends. These radials form the most ventral part of the skeleton of the tail and no doubt the modifications and the absence of dermal fin-rays are connected with the fact that this part of the tail dragged on the ground when the animal was walking.

The dermal fin-rays (*Dfrb*, figs. 2—7, 8D, pls. 2—6), which are supported by the radials and most posteriorly by the urostyle, are much more (about 5—6 times) numerous than the radials. They are generally of about the same length as the radials or are slightly shorter and may be characterized as comparatively short and stout. They are nearly round, as seen in transverse section, and taper somewhat towards the distal end, which as a rule seems to be pointed. However, they never become so very thin towards the periphery as they do in many fishes, and, in fact, they are most suggestive of the comparatively long proximal segments of the fin-rays for example in *Osteolepiformes* and dipnoans (figs. 8, 10; GOODRICH 1904; JARVIK 1950c, fig. 7, pl. 5: 3).

Like these segments, they are—as far as can be seen—unbranching and unjointed and their pointed proximal ends embrace the distal parts of the endoskeletal fin-supports. However, whereas in the said fishes the fin-rays, as far as known, overlap only the very distal ends of the endoskeletal fin-supports, in the ichthyostegids they overlap the radials to a considerable extent, only about one third of the rays extending beyond the distal tip of the radials. As evidenced by the section shown in fig. 4, the fin-rays contain distinct cell-spaces quite similar to those found in the fin-rays of many fishes (GOODRICH 1904, pl. 39).

Some scales are shown in No. A. 109 (*Sc*, figs. 2B; pls. 3, 4) but are too imperfectly preserved to be described and nothing definitely

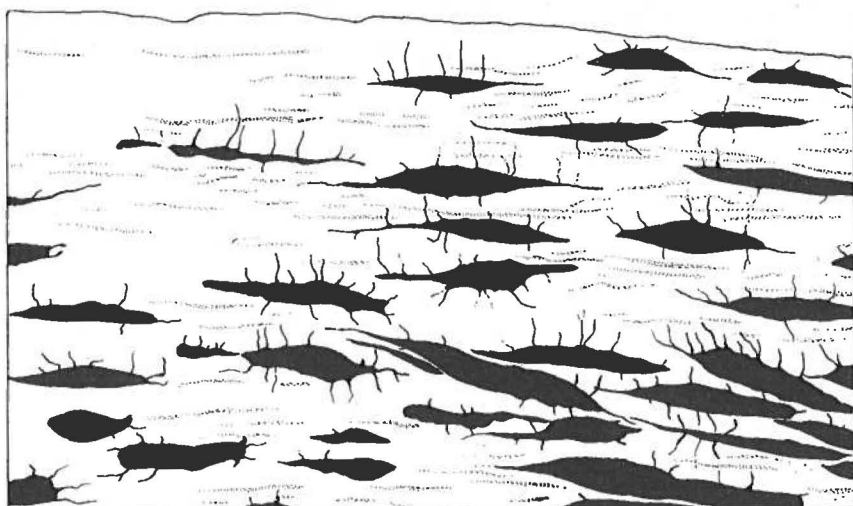


Fig. 4. *Ichthyostega* sp. Part of longitudinal section of dermal fin-ray, mainly showing cell-spaces. After a microphoto (S. 1214). Specimen No. A.69. Ca. 700/1.

can be said as regards their arrangement. They are small and thin and at least most probably rounded. In the present state of preservation they are found proximally to the dermal fin-rays, between the endoskeletal elements of the tail, and it may be assumed that the whole tail was scale-covered as shown in the restoration (fig. 7). It may be mentioned in this connection that in another specimen, No. A. 115, which is one of the best preserved and most complete specimens at my disposal, numerous detached scale-like structures, rectangular or rounded in shape, are found at and below the distal ends of the ribs, and probably the ventral side of the animal was covered with scales as it is in many post-Devonian stegocephalians (see e.g. ROMER 1947, p. 80).

The continuous median fin (figs. 2, 3, 6, 7; pls. 1—6), supported by the radials, the urostyle, and the short and stout dermal fin-rays, is comparatively low and rigid. On the dorsal side it extends from the tip of the tail to a point a little behind the postsacral ribs but its anterior part is not well preserved in any of the specimens and it has been impossible to determine exactly where it ends anteriorly. On the ventral side it may be regarded to end anteriorly at the most anterior of the ventral radials, but as may be gathered from the descriptions above and from the figures only the posterior part of it contains dermal fin-rays. On the dorsal side are two shallow depressions, one posterior where the tip of the tail is upturned and one anterior in which the dermal fin-rays are comparatively short, hardly extending beyond the distal ends of the radials. The latter depression may possibly correspond to the notch occurring at the growth of the tail in the dorsal margin of the caudal

fin or of the continuous dorsal fin in fossil and recent dipnoans (see JARVIK 1948a, p. 105, fig. 31). However, it is more likely to mark the boundary between two incompletely separated fins, one fairly long dorsal fin (*df*) and a heterocercal caudal fin (*cdf*, *cvf*) with a relatively long dorsal and a shorter ventral lobe (cf. p. 24).

In specimens Nos. A. 109 and A. 156 one of the pelvic bones, in No. A. 109 the right and in No. A. 156 the left (together with the left hind foot), are preserved in a position which no doubt is nearly the natural one (fig. 5). Specimen No. A. 109 (fig. 5A; pl. 2) in addition presents parts of the left pelvic bone (*Pb.l*) together with a well preserved hind limb, but these structures have obviously slid somewhat downwards. The pelvic bones are all incomplete in the said specimens but enough is shown to allow the outline to be restored.

Knowing considerable parts of the postcranial skeleton in four specimens and knowing the size and position of the pelvis in two of them, we are able to restore the skeleton of the tail in the ichthyostegids with a fairly high degree of certainty (fig. 6). The tail is fairly small as compared with the pelvic bone (fig. 5), being not quite three times as long as that bone. The number of vertebrae could not be definitely established, but judging from the number of radials, postsacral ribs and ventral vertebral arches in the various specimens it seems likely that there were about 35 vertebrae behind the articular area, conceivably for a postsacral rib, on the inner side of the pelvic bone backwards to the hindmost radial observed. If we assume that the part of the urostyle situated behind that radial contains about 3 vertebrae, the total number of vertebrae in the tail was about 38, that is about the same number as in *Eryops*, judging from ROMER's figure (1943, pl. 2: 2) of that form.

In the two specimens in fig. 5, and in all other specimens in the material showing the position of the hind foot, the toes are directed backwards and the fifth toe is situated nearest to the body. In No. A. 109 (pl. 2) and, as far as I can see, in most other specimens as well the foot, moreover, is so situated in the fossil that its upper face is directed dorso-laterally and its lower face correspondingly ventro-medially. The foot is thus situated exactly as the paired fins in osteolepiform crossopterygians (figs. 8E, 10; pl. 7; JARVIK 1948a, p. 19, figs. 1—3). This may be accidental, but it is also possible that the foot was held in this position when the animal was swimming and in the attempted restoration shown in fig. 7 the foot has been drawn in this position.

The fore limb, too, has been restored and given the position it actually has in the fossils. The shoulder-girdle and the bones of the arm are found articulated in one specimen (No. A. 115) and are well shown and almost completely preserved on both sides. The shoulder-girdle is situated as indicated in the restoration (fig. 7), but since no dermal bones

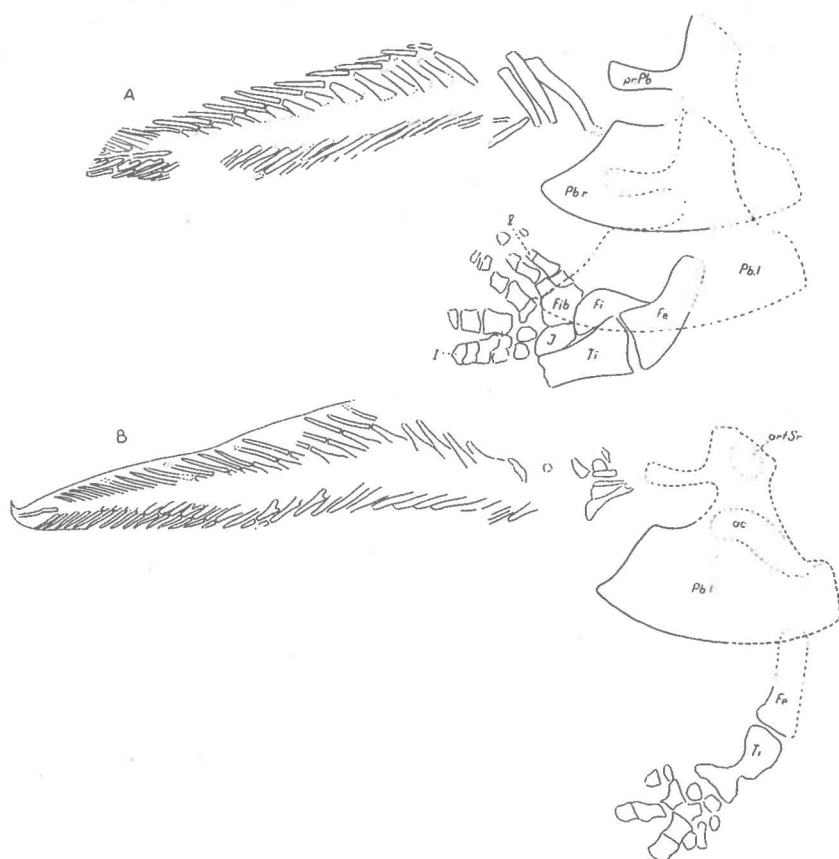


Fig. 5. *Ichthyostega* sp. The position of the pelvis and hind limb in relation to the tail in two specimens. 1/3. A, specimen No. A.109 (fig. 2A; pls. 2—4). B, specimen No. A.156 (fig. 2B; pl. 5).

Fe, femur; *Fi*, fibula; *Fib*, fibulare; *I*, intermedium; *Pb.l*, pelvic bone of left side; *Pb.r*, pelvic bone of right side; *Ti*, tibia.

ac, acetabulum; *art.Sr*, articular area on the inner side of the pelvic bone, conceivably for a sacral rib; *pr.Pb*, posterior process of pelvic bone.

I, V, first and fifth toes.

have been found connecting the dorsal end of the cleithrum with the skull, it is possible that this end was situated slightly farther forwards or backwards. In the fossil, the humerus, which is a long stout bone, very complicated in structure, extends straight backwards from the glenoid, and the radius and ulna, which are both comparatively short, meet the distal parts of the humerus at about right angles. The carpals are incompletely shown in No. A. 115, but judging from another specimen the carpus was developed much as the tarsus and no doubt the fore foot was broad as was the hind foot. The fingers are unknown.

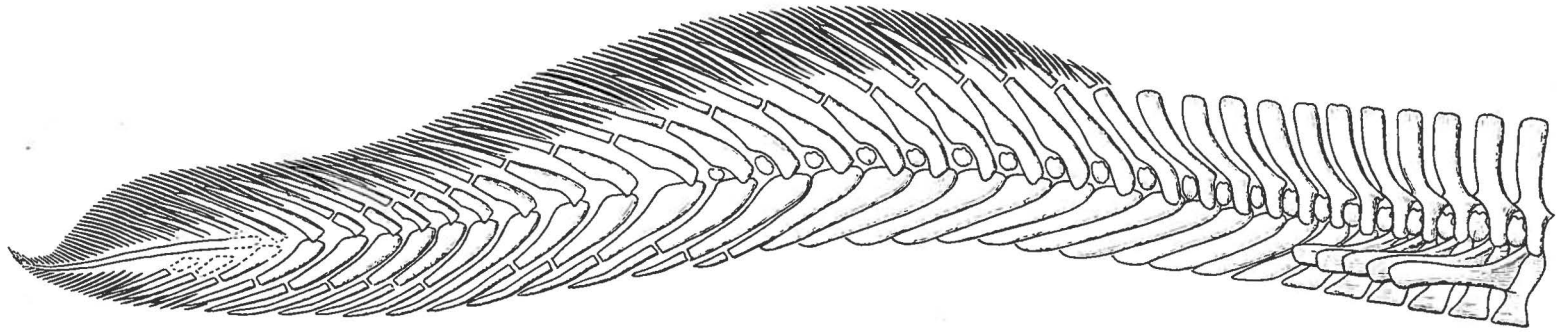


Fig. 6. *Ichthyostega* sp. Attempted restoration of the skeleton of the tail in lateral aspect. Scales omitted. Mainly after the specimens shown in figs. 2, 3, 14, 15. Ca. 5/6.

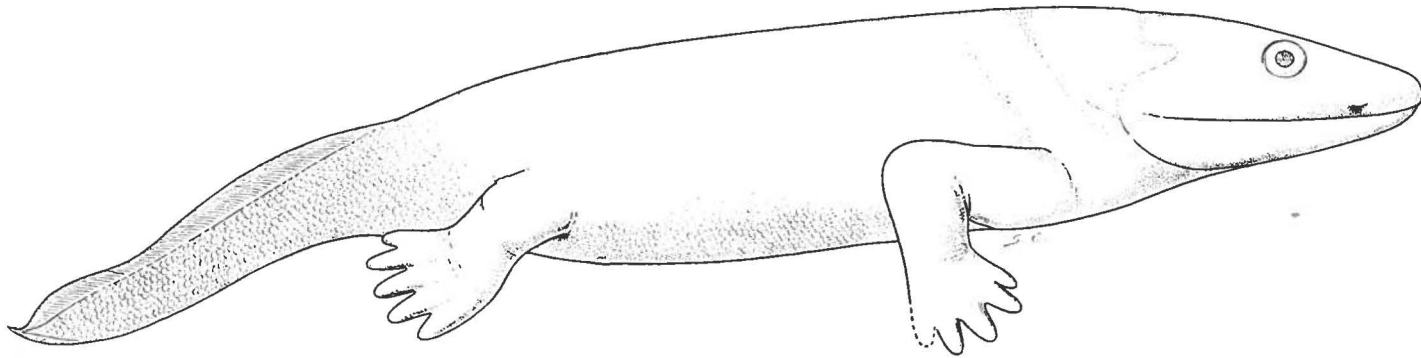


Fig. 7. *Ichthyostega* sp. Attempted restoration of the animal in lateral aspect. The limbs shown in the position they have in the fossils. The number of fingers unknown. The triangular bone indicated between the postero-ventral corner of the skull and the shoulder-girdle is the subopercular (cf. foot-note 1 on p. 21 and fig. 35A). Ca. 1/3.

The restoration of the presacral part of the animal is also in other respects based chiefly on No. A. 115, but several other specimens have been used as well¹⁾. As evidenced by the size and shape of the skull, the shoulder-girdle, the ribs and the pelvic bone, the animal was comparatively high and narrow—probably at least 1.25 times as high as broad in the pelvic region—and on the whole fairly fish-like. However, as in other tetrapods in which the body is carried mainly by the two pairs of legs, the vertebral column and the back of the animal are more convex in lateral view than they usually are in fishes.

Comparisons and discussion.

The presence of a real median fin, as in fishes supported by radials and dermal fin-rays, in the Upper Devonian ichthyostegid stegocephalians, that is in the oldest known tetrapods, is no doubt a primitive character inherited from not too remote fish ancestors. Also in many other respects (the presence of an independent preopercular bone; the fact that the sensory lines are enclosed in canals in the dermal bones, SÄVE-SÖDERBERGH 1932 b; the presence of a vestigial subopercular, foot-note 1 below; the development of the neural endocranium and the parasphenoid, see p. 36; etc.) the ichthyostegids are clearly primitive and fish-like or intermediate between fishes and tetrapods and they are undoubtedly more closely related to the fishes than are any other tetrapods. However, the paired fins characteristic of fishes have already been transformed into typical tetrapod limbs and since in many other respects, too, the ichthyostegids have clearly reached the tetrapod stage of evolution, they cannot be classified as fishes but are to be regarded as true tetrapods. It is of particular interest that in certain respects (e.g. in the position of the external nares, see foot-note 1 on p. 80, and in the development of the occiput, see pp. 82—83) they have become specialized and, as discussed elsewhere (JARVIK 1942, p. 630; 1948b, p. 6), they are most likely not the direct ancestors of any of the known members of later tetrapods but represent a blind early side-branch of the stem of the labyrinthodont stegocephalians.

As was already pointed out by SÄVE-SÖDERBERGH (1932b, p. 94) and as is confirmed by the new material at my disposal, the ichthyostegids

¹⁾ The small dermal bone pointed posteriorly, indicated in the restoration (fig. 7; see also fig. 35A) between the ventralmost part of the cheek and the shoulder-girdle, is situated as the subopercular in the *Osteolepiformes* and conceivably it represents a vestigial subopercular. This bone, previously unknown in tetrapods, is well shown on both sides in No. A. 89.

are closely related to the rhipidistid crossopterygians and no doubt they developed from them or from allied forms. The *Rhipidistia* comprise two distinct groups, the *Porolepiformes* and the *Osteolepiformes* (JARVIK 1942), the only groups of fishes with an indisputable choana¹). Even the earliest representatives of these two groups, from the Lower and Middle Devonian respectively, are highly specialized and no doubt the *Porolepiformes* and the *Osteolepiformes* developed independently of each other from early Devonian or pre-Devonian times. In a previous paper (1942) I have shown that as regards the structure of the snout the *Porolepiformes* agree closely with the *Urodela*, whereas the *Osteolepiformes* strongly resemble the *Anura*. The agreements found to exist between *Porolepiformes* and *Urodela*, on the one hand, and *Osteolepiformes* and *Anura*, on the other, are not confined merely to general similarities but go far into details and include all important specialized features. On the basis of this very strong evidence it was concluded that the *Urodela* are closely related to the *Porolepiformes* and developed from early representatives of that group, whereas the *Anura* arose from primitive *Osteolepiformes*. It was also maintained (op. cit. p. 630) that the ichthyostegids belong to the *Osteolepiformes-Anura* stock, but the evidence supporting this

¹) In the *Coelacanthiformes*, which in several respects differ considerably from the rhipidistids and consequently only with doubt can be referred to the *Crossopterygii* (JARVIK 1942, pp. 593—597), there is no choana, and as regards the presumed choana in the *Dipnoi* all evidence available strongly supports the view advanced by ALLIS that this opening represents the posterior external nostril, which migrated secondarily into the roof of the mouth (op. cit. pp. 270—280). Since a true choana is lacking in the *Coelacanthiformes* and, in my opinion, in the *Dipnoi* as well, neither of these two groups can include direct ancestors of any tetrapod, which latter have a true choana developed very much as in the rhipidistids (cf. p. 40 and SÄVE-SÖDERBERGH 1945, pp. 38—39; 1951).

Fig. 8. A—D. The skeleton of the tail of various forms in lateral aspect. A, *Neoceratodus forsteri*. From GÜNTHER (1871, pl. 30). B, *Fleurantia denticulata*. From GRAHAM-SMITH and WESTOLL (1937, fig. 1). C, *Eusthenopteron foordi*. The same as in fig. 10. D, *Ichthyostega* sp. The same as in fig. 6. E, *Osteolepis macrolepidotus*.

Restoration of the fish in lateral aspect. From JARVIK (1948a, fig. 26 B).

Dfrb, elongated basal segment of dermal fin-ray; *Ido*, interdorsal; *N.a*, neural arch (basidorsal); *R*, dorsal rib; *Rd*, dorsal radial; *Rdd*, *Rdm*, *Rdp*, distal, middle, and proximal series of ditto; *Rd + nsp*, dorsal radial fused with neural spine; *R.pl*, pleural rib; *Rv*, ventral radial; *Rvd*, *Rvm*, *Rvp*, distal, middle, and proximal series of ditto; *Rv + hsp*, ventral radial fused with haemal spine; *V.a*, ventral vertebral arch (haemal arch), probably representing both the basiventral and the interventral. *af*, anal fin; *df*, dorsal fin; *cdf*, *cvf*, dorsal and ventral lobes of caudal fin; *f.df*, first dorsal fin; *hsp*, haemal spine; *nsp*, neural spine; *pf*, pectoral fin; *pvf*, pelvic fin; *ri.dm*, dorso-median ridge, probably representing potential anterior dorsal fin; *s.df*, second dorsal fin.

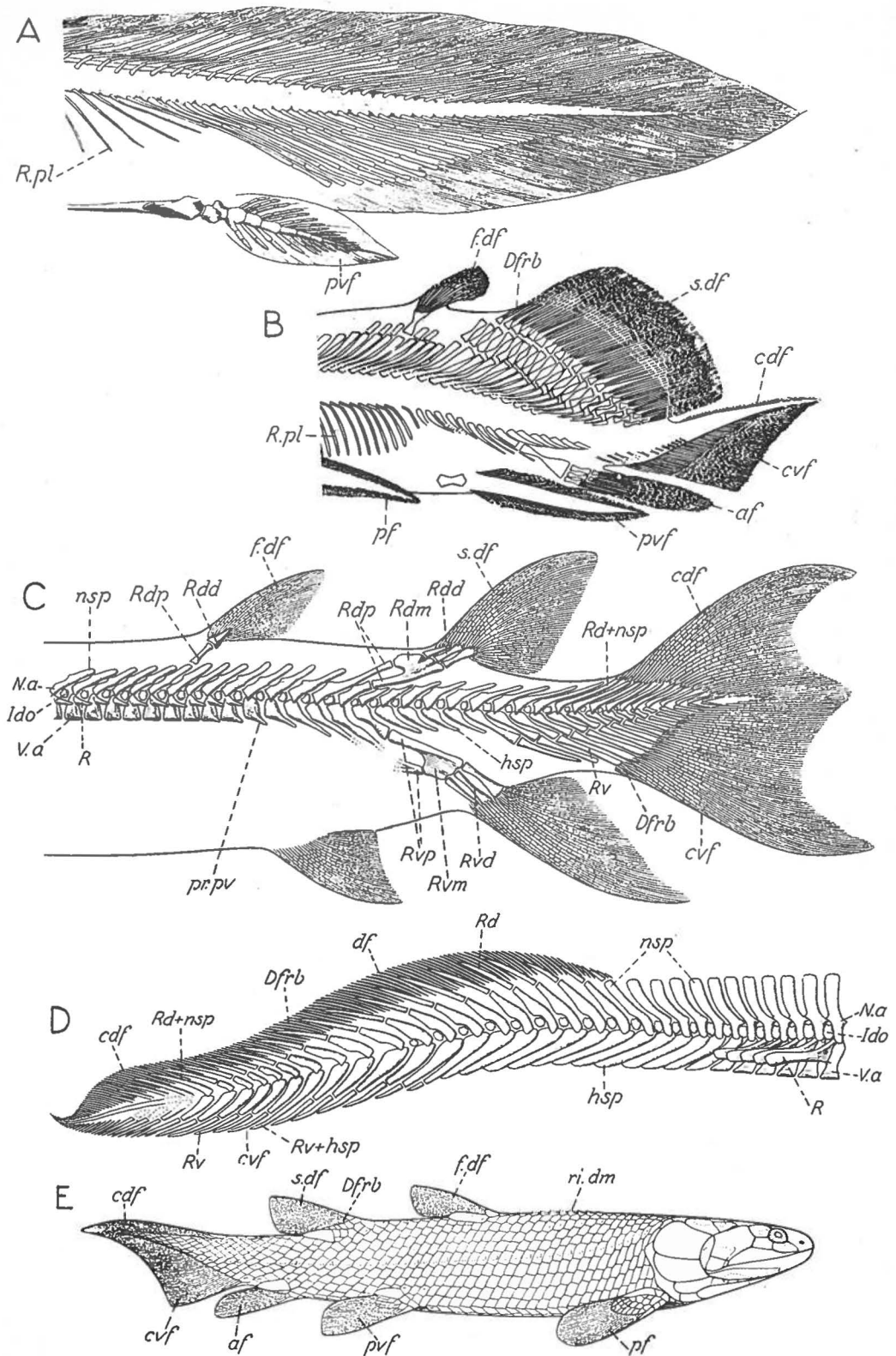


Fig. 8.

view was not particularly strong¹⁾ and, therefore, it would have been of great interest in this connection to compare the skeleton of the tail in the ichthyostegids with that in primitive and advanced representatives both of the *Porolepiformes* and the *Osteolepiformes*. Unfortunately this cannot be done, since the endoskeleton of the tail is practically unknown in most rhipidistids, and in the subsequent account the ichthyostegids, as far as the endoskeleton of the tail is concerned, can be compared mainly with *Eusthenopteron* among the *Osteolepiformes*. Since previous descriptions and restorations of the postcranial skeleton of *Eusthenopteron foordi* (WHITEAVES 1889; HUSSAKOF 1912; BRYANT 1919; GREGORY & RAVEN 1941) are incomplete and partly incorrect, it has been necessary to make a new restoration of the endoskeleton of the main posterior part of the body and to give a brief description of the vertebral column and the median fin-supports of that form. In addition new data will be given with regard to the structure of the vertebral column in early dipnoans.

The continuous median fin of the ichthyostegids (figs. 2, 3, 6, 7, 8D) has a distinct dorsal depression, as we have already seen, and is thus incompletely divided into two fins, a dorsal fin and a caudal fin. The latter fin consists of a relatively short dorsal lobe (*cdf*) with a partly concave margin and a much longer ventral lobe (*cvf*) with a convex margin, and the body axis is distinctly upturned. This fin is thus clearly heterocercal and is suggestive of the heterocercal caudal fin in *Porolepiformes* (*Holoptychius*, TRAQUAIR 1896, pl. 2: 4), early *Osteolepiformes* (*Osteolepis*, *Thursius*, fig. 8E; JÄRVIK 1948a, figs. 1, 26, 27, 47, 57, 61, 64, 70) and early *Dipnoi* (fig. 8B; FORSTER-COOPER 1937, fig. 1). The presumed dorsal fin (*df*) is situated much as the second dorsal fin (*s.df*) in rhipidistids and early dipnoans. However, it is comparatively long and continuous with the caudal fin, and contrary to the conditions at any rate in *Eusthenopteron* (figs. 8C, 10; pl. 7) there is no concrescence in the radial series or other signs of concentration of the fin (cf. GOODRICH 1930, pp. 113—122). In order to explain these differences the structure and ontogenetic development of the median fins in fishes in general will be briefly considered.

As is well known, the median fins in many early fishes are short and separate and often more or less concentrated, whereas in advanced forms, for example in advanced dipnoans (fig. 8A) and many teleosts, they are often more or less extended and sometimes continuous (GOODRICH

¹⁾ It may be added here that as regards the post-ethmoidal part of the skull, which I did not consider in 1942, the ichthyostegids in several respects agree more with the *Osteolepiformes* than with the *Porolepiformes* (e. g. in the number and arrangement of the dermal bones of the cheek; cf. figs. 26, 34, 35; JÄRVIK 1944a, fig. 18; 1948a, fig. 33B; 1950a, fig. 31).

1930, p. 117). Apparently an elongation of the median fins took place in phylogeny in various lines of evolution and it is therefore likely that also the fins in the ancestors of the ichthyostegids underwent a corresponding evolution, resulting in elongation and incomplete fusion of the dorsal and caudal fins. However, the radials (*Rd*, fig. 8D) in the dorsal fin of the ichthyostegids are independent and if the ichthyostegids developed from early *Osteolepiformes* we must assume either that they originated from forms in which the radials of the second dorsal fin had not yet fused or that the concrescence of the radials of the kind seen for example in *Eusthenopteron* (*Rdm*, fig. 8C; pl. 7: 2) may disappear secondarily. Since the postcranial endoskeleton in the Middle Devonian *Osteolepiformes* is unknown, the first alternative may be true, but it is also possible that the ichthyostegids really developed from forms in which, as in *Eusthenopteron*, the basal skeleton of the second dorsal fin is concentrated. The median fins in recent fishes are formed by differentiations in a continuous embryonic fin-fold, segmental in structure with regard to muscles, nerves and skeletal elements (see e.g. GOODRICH 1930, pp. 113—122) and for numerous reasons—the varying position of the median fins even in closely related forms (e.g. in *Osteolepis* and *Thursius* among the *Osteolepiformes*; JARVIK 1948a, pp. 103—104, 113, fig. 27), the presence of a vestigial dorsal fin in front of the first dorsal in *Osteolepis* (*ri.dm*, fig. 8E; JARVIK 1948a, pp. 102—104), the isolated appearance of long fins in such forms as *Tarassius* (MOY-THOMAS 1934, p. 374, fig. 1) and *Scanilepis* (ALDINGER 1937, pp. 220—221, 229) among the *Palaeonisciformes*, etc.—it is to be assumed that such an embryonic fin-fold was formed in fossil fishes as well and was laid down in each individual ontogeny. If we now imagine that in a form like *Eusthenopteron*, in which the skeleton of the second dorsal fin is concentrated, the segmental primordia of the radials formed in the embryonic fin-fold in connection with a beginning elongation of the second dorsal failed to fuse¹⁾ in the region of that fin, a series of segmental radials would obviously arise in the adult. As is then readily seen, a further elongation of the second dorsal fin would lead to conditions similar to those actually found in the ichthyostegids²⁾.

¹⁾ In a similar way the primordia of the dermal bones sometimes fail to fuse in early ontogenetical stages, which results in a comparatively large number of independent dermal bones in the adult (see JARVIK 1948a, p. 79).

²⁾ In *Dipnoi* a similar elongation of the median fins obviously took place in phylogeny (see e.g. GOODRICH 1930, p. 103; GRAHAM-SMITH & WESTOLL 1937, pp. 262—265; WESTOLL 1949, pp. 169—171; SÄVE-SÖDERBERGH 1951, fig. 4). Since in early *Dipnoi* (fig. 8B) the radials, at any rate in the first dorsal and anal fins, have fused in a similar way as in *Eusthenopteron* (figs. 8C, 10), whereas the radials in advanced forms (fig. 8A) in the regions of these fins are segmental, it is reasonable to assume that the elongation of the fins was accompanied by a secondary loss of the

In their histological structure (fig. 4) the dermal fin-rays of the ichthyostegids (figs. 2, 3, 6, 8D) agree with the corresponding formations in rhipidistids and dipnoans (GOODRICH 1904, pl. 39: 40—44) and as in these forms they are much more numerous than the corresponding radials. However, they are unbranching and unjointed and comparatively short and stout; as already pointed out they are very suggestive of the elongated basal pieces (*Dfrb*, fig. 8B, C, E) of the fin-rays in the said groups of fishes and very likely they correspond to those pieces. The absence of the dermal fin-rays in the anterior part of the ventral lobe of the caudal fin and the modifications of the radials in this region of the tail, that is the region which no doubt rested or dragged on the ground when the animal was on land or in shallow water, renders it likely that the fin-rays in this part were reduced and disappeared in connection with the change from water life to an amphibious mode of life. It is then natural to assume that the distal, soft and thin portions of the fins of the piscine ancestors of the ichthyostegids disappeared at the same time.

The vertebral column, the ribs, and the median fin-supports in *Eusthenopteron foordi*.

Before proceeding to a discussion of the endoskeleton of the tail and the vertebral column in the ichthyostegids¹⁾ it is necessary to get a more detailed knowledge of these structures in *Eusthenopteron foordi* than what may be obtained from previous figures and descriptions (WHITEAVES 1889; HUSSAKOF 1912; BRYANT 1919; MOY-THOMAS 1939; GREGORY, ROCKWELL & EVANS 1939; GREGORY & RAVEN 1941; NILSSON 1943; GREGORY 1951), which in some respects are incomplete and incorrect. The new description and the restorations (figs. 8C, 10, 13C—E) are based mainly on specimen No. P. 222 (fig. 9A—C; pl. 7) in the possession of the Paleozoological Department of the Swedish Museum of Natural History, Stockholm (cf. JARVIK 1948a, fig. 2). In addition, inter alia the following specimens have been used: Nos. P. 379 (fig. 12), P. 797

concrecence of the elements in the radial series. The opinion advanced by GRAHAM-SMITH & WESTOLL (1937, p. 264) that the radials in connection with elongation of the second dorsal fin "spread forwards" to the region of the first dorsal fin after the latter had become obliterated cannot possibly be true. The fact that in advanced dipnoans (fig. 8A) a fin, segmental in structure, occurs in a region corresponding to that of the first dorsal of early forms (fig. 8B) is certainly due to the persistence of the embryonic fin-fold and no doubt the radials in this region arose and remained in the segments to which they belong.

¹⁾ The vertebral column in the post-Devonian stegocephalians will not be discussed in this paper.

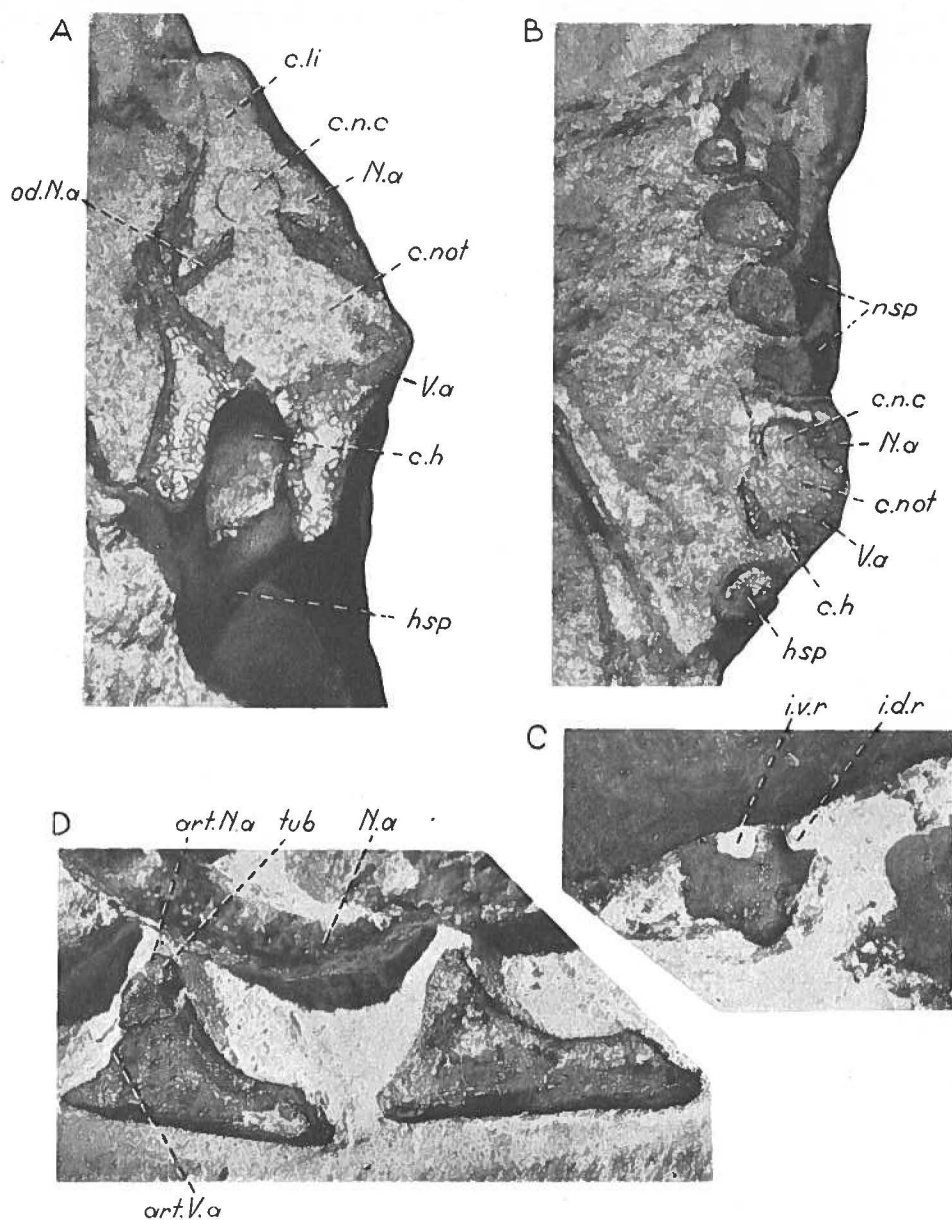


Fig. 9. *Eusthenopteron foordi*. A, B, transverse sections through the vertebral column in specimen No. P. 222, Stockh.: A, at the vertical crack below the posterior part of the second dorsal fin (pl. 7) and B, at the crack close in front of the caudal fin. Photographed in alcohol. 5/1. C, the next hindmost interdorsal seen in the same specimen. Photographed in alcohol. 15/2. D, two detached ribs in antero-lateral aspect. Unregistered specimen, Edinburgh. 5/1.

N.a, neural arch (basidorsal); *V.a*, ventral vertebral arch (haemal arch).
art.N.a, area of rib, probably articulating with ventral extremity of neural arch;
art.V.a, area articulating with ventral vertebral arch; *c.h*, haemal canal; *c.li*, canal for dorsal ligament; *c.n.c*, neural canal; *c.not*, notochordal canal; *hsp*, haemal spine; *i.d.r*, notch for dorsal root of spinal nerve; *i.v.r*, notch for ventral root of ditto; *nsp*, neural spine; *od.N.a*, dorsal portion of ventral vertebral arch overlapped by neural arch; *tub*, dorsal of head of rib, conceivably representing tuberculum.

and P. 4145 Stockh., Nos. 1887. 20. 19 (fig. 11), 1897. 51. 201 and one unregistered (fig. 9D), belonging to the Royal Scottish Museum, Edinburgh. The pelvic bone and the elements of the pelvic fin, which are detached in No. P. 222, have been omitted in the restoration (fig. 10).

The vertebral column in *Eusthenopteron* (figs. 8C, 9, 10, 13C—E; pl. 7) is composed of arcualia, whereas no independent "centra" are developed comparable to those found in early *Dipnoi* (see pp. 40—48) and many other fishes. As in fishes in general (see e. g. SCHAUINSLAND 1905; GOODRICH 1930; REMANE 1936) two dorsal elements, one anterior, the interdorsal (*Ido*, fig. 13C), and one posterior, the basidorsal or neural arch (*N.a*), are developed in each segment. Opposite the two dorsal elements there is a single ventral element, which in order to avoid confusion will be called simply the ventral vertebral arch (*V.a*; intercentrum, GREGORY, ROMER). In the posterior part of the lateral face of the latter there is a distinct vertical groove (*gr.i.a*), no doubt for the intersegmental artery. This groove thus marks the position of the boundary between two consecutive body segments. Thence it follows that each ventral vertebral arch very likely belongs to two segments and that the small posterior portion of the arch, which is situated behind the groove, represents the interventral, whereas the main anterior portion is the basiventral of the segment next in front (cf. *Saurichthys*, STENSIÖ 1925, pp. 118—119, fig. 27). Provided that this interpretation is correct, each basiventral has fused with the interventral lying next behind it, that is as in tetrapods, according to GOODRICH (1930, pp. 38—39).

Each neural arch (*N.a*, figs. 8C, 9A, B, D, 10, 11, 13C—E; pl. 7:2), both in the trunk and the tail¹), consists of two halves, ventrally enclosing the neural canal (*c.n.c.*) and the canal for the dorsal ligament (*c.li*) and dorsally fused into a median neural spine *nsp*). At the ventralmost part of the neural spine the antero-dorsal margin forms a small unpaired process (*pr.d*) overhanging the anterior opening of the canal for the dorsal ligament. Ventrally to this process the paired ventral part of the antero-dorsal margin often presents two shallow depressions, one dorsal at the anterior opening of the said canal and one ventral marking the position of the anterior opening of the neural canal of the arch. Behind the small paired process (*pr.a*), which separates these depressions, and in a corresponding position in relation to the neural canal there is sometimes a similar small paired process (*pr.p*) in the postero-ventral margin of the neural arch. These small paired anterior and posterior processes, which are lacking in the main posterior part of the tail, are in the position of pre- and postzygapophyses, respectively, and probably they

¹) The tail in *Eusthenopteron* refers to the part of the fish situated behind the vertebra supporting the first dorsal fin.

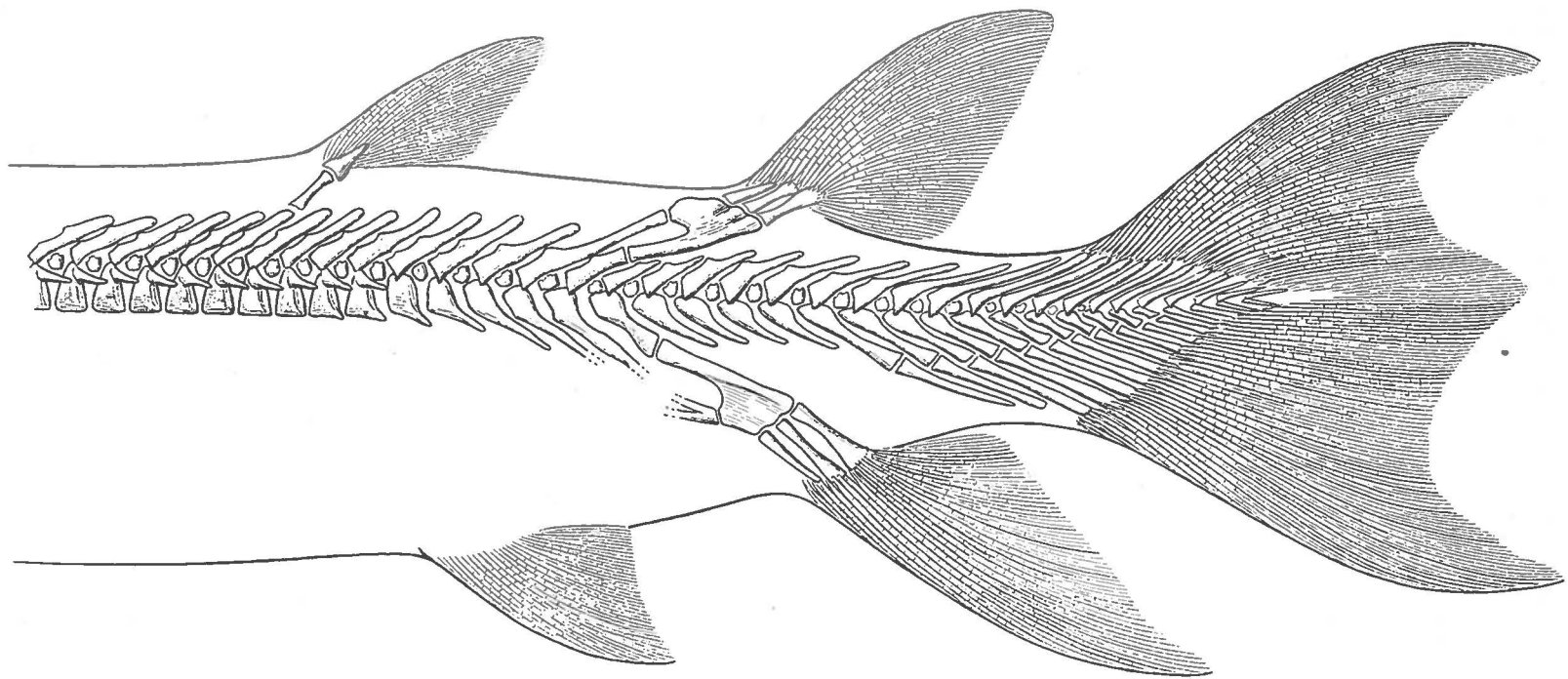


Fig. 10. *Eusthenopteron foordi*. Restoration of the skeleton of the posterior part of the trunk and the tail in lateral aspect. The scales, the pelvic bone and the endo-skeleton of the pelvic fin omitted. Based mainly on the specimen shown in pl. 7. For explanations see that plate and figs. 8C and 13C—E. 7/10.

represent zygapophyses in an initial stage of development. Ventrally to the posterior small paired process the posterior margin of the arch is often slightly concave as seen in lateral aspect. The paired ventral end of the neural arch is more or less pointed and both in the trunk and in the tail it meets and overlaps the dorsal part of the ventral vertebral arch (the area *od.N.a.*, fig. 9A; pl. 7: 2). The lateral face of the very ventral tip of the neural arch, which is often damaged, sometimes shows traces of a small lateral protuberance, probably articulating with the rib. In front of its ventral end the neural arch has a short, straight or slightly concave anterior margin, which meets the antero-dorsal margin of the arch at about right angles.

The interdorsal (*Ido*, figs. 8C, 9C, 10, 11, 13C, pl. 7: 2) is a fairly small paired element generally somewhat rectangular or sometimes triangular in shape as seen in lateral view and more or less rounded. It is situated in the space between the short anterior margin of the neural arch and the concave ventral part of the postero-ventral margin of the arch next in front. Its ventral part lies between the dorsal ends of two adjoining ventral vertebral arches. In the most posterior part of the tail no interdorsals have been observed. The interdorsal generally presents two more or less distinct notches, one antero-dorsal and one postero-dorsal. The antero-dorsal notch (*i.v.r.*), which obviously was situated close behind the intersegmental artery, no doubt transmitted the ventral root of the spinal nerve, whereas the postero-dorsal one (*i.d.r.*), which was situated outside the nerve-cord, marks the exit of the dorsal root. The interdorsal thus lies between the ventral and dorsal roots, which is the proper position of this element (SCHAUINSLAND 1905, pp. 415, 434; GOODRICH 1930, pp. 44—45).

The ventral vertebral arch (*V.a.*, figs. 8C, 9A, B, 10—12, 13C—E; pl. 7: 2), as we have seen (p. 28), is probably compound and consists of a basiventral, which has fused with the interventral of the segment next behind. In the trunk and the anterior part of the tail it consists of a paired piece, somewhat triangular in shape as seen in lateral view. The dorsal end of each half of the arch, which rarely is well shown, meets and is overlapped by the ventral end of the overlying neural arch but is always well separated from the dorsal end of the other half by an opening, which in the fossil state of preservation connects the wide notochordal canal (*c.not*) with the neural canal. Ventrally, on the other hand, the two halves always meet and, as is evidenced by some specimens, sometimes fuse and form a horse-shoe-shaped structure, open dorsally and enclosing the notochordal canal. The ventral face formed by the two halves is more or less plane or presents a shallow median depression continued backwards by the haemal canal. At about the vertebra supporting the first dorsal fin the ventral vertebral arches

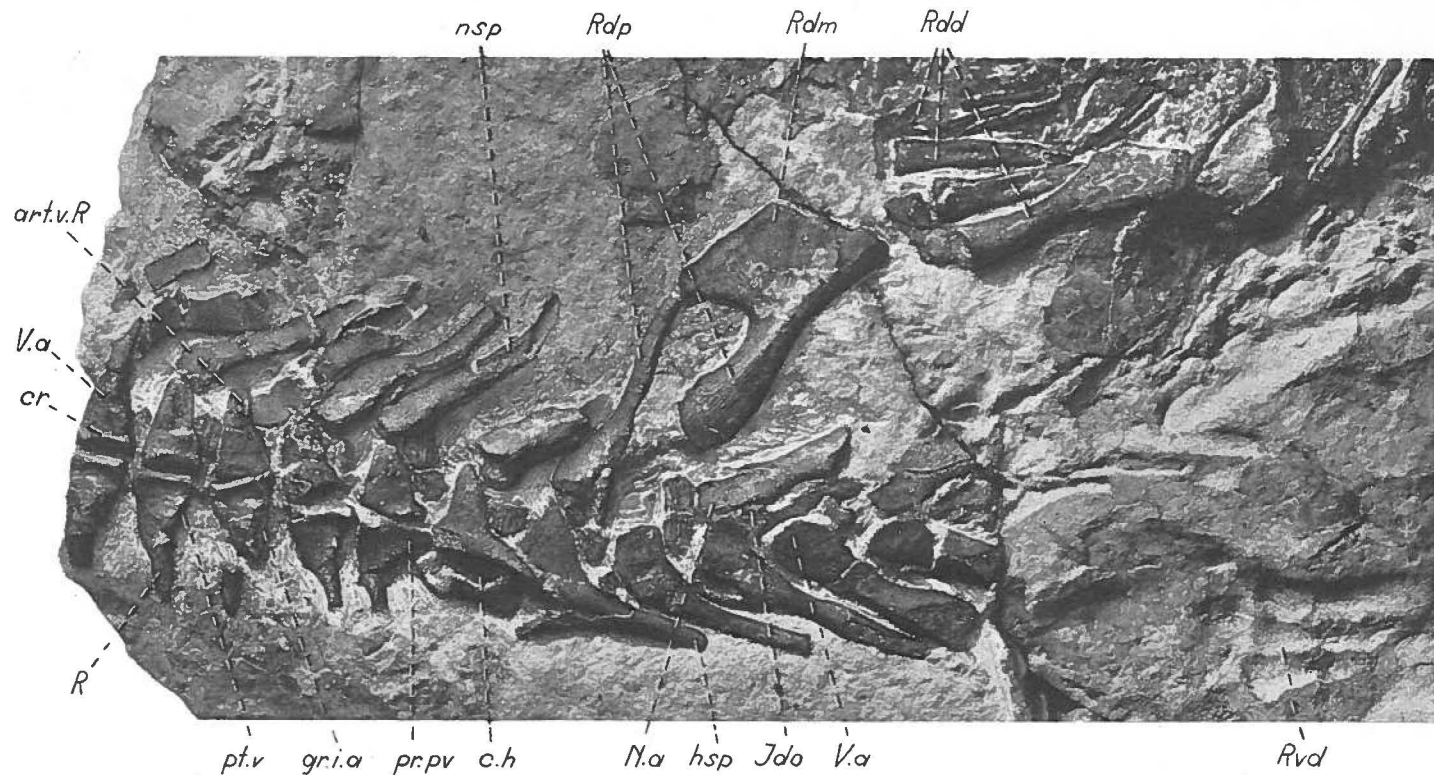


Fig. 11. *Eusthenopteron foordi*. Specimen compressed dorso-ventrally, showing mainly the vertebral column of the anterior part of the tail in ventral aspect and the radials of the second dorsal fin. Specimen No. 1887.20.19. Edinburgh. 5/4.

Ido, interdorsal; *N.a*, neural arch (basidorsal); *R*, rib; *Rdd*, distal series of radials supporting second dorsal fin; *Rdm*, middle series of ditto, fused into a single plate; *Rdp*, proximal series of ditto; *Rvd*, impression of distal series of radials supporting anal fin; *V.a*, ventral vertebral arch (haemal arch).

art.v.R, area of ventral vertebral arch articulating with rib; *c.h*, haemal canal; *cr*, ventro-medial crest of ventral vertebral arch; *gr.i.a*, groove for intersegmental artery; *hsp*, haemal spine; *nsp*, neural spine; *pr.pv*, postero-ventral process of ventral vertebral arch; *pt.v*, ventral protuberance of lateral side of ventral vertebral arch.

begin to change and are gradually transformed backwards into the ventral arches with haemal spines characteristic of the tail (see fig. 11). In the foremost modified ventral vertebral arch each half is ventro-medially provided with a low longitudinal crest (*cr*), which together with its fellow of the other side forms a median groove. In the arches following next behind the posterior part of this crest gradually increases in height and becomes extended into a paired postero-ventral process (*pr.pv*). Further back this process fuses with its fellow ventrally to the median groove, converting this groove into the haemal canal (*c.h*) and forming the haemal spine (*hsp*). The dorsal part of the arch, which bounds the notochordal canal and in the trunk forms the entire arch, also gradually changes backwards and becomes more or less rectangular in shape as seen in lateral view. Along the dorsal margin of the rectangular part a fairly high depressed area (*od.N.a*, fig. 9A; pl. 7:2) overlapped by the ventral part of the neural arch is sometimes found.

The groove (*gr.i.a*) in the posterior part of the lateral face of the ventral vertebral arch assumed to have contained the intersegmental artery is well developed in the trunk and in the anterior part of the tail. The portion of the arch carrying this groove is generally considerably depressed and the groove may therefore easily be overlooked in imperfectly cleaned specimens. In the tail the portion behind the groove gradually becomes narrower backwards to disappear about at the first arch with unpaired haemal spine. A little further back the groove, which in this region is represented by a faint impression in the posterior margin of the arch, disappears as well. The groove for the intersegmental artery generally runs in a distinct curve, concave posteriorly, and in those arches provided with a postero-ventral process the groove continues downwards medially to that process to the ventral median groove. In the trunk and in the anterior part of the tail the raised anterior portion of each ventral vertebral arch close in front of the dorsal part of the groove for the intersegmental artery is provided with a distinct protuberance with a fairly large articular area for the rib. This articular area (*art.v.R*), which faces postero-laterally, dorsally ends about at the ventral end of the area overlapped by the neural arch. Ventrally to the said protuberance, and separated from it by a more or less distinct notch, another protuberance (*pt.v*) is often found on the lateral face of the ventral vertebral arch.

The canal for the notochord (*c.not*, figs. 9A, B, 13D, E), which, as already pointed out, in the fossil state of preservation dorsally is continuous with the neural canal, anteriorly attains nearly the same width as its continuation forwards in the ventro-medial part of the neural endocranium. Posteriorly it decreases slowly in width but at any rate as far back as in the region of the anterior part of the caudal fin (fig. 9B)

it is still fairly wide and obviously it continues backwards to or almost to the very tip of the body axis of that fin.

The ribs (*R*, figs. 8C, 9D, 10, 11, 12, 13C, D; pl. 7:2), which have been overlooked by previous writers, are well shown in several specimens of *Eusthenopteron* at my disposal. It could not be ascertained whether the foremost vertebra carries a rib, but from the second vertebra ribs are found on each vertebra as far back as shown in the restoration (fig. 10). Judging from their position in the fossils and the development of the articular area (*art.v.R*) for the rib on the ventral vertebral arch they were situated almost horizontally and were directed postero-laterally. On account of their position and in view of the fact that the hindmost ribs are connected with the ventral vertebral arches provided with a postero-ventral process (*pr.pv*), which latter posteriorly is converted into the haemal spine, the ribs are no doubt dorsal ribs, as in the tetrapods (cf. e.g. GOODRICH 1930, p. 75). Each rib is fairly short and somewhat triangular in shape as seen in antero-lateral view. A concave dorsal, an almost straight ventral, and a vertical antero-medial margin are distinguishable. The antero-medial part of the rib is much expanded dorso-ventrally, forming a head articulating with the ventral vertebral arch (the area *art.v.R*). As evidenced by the ribs shown in fig. 9D, the head of the rib dorsally to the area (*art.V.a*) articulating with the ventral vertebral arch, at any rate sometimes presents another but smaller area (*art.N.a*) devoid of periosteal lining. This area lies close to the small protuberance traceable at the ventral end of the neural arch and very likely the rib articulated with the neural arch as well. If this is true, which needs confirmation, the antero-dorsal part of the head represents the tuberculum (*tub*) and the ventral part the capitulum of the rib.

Fin-supports (figs. 8C, 10, 11, 12; pl. 7:2).—As is well shown in No. P. 222 and other specimens of *Eusthenopteron foordi* the first dorsal fin (*f.df*) is supported by two radials, one proximal (*Rdp*), articulating with the distal end of a neural spine, and one distal (*Rdd*), partly embraced by the proximal elongated basal pieces of the dermal fin-rays.

The fin-supports of the second dorsal (*s.df*) and anal (*a.f*) fins may be regarded to consist of three series of radials, proximal, middle, and distal. The proximal series in the second dorsal fin consists of two (*Rdp*) and in the anal fin of three (*Rvp*) elements. In both fins the posterior element is continuous with the plate formed by the fusion of the elements of the middle series, whereas the anterior one (second dorsal) or two (anal fin) elements, which have been overlooked previously, articulate with that plate. As evidenced by the specimen shown in fig. 11, the anterior element of the proximal series of radials in the second dorsal fin is continuous with the neural spine next in front of that articulating with the posterior element of that series. In No. P. 222 (pl. 7:2) it is

broken and is in the fossil directed forwards, as are the two anterior elements of the proximal series of the anal fin. Conceivably the latter elements, which have been encountered in this specimen only, have been continuous with, or have articulated with, two haemal spines. Distally they have fused with each other. In this connection it may be mentioned that the stout haemal spine, which forms the main support

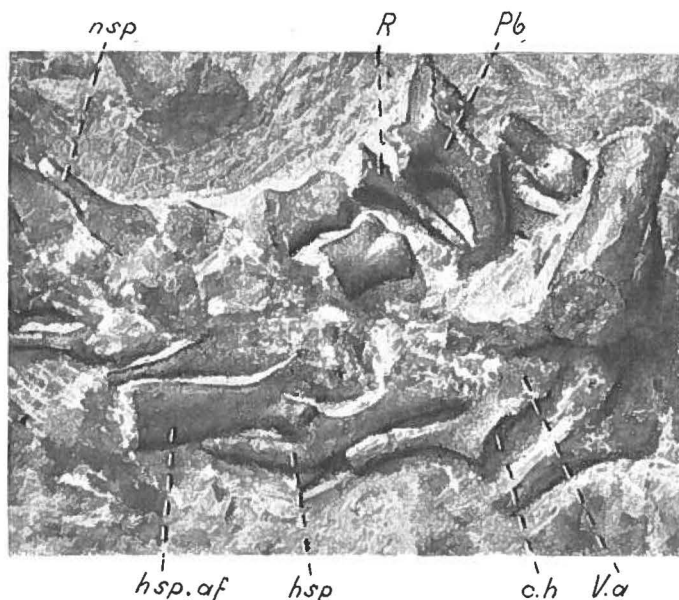


Fig. 12. *Eusthenopteron foordi*. Part of compressed specimen, showing the haemal spines supporting the anal fin, adjoining parts of the vertebral column, one of the pelvic bones and parts of the endoskeleton of the pelvic fin. Specimen No. P. 379 Stockh. 3/1.

Pb, pelvic bone; *R*, rib; *V.a*, ventral vertebral arch.

c.h, haemal canal; *hsp.af*, thickened haemal spine forming the main support of the anal fin; this spine is provided with a distinct anterior process articulating with a posterior process of the haemal spine (*hsp*) next in front; *nsp*, neural spine.

of the anal fin, sometimes articulates with the haemal spine next in front of it in the manner shown in fig. 12. The elements of the middle series of radials (*Rdm*, *Rvm*), apparently three in number, have in both fins fused with each other forming a single plate. The distal series of radials (*Rdd*, *Rvd*) in both the second dorsal and the anal fins consists of three elements proximally articulating with the said plate and distally to some extent embraced by the dermal fin-rays. They are situated entirely within the body as is the distal radial of the first second fin as well and do not extend so far into the fins as is shown in the restoration given by GREGORY & RAVEN (1941, fig. 10).

The dorsal and ventral lobes of the caudal fin are each supported by a series of radials, consisting in the dorsal lobe of at least 12 and in the ventral of at least 15 elements. However, in the dorsal series all

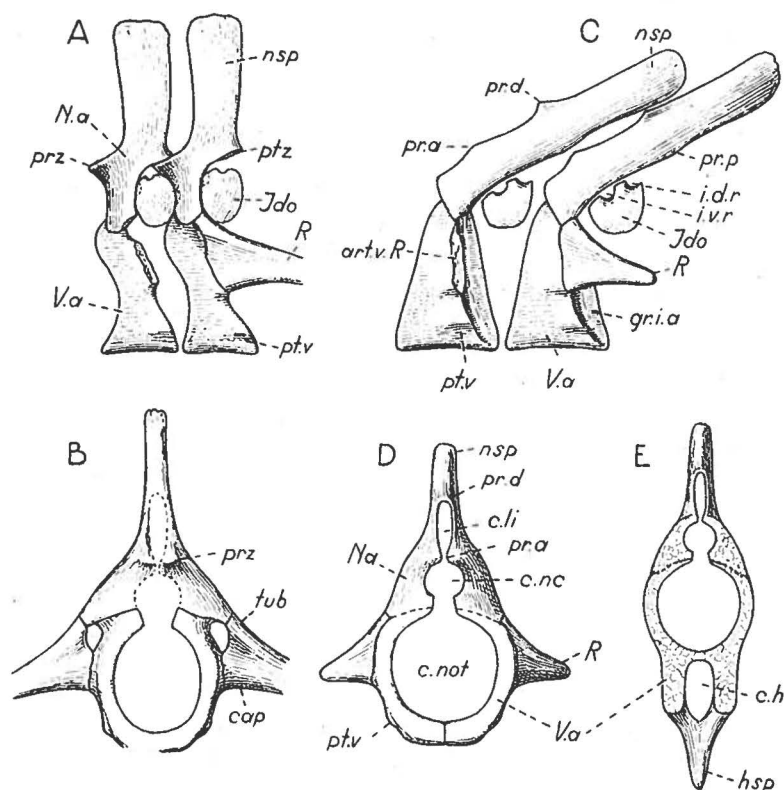


Fig. 13. A, B. *Ichthyostega* sp. Restorations of two vertebrae from the most anterior part of the tail in lateral and anterior aspects. The dorsal parts and the rib mainly after the specimens shown in fig. 14, the ventral parts mainly after the specimen shown in fig. 15. Ca. 4/3. C-E. *Eusthenopteron foordi*. C, D, restorations of two vertebrae from about the same region as in A in lateral and anterior aspects. 2/1 E, restoration of the section shown in fig. 9 A. 2/1.

Ido, interdorsal; *N.a*, neural arch (basidorsal); *R*, rib; *V.a*, ventral vertebral arch (basiventral + interventral; haemal arch).

art.v.R, area of ventral vertebral arch articulating with capitulum of rib; *cap*, capitulum; *c.h*, haemal canal; *c.li*, canal for dorsal ligament; *c.nc*, neural canal; *c.not*, notochordal canal; *gr.i.a*, groove for intersegmental artery; *hsp*, haemal spine; *i.d.r*, notch for dorsal root of spinal nerve; *i.v.r*, notch for ventral root of ditto; *nsp*, neural spine; *pr.a*, anterior paired process of neural arch, probably corresponding to the prezygapophysis; *pr.d*, anterior unpaired process of neural arch; *pr.p*, posterior paired process of neural arch probably corresponding to the postzygapophysis; *prz*, prezygapophysis; *pt.v*, ventral protuberance on lateral side of ventral vertebral arch; *ptz*, postzygapophysis; *tub*, tuberculum of rib.

(*Rd* + *nsp*) and in the ventral series the hindmost radials (*Rv* + *hsp*) have fused with the corresponding neural and haemal spines and only the eleven anterior elements of the ventral series (*Rv*) are independent.

The vertebral column in the ichthyostegids.

The vertebral column in the ichthyostegids (figs. 2, 3, 6, 8D, 13A, B, 14, 15; pls. 1—6) is on the whole imperfectly preserved in the material available. However, as is evidenced by some specimens, mainly those shown in figs. 14 and 15 and pls. 1—6, each vertebra, both in the trunk and in the tail, is composed of three elements, two dorsal and one ventral very suggestive of those in *Eusthenopteron*. As in that form, the notochordal canal is wide and is continued forwards by a wide canal (*c.not.*, fig. 36) in the ventro-medial parts of the large ossification which forms the posterior part of the neural endocranium¹). The lateral wall of the notochordal canal of the endocranium posteriorly forms a small but distinct paired occipital condylus (*oc.c*).

The neural arch (*N.a.*, figs. 2, 3, 6, 8D, 13A, B, 14; pls. 1—6) of the ichthyostegids is well shown in the trunk in several specimens, whereas in the tail the ventral parts, as indicated above, generally are imperfectly preserved. In the trunk the neural spine is fairly broad in lateral aspect and has a dorsal direction. The dorsal end appears to be rough, as in many post-Devonian stegocephalians. From the sacral region back-

¹) As clearly shown in several specimens (fig. 36; cf. SÄVE-SÖDERBERGH 1932b, pl. 17: 2), the neural endocranium close behind the region of the hypophysis is divided transversely into two large ossifications, anterior and posterior. The anterior ossification (*Et.*, fig. 36), which extends forwards almost to the tip of the snout (the ethmoidal region is thus ossified), apparently corresponds to the ethmosphenoid in *Eusthenopteron* and other rhipidistids, whereas the posterior one (*Ot-oc*) represents the otico-occipital. No other traces of sutures in the neural endocranium have been observed so far. As in the *Osteolepiformes* (fig. 29), the parasphenoid is short and narrow and ends posteriorly close behind the canal for the ventral tube of the hypophysis, which pierces the bone. However, as discussed elsewhere (JARVIK 1942, p. 629), the parasphenoid of the ichthyostegids does not extend as far forwards as in the *Osteolepiformes*.

Fig. 14. *Ichthyostega* sp. A. Postsacral ribs and adjoining dorsal parts of the vertebral column. Specimen No. A. 54. Photograph of cast in plastic material according to the method of STÅHL (1951). 1/1. B, C. Part of the vertebral column of the trunk. Specimen No. A. 140. B, Photograph of cast in plastic material (cf. A). 1/1. C, Small part of the specimen photographed in alcohol. 12/5.

N.a., neural arch; *Ido*, interdorsal; *R*, rib.

art.d.R., area of neural arch articulating with tuberculum of rib; *cap*, capitulum of rib; *i.d.r.*, notch for dorsal root of spinal nerve; *i.v.r.*, notch for ventral root of ditto; *nsp*, neural spine; *prz*, prezygapophysis; *ptz*, postzygapophysis; *tub*, tuberculum of rib.

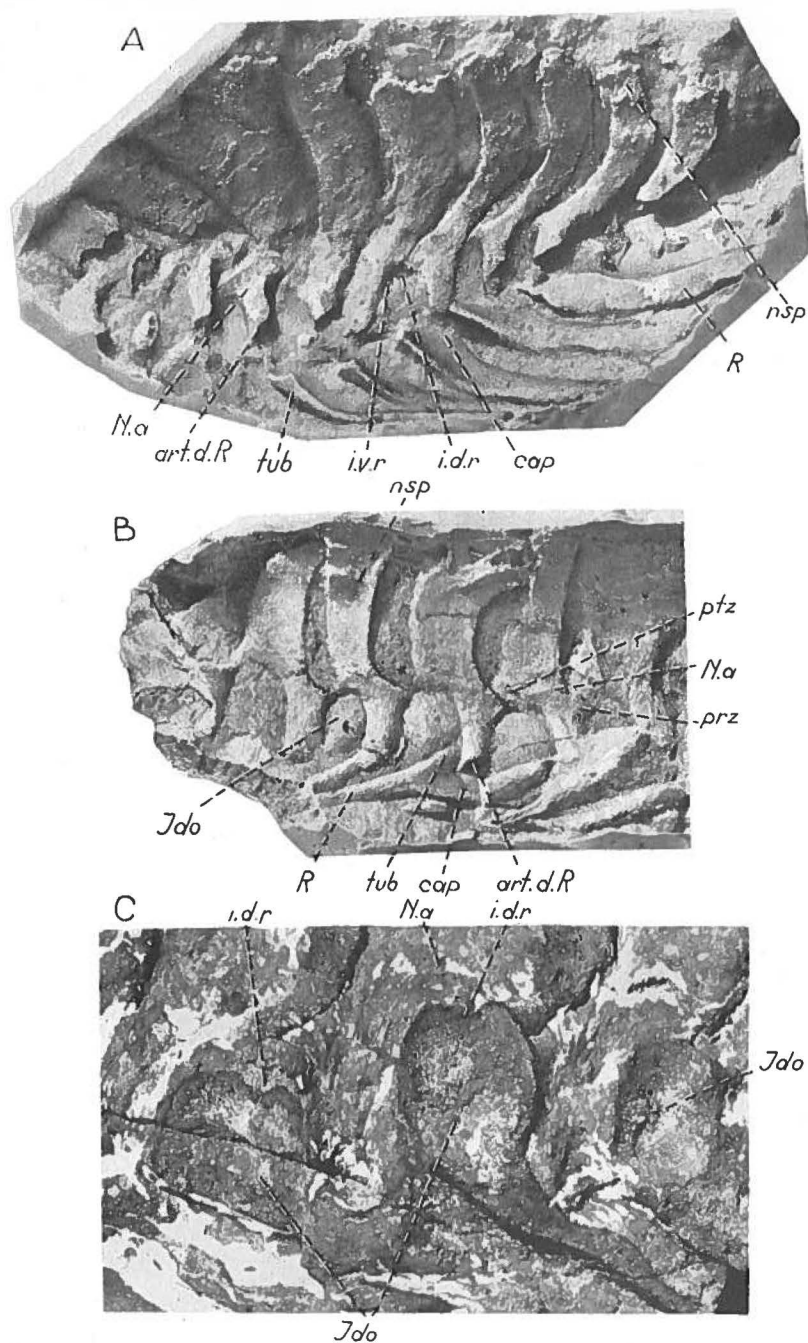


Fig. 14.

wards the neural spines gradually become narrower and more inclined backwards and are converted into the comparatively narrow spines, round in section, which in the tail articulate with the radials (p. 14). The latter strongly resemble the neural spines in *Eusthenopteron* (figs. 10, 13C—E). The pre- and postzygapophyses (*prz*, *ptz*) arise just above the neural canal lying very close to their fellows of the other side. They are well developed in the trunk but apparently they are lacking in the main part of the tail as are the correspondingly situated small processes (*pr.a*, *pr.p*, fig. 13C, D) in *Eusthenopteron*. However, contrary to the conditions in that form, the posterior process articulates with the dorsal face of the anterior process of the neural arch following next behind. In other respects the ventral part of the neural arch is developed much as in *Eusthenopteron* and ventrally it overlaps the underlying ventral vertebral arch. However, the distinct anterior corner of the ventral part of the arch found in *Eusthenopteron* is replaced by a more or less convex or straight anterior margin and the articular area (*art.d.R*) for the tuberculum of the rib is distinct.

The interdorsal (*Ido*, figs. 2B, 3, 6, 8D, 13A, 14; pls. 3, 5; "pleurocentrum", cf. GOODRICH 1930, figs. 51, 52D; ROMER 1945, fig. 94C) is well shown in Nos. A. 54 and A. 140 (fig. 14), whereas in other specimens showing the neural arches it generally is imperfectly preserved or missing. Both as to position and shape it agrees closely with the corresponding element in *Eusthenopteron*, and as in that form it is notched postero-dorsally (*i.d.r*), and conceivably antero-dorsally (*i.v.r*) as well, for the dorsal and ventral roots of the spinal nerve.

Also the ventral element, provisionally termed the ventral vertebral arch ("intercentrum"; *V.a*, figs. 2, 3, 6, 8D, 13A, B, 15; pls. 1—6), both in the trunk and in the tail, in most respects closely resembles the corresponding element in *Eusthenopteron*. In the trunk and the anterior part of the tail the two halves, judging from the scanty material available, have always fused with each other ventro-medially and form a horse-shoe-shaped structure, open dorsally where in the fossil state of preservation the wide notochordal canal is continuous with the neural canal, exactly as in *Eusthenopteron*. At the top of each half there is a rough area (*od.N.a*, fig. 15) overlapped by the neural arch. This area faces dorso-laterally or dorsally. On the lateral face of the arch, which decreases in width dorsally, two protuberances are found along the posterior margin, one dorsal provided with a distinct articular area (*art.v.R*) for the capitulum of the rib, and one ventral (*pt.v*), thus as in *Eusthenopteron*. No groove for the intersegmental artery has been found on the very few ventral vertebral arches presenting the lateral side, but conceivably this artery crossed the ventral elongated part of the arch behind the ventral protuberance. In the tail, too, the ventral vertebral

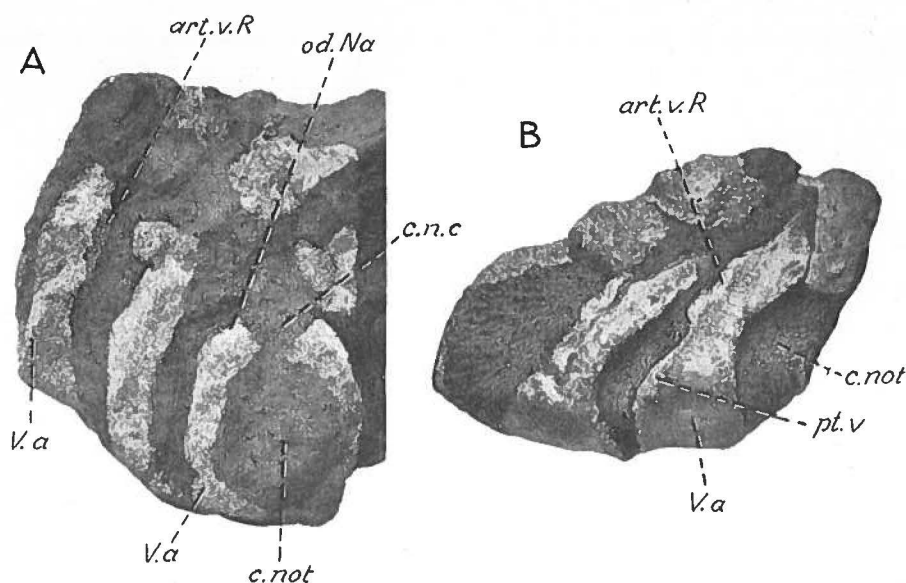


Fig. 15. *Ichthyostega* sp. Three ventral vertebral arches probably from the anterior part of the tail. Specimen No. A.109. Same specimen as in pls. 2—4. 2/1. A. The hindmost arch in transverse section and the left lateral side of the two arches next in front. Posterior view. B. The right halves of the two anterior arches shown in A in ventro-lateral aspect.

V.a, ventral vertebral arch.

art.v.R, area articulating with capitulum of rib; *c.n.c*, neural canal; *c.not*, notochordal canal; *od.N.a*, area overlapped by neural arch; *pt.v*, ventral protuberance of lateral side.

arches, as far as could be ascertained, strongly resemble the corresponding elements in *Eusthenopteron*, and as in that form the haemal spines articulate with the radials.

The ribs of the trunk in the ichthyostegids are powerful bicipital elements, which encircle the body cavity and are provided with strong posterior laminae covering the two or three ribs following behind (see STENSIÖ 1931, pl. 36, which shows some ichthyostegid ribs and part of the cleithrum). No sacral rib has been found, but as pointed out above the inner face of the iliac portion of the pelvic bone presents a distinct articular area (*art.Sr*, fig. 5B) with raised margins and no doubt the pelvis in some way articulated with the vertebral column. The postsacral ribs (p. 14, *R*, *R.ps*, figs. 2B, 6, 8D, 13A, B, 14A; pls. 2, 3), fairly well shown in No. A. 54 (fig. 14A) and probably five in number, are situated almost horizontally and are directed postero-laterally as are the ribs in *Eusthenopteron*. As pointed out (p. 14) above, the postsacral ribs in the ichthyostegids resemble the posterior process (*pr.Pb*, fig. 5; pls. 2, 3) of the iliac portion of the pelvic bone, which thus presumably represents a postsacral rib secondarily incorporated in the pelvis.

The median fin-supports in the ichthyostegids (p. 16, figs. 6, 8D) resemble those in the caudal fin in *Eusthenopteron* (pp. 35—36, figs. 8C, 10) and as in that form the radials would appear sometimes (e.g. in the most posterior part of the tail) to have fused with the neural or haemal spines ($Rd + nsp$, $Rv + hsp$).

As may be gathered from the descriptions now given and from the figures, the vertebral column in the ichthyostegids even in many details agrees closely with that in *Eusthenopteron* and in both the latter and the ichthyostegids the ribs are dorsal ribs.

The vertebral column in early *Dipnoi*.

In *Dipnoi*, which as regards the median fin-supports in several respects agree fairly well with the ichthyostegids and *Eusthenopteron*, the ribs are of the pleural type (see e.g. GOODRICH 1930, p. 75). As regards the ribs there is thus an important difference between *Dipnoi* on the one hand and *Eusthenopteron* and the ichthyostegids on the other, and as we shall now see, the structure of the vertebral column is very different as well. In early *Dipnoi* the vertebral column thus, besides arcualia, comprises strong independent centra, unparalleled in *Eusthenopteron* and the ichthyostegids and comparable to those found in sharks and many actinopterygians¹).

In recent *Dipnoi* (figs. 8A, 19C—E; SCHAUINSLAND 1905; GOODRICH 1930) no vertebral centra are developed²). In fossil *Dipnoi* such structures have been recorded in *Dipterus* (PANDER 1858, p. 17; pl. 1:1; pl. 2:6)

¹) The structure of the vertebral column and the presence of pleural ribs in the *Dipnoi* strongly contradict the assumption (see e.g. ROMER 1945, pp. 114—115; 1946, p. 58; WESTOLL 1949, pp. 122—123) that the *Dipnoi* are closely related to the rhipidistids, as do the great differences in structure between dipnoans, on the one hand, and both the *Porolepiformes* and the *Osteolepiformes*, on the other, as regards the dentition, the palate (cf. foot-note on p. 48), the lower jaw, the snout (see foot-note on p. 22 and JARVIK 1942), etc. Moreover, the neural endocranium in early dipnoans, as may be gathered from SÄVE-SÖDERBERGH's excellent restorations of this structure in *Chirodipterus* (cf. foot-note on p. 48), in numerous important respects differs considerably from that in the rhipidistids. The main reasons for a close relationship between dipnoans and rhipidistids seem to be the similar development of the fins, including concrescence of the radial elements and similarities in the histology of the dermal bones and scales. However, the fins in fishes may be easily modified (cf. p. 24—25) and concrescence of the radial elements or of the corresponding elements in the paired fins is a normal phenomenon in fishes. The resemblances in histology (see JARVIK 1950a, pp. 31—51) to a considerable extent seem to be shared with such remote forms as the tremataspids, which renders the importance also of these resemblances very doubtful.

²) In the tail cartilage blocks occur which according to MILLER (1930) represent vestigial vertebral centra.

and *Rhynchodipterus* (SÄVE-SÖDERBERGH 1937, p. 8), but they have remained practically unknown. Under these circumstances it may be justifiable to give here a description of these structures in early *Dipnoi*. For that purpose I have been permitted to use the material of dipnoans from the Upper Upper Devonian of East Greenland, in which the vertebral centra are well represented.

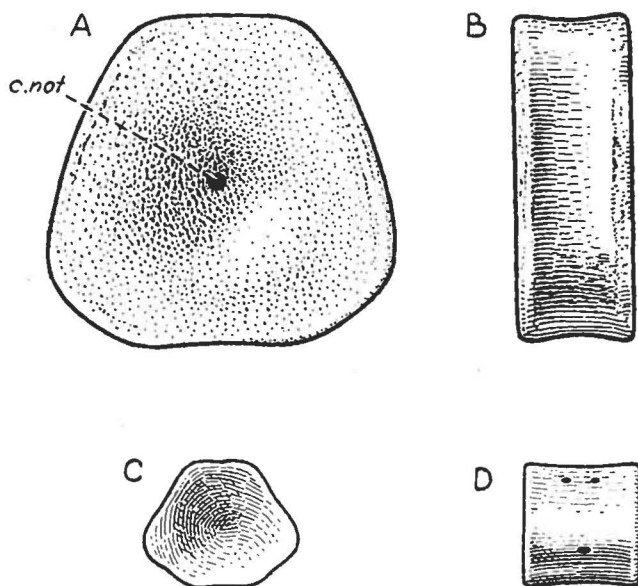


Fig. 16. Undetermined dipnoans from the Upper Devonian of East Greenland. Restorations of vertebral centra in posterior and lateral aspects. A, B, form A (pl. 8: 7—9). 2/1. C, D, form B (pl. 8: 1—6). 2/1.

c.not, canal for the constricted notochord.

The Greenland material of *Dipnoi*, which originates from the Remigolepis Series, that is from the same strata as the ichthyostegids, includes remains of two different forms, form A and form B. Form A, according to SÄVE-SÖDERBERGH (1937) related to *Rhynchodipterus* and represented inter alia by a magnificent cranial roof measuring almost 30 cm. in length, is characterized by a fairly broad cranial roof and a long, but broad, snout. In form B, which is smaller, the cranial roof is comparatively narrow and the snout is long and narrow and on the whole rather *Fleurantia*-like in external shape. Whether also the latter form belongs to the rhynchodipterids I would not venture to decide.

Well developed vertebral centra are represented in both forms but no arcualia have been recognized with certainty. It may be mentioned, however, that long ribs resembling those in *Fleurantia* (fig. 8B) occur together with the material of form A. The centra of the latter form are

all detached and are generally split more or less transversally. In order to make out the general shape the hard tissue of both part and counterpart of one centrum has been removed and a cast in latex has been made (pl. 8:7, 8). Centra of form B have been found in one specimen only (pl. 8:1—6). However, in this specimen a long anterior portion of the vertebral column is preserved. This portion, which anteriorly articulates with the skull, comprises 21 centra, obviously almost in their natural position. The most posterior part of this unique vertebral column, which is presented in ventral view, has been removed from the matrix, but unfortunately the most dorsal parts of the centra remained in the counterpart and had to be removed by negative preparation. The 20th vertebra and parts of the 19th and 21st have been completely ground through transversely and the sections have been studied at close intervals.

In both forms the state of preservation is unfavourable for histological purposes and the minute structure of the hard tissue forming the centra could not be made out. However, as is clearly seen in the sections (fig. 18B, pl. 8:6), the centra consist of trabecular tissue with comparatively much larger spaces between the trabecles in the interior than towards the ends and along the periphery, where the interspaces are very small. The main trabecles run parallel with each other and the periphery, the centra thus being clearly concentric in structure (cf. e.g. *Squatina*, LERICHE 1936, pl. 27:1). No distinct traces of a periosteal bone layer have been noticed on the external faces, and on the cranial and caudal ends, which are concave and have pitted faces (pl. 8:9), such a layer was certainly lacking. It is difficult to say whether this tissue consists of bone or of calcified cartilage (cf. *Bobasatrania*, ØRVIG 1951, p. 431, pl. 8:2).

In both forms the centra consist of amphicoelus discs (figs. 16—18; pl. 8), the external appearance in many respects suggestive of those in such forms as *Esox* (see GOODRICH 1930, fig. 49A, B) among the teleosts. The discs attain their greatest breadth near the ventral margin. In form A (fig. 16A, B) they are considerably larger (height about 21 and breadth about 23 mm.) than in the other form (fig. 16C, D; height about 8 and breadth about 10 mm.) but they are relatively much shorter. They are thus about 3 times as broad as long in form A, whereas the corresponding ratio in form B is only about 1.3. Another difference is that the centra in form A are pierced by a narrow notochordal canal (*c.not.*, fig. 16A; pl. 8:8, 9). In form B (fig. 18; pl. 8:4, 6) such a canal is absent and evidently the notochord in this form was completely obliterated in the regions of the centra.

The dorsal, ventral and lateral sides of the discs are well shown only in the continuous column of form B (figs. 17, 18B; pl. 8:1—6). On the dorsal side of each disc there is a longitudinal median groove (*gr.n.c.*),

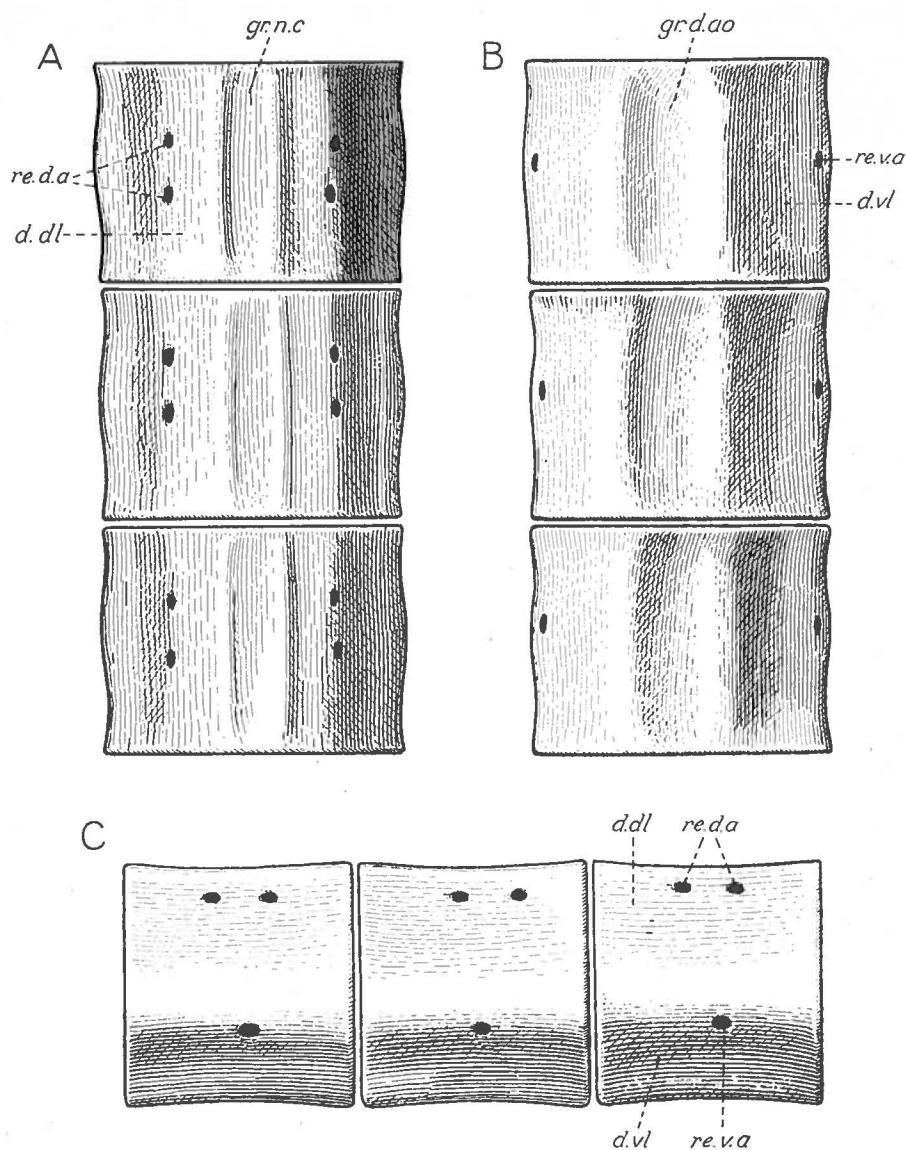


Fig. 17. Undetermined dipnoan from the Upper Devonian of East Greenland. Form B. Restorations of three vertebral centra in, *A*, dorsal, *B*, ventral, and *C*, lateral aspects. 4/1.

d.dl., dorso-lateral depression; *d.vl.*, ventro-lateral depression; *gr.d.a.o.*, longitudinal, ventro-medial groove, probably for the dorsal aorta; *gr.n.c.*, longitudinal, dorso-medial groove forming the floor of the neural canal; *re.d.a.*, canal-like pits, probably housing the proximal cartilaginous parts of the dorsal arcualia (basidorsal, interdorsal); *re.v.a.*, canal-like pit housing the proximal cartilaginous parts of the ventral arch (probably basiventral + interventral).

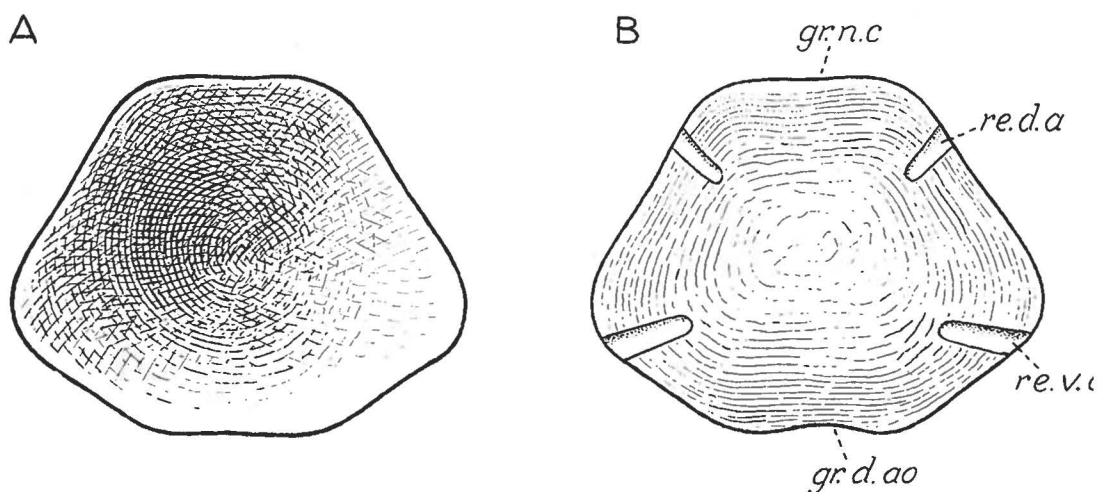


Fig. 18. Undetermined dipnoan from the Upper Devonian of East Greenland. Form B. Restorations of vertebral centrum. *A*, posterior view. *B*, transverse section. 4/1. *gr.d.a.*, ventro-median groove, probably for the dorsal aorta; *gr.n.c.*, longitudinal groove forming the floor of the neural canal; *re.d.a.*, *re.v.a.*, canal-like pits for the cartilaginous proximal parts of the arcualia.

no doubt as the corresponding groove in *Esox* forming the ventral boundary of the neural canal. The ventral side presents a median groove (*gr.d.a.*) similar to that found in the corresponding position in *Esox* but less deep. This groove contained or was situated close dorsally to the dorsal aorta (cf. fig. 19A). On each side of the dorsal groove the dorso-laterally facing side of the disc is somewhat depressed (*d.dl*) and a similar paired depression (*d.vl*) is found on the ventro-lateral side, laterally to the groove for the dorsal aorta. In *Esox* dorso-lateral and ventro-lateral depressions are represented, as well, and are in this form situated below the basidorsal and below the basiventral, respectively. In the most dorsal part of the dorso-lateral depression there are two rather wide foramina (*re.d.a.*), the one behind the other, whereas close dorsally to the ventro-lateral depression one similar foramen (*re.v.a.*) is found. These foramina did not transmit the roots of the spinal nerves or vessels, as might perhaps be suspected, but are the openings of deep and narrow canal-like pits, which from the opening run inwards towards the central parts of the disc (fig. 18B; pl. 8:6). These canal-like pits almost certainly contained the cartilaginous basal parts of the arcualia (fig. 19B), which exactly as in such forms as *Amia* and *Esox* (SCHAUINSLAND 1905, pp. 444, 471—472; figs. 243, 263; GOODRICH 1930, p. 43; figs. 40, 49B) during the growth of the centra gradually became buried in the trabecular tissue (cf. also selachians, fig. 19F; HASSE 1882, pl. 23:5; pl. 26:22—24;

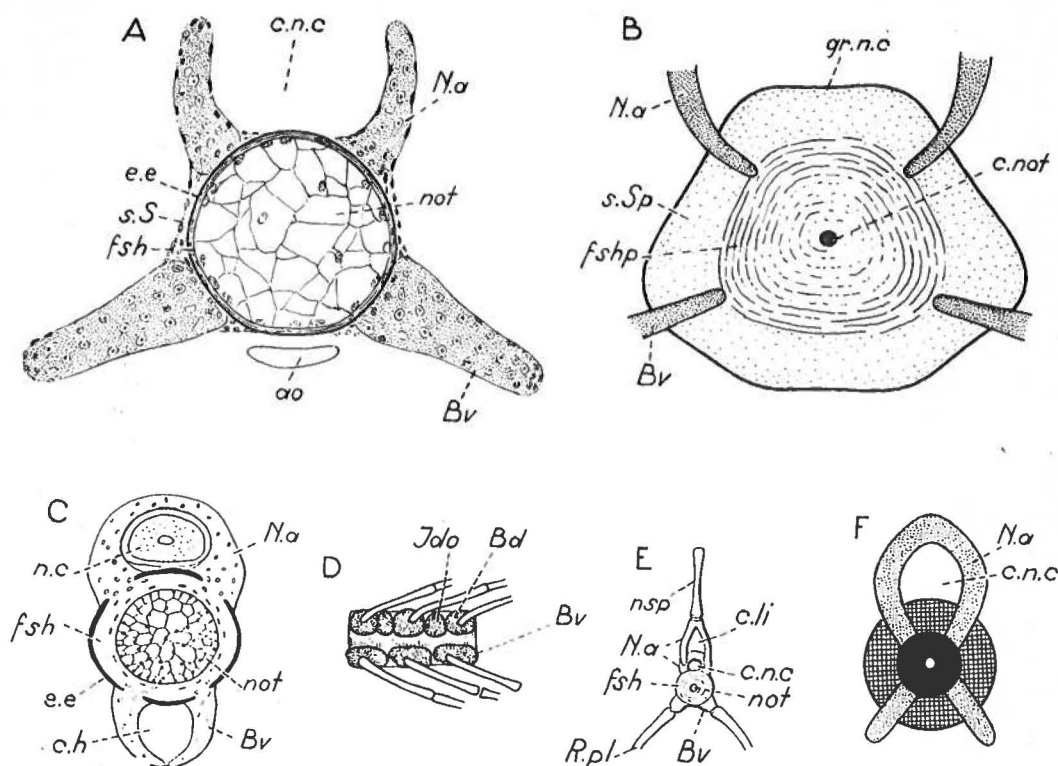


Fig. 19. *A.* Transverse section of vertebral column of a young *Neoceratodus forsteri* (14 mm. long). From SCHAUINSLAND (1905, fig. 274 a, simplified). *B.* Diagrammatic transverse section of vertebral centrum of undetermined dipnoan from the Upper Devonian of East Greenland (cf. figs. 16—18). The cartilaginous proximal parts of the arcualia restored. *C.* Transverse section of vertebral column of young *Protopterus*, showing the invasion of the fibrous notochordal sheath by the mesoblastic cells. From GOODRICH (1930, fig. 10 A). *D.* *Neoceratodus forsteri*. Left-side view of vertebral column of caudal region. From GOODRICH (1930, fig. 33). *E.* *Neoceratodus forsteri*. Transverse section of vertebral column (abdominal region). From GOODRICH (1930, fig. 10 C). *F.* Diagrammatic transverse section of vertebra, showing the typical composition in a selachian. From REMANE (1936, fig. 11 a).

Bd, basidorsal; *Bv*, basiventral (+ interventral); *Ido*, interdorsal; *N.α*, neural arch (basidorsal); *R.pl*, pleural rib.

ao, dorsal aorta; *c.h*, haemal canal; *c.li*, canal for dorsal ligament; *c.n.c*, neural canal; *c.not*, notochordal canal; *e.e*, elastica externa of notochord; *fsh*, fibrous sheath of notochord; *fshp*, part of vertebral centrum formed inside the elastica externa (chordacentral part; black in *F*); *gr.n.c*, groove, forming floor of neural canal; *n.c*, nerve-cord; *not*, notochord; *n.sp*, neural spine; *s.S*, "skeletoblastische Schicht" of SCHAUINSLAND; *s.Sp*, part of vertebral centrum probably formed in tissue corresponding to the "skeletoblastische Schicht" (autocentral part; cross-ruled in *F*).

pl. 30:34, 35, etc.; LERICHE 1936, p. 392, pl. 17:10). Since there are two pits dorsally, it is to be assumed that the basidorsals and interdorsals were independent, as they are in the tail of *Neoceratodus* (fig. 19D). This would mean that, at any rate in form B in which the centra are much longer, relatively speaking, than in form A, there was only one disc for each neural arch. Provided the interpretation of the canal-like pits now given is correct, the peripheral parts of the centra (*s.Sp*), which enclosed the cartilaginous thin basal parts of the arcualia (see

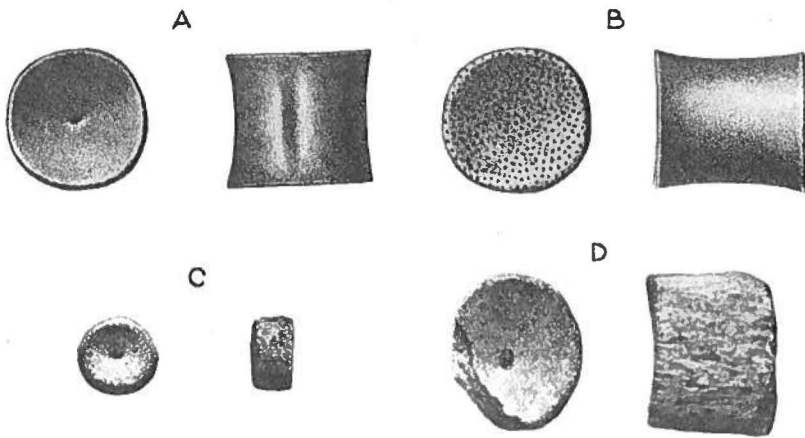


Fig. 20. Devonian vertebral centra, probably of dipnoans. *A, B*, from the banks of the Prickscha, Russia. Magnified. *C*, from Neuhausen, Estonia. 2.3/1. *D*, from Oos (Eifel), Germany. 2.3/1. *A, B*, after PANDER (1858, pl. 4: 3, 4), *C, D*, after Gross (1936, fig. 9: 6, 7).

figs. 18B, 19B), were formed outside the elastica externa of the notochord, apparently in a layer corresponding to the "skeletoblastische Schicht" (*s.S*, fig. 19A; SCHAUINSLAND 1905, figs. 274—276), which in recent *Dipnoi* is found between the bases of the arcualia outside the elastica externa. However, as is well known (see e. g. SCHAUINSLAND 1905, p. 485; GOODRICH 1930, p. 31), the thick fibrous sheath of the notochord in recent dipnoans (*fsh*, fig. 19E) is to a considerable extent invaded by mesoblastic cells (fig. 19C), which in advanced stages become arranged in more or less concentric rows. It is reasonable to assume, therefore, that the central parts of the discs (*fshp*, fig. 19B) were formed inside the elastica externa and that these parts correspond to the thick fibrous sheet in modern *Dipnoi*. If this is true, the vertebral centra in early *Dipnoi* were chordacentral + autocentral + arcocentral (REMANE 1936, pp. 14—16) and then conform very well with type a (fig. 19F), repres-

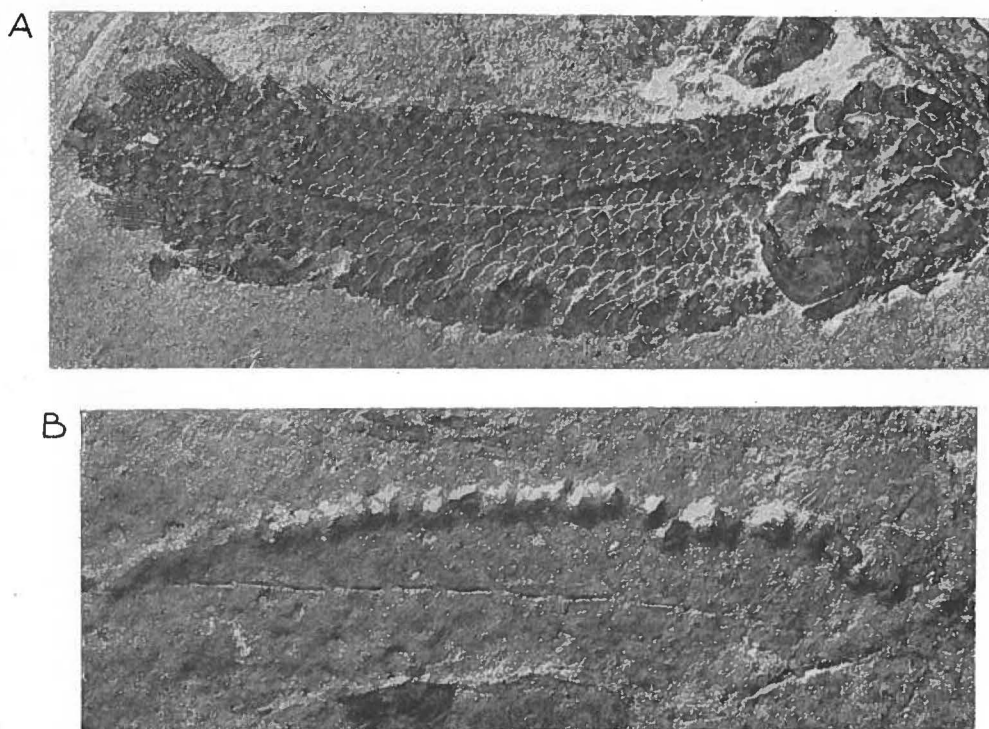


Fig. 21. Two dipnoans from the Middle Devonian of Scotland, showing vertebral column with vertebral centra. The centra are covered by scales and no details are known. *A*, *Dipterus valenciennesi* SEDG. & MURCH. Compressed fish in lateral view. The vertebral column (visible as a ridge) extends from the skull to the posterior end of the part of the tail preserved. Specimen No. 53402 Geol. Surv., London. From Banniskirk. 3/2. *B*, *Dipterus* sp. Part of compressed specimen in lateral aspect. Separate vertebral centra are distinctly seen. Specimen No. 1886. 31.5 Edinburgh. Locality unknown. 9/4.

enting the normal selachian condition in REMANE's scheme (1936, fig. 11) of the main types of vertebral centra¹).

Amphicoelous vertebral centra very similar to those now described in the Upper Devonian dipnoans from East Greenland are known from the Russian, Baltic, and German Devonian (fig. 20; PANDER 1858, pp. 15—19; GROSS 1936, pp. 76—77) and probably these and most or all the other centra figured by PANDER and GROSS also belong to dipnoans²). It is of great interest that vertebral centra, apparently of the

¹) It is worth while mentioning in this connection that ossifications inside the elastica externa have recently been described by ROMER (1942, p. 225) in a paleozoic shark vertebra.

²) Some of the centra figured by PANDER (1858, pl. 4: 14, 17, 18) have a wide notochordal canal and are somewhat suggestive of the ring-shaped ossifications in *Strepsodus* and certain other rhipidistids (see e. g. GREGORY and others, 1939, figs. 1, 2).

same type, were already developed in the vertebral column—from the skull to or almost to the tip of the tail—in the Middle Devonian genus *Dipterus*, as is evidenced by the two specimens shown in fig. 21 and some specimens figured by PANDER (1858, p. 17; pl. 1:1; pl. 2:6).

As we have now seen, independent vertebral centra of trabecular hard tissue (conceivably bone) were developed in early *Dipnoi*, but otherwise the vertebral column seems to have been very much as in modern forms (cf. GRAHAM-SMITH & WESTOLL 1937, pp. 262—264). The main difference between ancient and modern dipnoans as to the structure of the vertebral column would thus appear to be that the endoskeleton exactly as in the skull¹⁾ has developed regressively in phylogeny (cf. JARVIK 1942, pp. 422, 551, 592; ØRVIG 1951, pp. 379—380). In connection with the degeneration of the hard skeleton the subdivision in separate centra, which was necessary, when they were formed by hard tissue, has disappeared.

Concluding remarks.

As has been demonstrated above the ichthyostegids and the *Osteolepiformes* agree very closely with each other as to the structure of the vertebral column. No independent vertebral centra comparable to those in early *Dipnoi* are developed and the ribs are of the dorsal type. Also the endoskeletal supports of the median fins are very similar and the dermal fin-rays (lepidotrichia) of the ichthyostegids are suggestive of the long basal segments of the fin-rays in *Osteolepiformes*. These and other new data (cf. pp. 59, 64, 66, foot-notes on pp. 21, 24, 36, 80), together with the fact that the caudal fin in the ichthyostegids is heterocercal and resembles that in certain early *Osteolepiformes*, strongly confirm the assumption (cf. p. 22) that the ichthyostegids are closely related to the *Osteolepiformes* and have evolved from primitive members of that group. If this is true, the main evolutionary changes in the skeleton of the tail during the phylogeny of the ichthyostegids may be supposed to have been as follows. In connection with the

¹⁾ In a posthumous paper by SÄVE-SÖDERBERGH (1951) elaborate restorations of the palate and—for the first time—of the neural endocranium in an early dipnoan, *Chirodipterus wildungensis* GROSS (lowermost Upper Devonian), are given. SÄVE-SÖDERBERGH states that the endocranium of this primitive form even as to details agrees very closely with that in *Neoceratodus*. The main difference is that it is more strongly ossified. Moreover, he demonstrates the great resemblances in the dentition and the palatal structure between early and modern *Dipnoi* and emphasizes the great disagreement in these respects between early *Dipnoi* and rhipidistids. He concludes that the dipnoans as regards the dentition, the palate, and the neural endocranium have been almost incredibly conservative, a conclusion which apparently applies to the vertebral column as well.

transformation of the paired fins into legs supporting the body the vertebral column became bent downwards behind the sacral region. The second dorsal fin became elongated and fused incompletely with the dorsal lobe of the caudal fin. The anal fin was reduced or was incorporated in the ventral lobe of the caudal fin. The thin, jointed and branching distal parts of the dermal fin-rays were reduced. In the main anterior part of the ventral lobe of the caudal fin, which supported the posterior part of the tail when the animal dwelt in shallow, water or on land, the long basal segments of the fin-rays disappeared as well, and the radials became slightly modified. The postsacral ribs became somewhat elongated and most probably the most anterior postsacral rib was incorporated in the pelvic bone, forming the posterior process of the iliac portion of that bone.

III. SYSTEMATIC DESCRIPTIONS

Some remarks on the terminology of the dermal bones.

In the subsequent account the dermal bones of the skull of both a tetrapod and a rhipidistid crossopterygian will be described and before entering upon these descriptions I find it advisable to make a few remarks on the much debated question of the homologies of the dermal bones of the cranial roof in fishes and tetrapods, and on the new terminology of these bones in the rhipidistids recently introduced by WESTOLL (1938; 1943). WESTOLL claims that he has correctly homologized the said bones in rhipidistids with those in tetrapods and maintains that his "considerations show beyond reasonable doubt that both the old 'orthodox' homologies and those of SÄVE-SÖDERBERGH are incorrect both in method and in fact" (1943, p. 82).

WESTOLL assumes that the bone in the rhipidistids (*Fr*, fig. 22A) which is pierced by the fenestra occupied by the pineal plates and which according to the 'orthodox' terminology is called frontal, is the true homologue of the bone in lower tetrapods that is pierced by the pineal foramen and which according to current views corresponds to the parietal in Man. The frontal in rhipidistids should therefore, according to WESTOLL, be called parietal, and simply using the pineal foramen as a landmark he renames most of the bones of the cranial roof of the rhipidistids. This new terminology, which thus implies a radical change of the current names, has been adopted inter alia by ROMER (1941; see also GREGORY 1951, p. 243), who used it in his well-known text-book (1945), where he made an attempt to apply the new terminology to the actinopterygians as well.

Provided that this new terminology is correct, as it is claimed to be, the frontal in *Eusthenopteron* (*Fr*, "*Pa*", fig. 22A), for example, would be the true homologue of the parietal in Man and other mammals (*Pa*, fig. 22B) and the hindmost nasal (*Na.7*, "*Fr*", fig. 22A) and the remaining elements of the nasal series (*Na.2*—*Na.6*) would correspond to the frontal and nasal respectively in Man. It is not my intention in this connection to discuss these homologies in detail, but I cannot for-

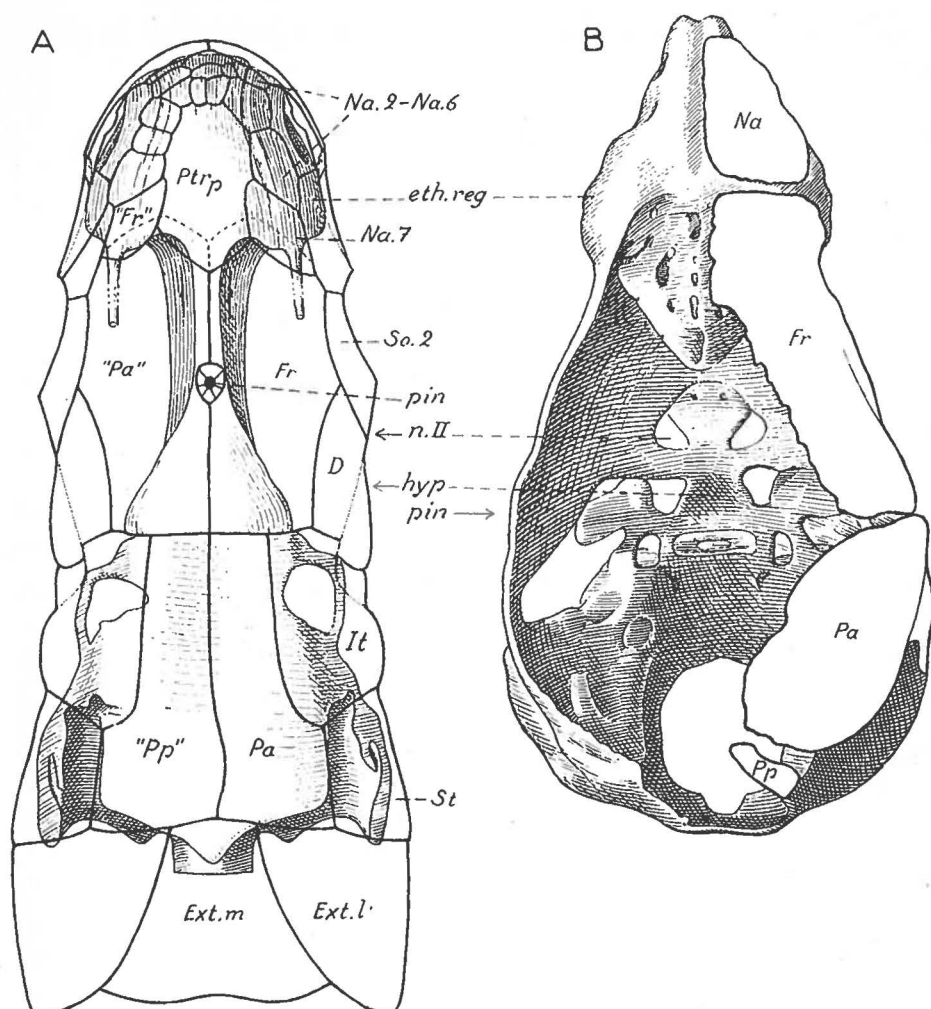


Fig. 22. Diagrammatic representations of the dermal bones of the cranial roof, showing their position in relation to each other, to the neural endocranium, and to certain other structures in (A) an osteolepiform crossopterygian and (B) a mammal. As is clearly seen, the bone generally called frontal (*Fr*) in the crossopterygian skull is situated almost exactly as the frontal in mammals. A. *Eusthenopteron foordi*. Restoration based mainly on the grinding series of the skull of specimen No. P.222 Stockh. (cf. pl. 7 and JARVIK 1942, fig. 34). Several details in the neural endocranium omitted. The anterior margin of the overlapped portion of the frontal indicated by a broken line. B. *Lepus cuniculus*. Embryo, 45 mm. long. After VOIT, from STADTMÜLLER (1936, fig. 640).

D, dermosphenotic; *Ext.l*, *Ext.m*, lateral and median extrascapulars; *Fr*, frontal; "*Fr*", dermal bone in the crossopterygian skull, by WESTOLL claimed to be the strict homologue of the frontal in mammals; *It*, intertemporal; *Na*, nasal; *Na.7*, nasal 7; *Na.2-6*, nasals 2-6; *Pa*, parietal; "*Pa*", dermal bone, by WESTOLL claimed to be the strict homologue of the parietal in mammals; *Pp*, postparietal; "*Pp*", dermal bone, by WESTOLL claimed to be the strict homologue of the postparietal in mammals;

So.2, posterior supraorbital; *St*, supratemporal.

eth.reg, ethmoidal region of neural endocranium; *hyp*, position of the hypophysis;

n.II, position of the exit of n. opticus; *pin*, position of the pineal organ.

bear observing that they are hardly in agreement with the actual position of the said bones in relation to the neural endocranium and other structures. As may be gathered from fig. 22, showing the dermal bones of the cranial roof, and the endocranium in a rhipidistid crossopterygian (*Eusthenopteron*) and a mammal (*Lepus*), the frontal (*Fr*) in *Eusthenopteron*, which should correspond to the parietal (*Pa*) in *Lepus*, is in fact situated almost exactly as the frontal in *Lepus*. As that bone, it covers the orbito-temporal region and the hindmost part of the ethmoidal region of the neural endocranium. It forms the main part of the exoskeletal roof of the orbit and backwards it extends only a little behind the region of the hypophysis (*hyp*, fig. 22). Moreover, the pineal organ (*pin*, fig. 22B) in *Lepus* is situated about opposite the posterior end of the frontal; in certain rhipidistids (see figs. 23, 26) it is situated between the posterior parts of the frontal (cf. foot-note on p. 53). It may now be questioned if the rhipidistid frontal in the phyletic development from fish to Man really moved backwards to be situated behind the region of the hypophysis in the otic region of the skull, where the parietal in *Lepus* both arises in ontogeny and remains in the adult (cf. DE BEER 1937, pp. 307—314); or did possibly other modifications take place in the long phyletic development from fish to mammal, which might explain the great difference in position between the rhipidistid frontal and the parietal in mammals, which bones according to WESTOLL are strictly homologous? Or is it perhaps after all so that earlier writers were correct in assuming that it is the frontal in rhipidistids and other fishes that corresponds to the frontal in Man? Another possible alternative to be seriously considered is that a posterior part of the rhipidistid frontal in phylogeny may have fused with an anterior part of the parietal, as suggested by SÄVE-SÖDERBERGH (1932 b, p. 92, fig. 18), and it is also worth serious consideration if SÄVE-SÖDERBERGH was not correct in assuming that several of the comparatively numerous dermal bones in the rhipidistids have fused, forming compound bones in tetrapods¹).

¹) These assumptions of SÄVE-SÖDERBERGH have, on several occasions, been severely criticized by ROMER (1936; 1946, p. 62; 1947, pp. 26—29) and WESTOLL (e.g. 1938; 1940; 1943; 1949; see also GREGORY 1951, p. 243). However, a subdivision of the frontal in the way postulated by SÄVE-SÖDERBERGH has recently (JARVIK 1947) been demonstrated in *Polypterus*, in which the frontal is very much as in *Eusthenopteron*, and anterior parts of the parietal and posterior parts of the frontal are often independent in *Osteolepiformes* and may fuse with each other in various combinations (JARVIK 1948a, pp. 64—66). That fusions of dermal bones in the way assumed by SÄVE-SÖDERBERGH really occur, and that such fusions are very common and have played an important role in the development of the different patterns of arrangement of the dermal bones in various groups, must now be regarded as a well established fact (JARVIK 1948a, pp. 62—85; 1950a, p. 53). All dermal bones grow and fuse in principally the same way, and it is only natural that there are no differ-

Or is it perhaps so that the numerous components entering into the formation of the dermal bones in rhipidistids and other fishes (JARVIK 1948a, pp. 76—85; 1950a, pp. 51—53) have been rearranged in tetrapods so that no homologues are traceable? It may also be questioned if the position of the pineal foramen really is a reliable landmark for bone identifications¹⁾ and if the correspondingly named bones in the various tetrapod groups really are homologous throughout (cf. JARVIK 1942, pp. 343—345, 415, 549—550)?

In reviewing these various alternatives, which in no way are exhaustive, I have not intended to take up a definite position with reference to any of the questions discussed but have only wanted to show that many fundamental problems still remain to be solved. In my opinion (cf. JARVIK 1948a, p. 81) the only way out of the difficulties would be to introduce a quite new terminology, not using any tetrapod names, and to try to follow the modifications of the bone patterns in the various lines of evolution from primitive forms upwards. However, this is a very intricate task, which is difficult to solve without a detailed knowledge

ences in these respects between different categories of dermal bones. However, WESTOLL (1949, p. 135) only admits that lateral-line bones may fuse, and maintains that "the evidence is overwhelmingly against fusions between lateral-line ossicles and adjoining 'general' dermal bones". The overwhelming evidence is that in *Dipterus* "no single example of fusion between bone 3 and L_2 , L_1 , K or X was ever seen in several dozen favorably preserved specimens". WESTOLL here overlooks the important fact that bone 3, which often is missing (see e.g. JARVIK 1950a, fig. 6), is situated above the orbit, where of course no fusions are to be expected because of the movements of the eye. Similar conditions are found in many other fishes, for example in *Eusthenopteron* (JARVIK 1944a, p. 12) and *Eusthenodon* (p. 62), in which the correspondingly situated bone, the posterior supraorbital, is often detached or missing and never fuses with the adjoining bones. The overwhelming evidence is thus no evidence at all. Besides, WESTOLL's sketches of the cranial roof in various dipnoans provide many good examples of fusion between different categories of bones.

¹⁾ In the *Osteolepiformes* the pineal foramen has a very varying position in relation to the position of the centra of radiation of the frontals (similar conditions are found in other fishes, e.g. in arthrodires; cf. HEINTZ 1932, figs. 12, 13; STENSIÖ 1945, figs. 8, 12; 1948, figs. 66, 68, 69, 70, 72, 73). It is remarkable that in the Middle Devonian genus *Osteolepis* (JARVIK 1948a, fig. 16), in which the frontal and the underlying orbito-temporal region of the neural endocranium are comparatively short, the pineal foramen is situated far forwards, distinctly in front of the frontal centra, whereas in *Eusthenopteron foordi* from the lowermost Upper Devonian (fig. 22A) and in *E'dalgleisiensis* (JARVIK 1950c, fig. 8; cf. also fig. 9C) and *Eusthenodon* (fig. 26) from the Upper Devonian, in which the orbito-temporal region has become much lengthened (as in lower tetrapods), it lies between (*E. foordi*), or more or less far behind, the said centra. The importance of these interesting variations, and the question whether a further migration backwards of the pineal foramen would lead to the conditions found e.g. in *Lepus* (fig. 22B), where the pineal organ is situated a little behind the region of the hypophysis, apparently about opposite to the posterior end of the frontal, are too intricate problems to be discussed here.

of the neural endocranium and the skull as a whole in the various forms, and under the present circumstances the only thing to do seems to me to be to retain, as far as possible, the current names in each group without claiming that correspondingly termed bones in the various groups are homologous.

Crossopterygii. Osteolepiformes.

Family Rhizodontidae.

Genus Eusthenodon n. g.

The generic name refers to the large and stout tusks in the upper and lower jaws.

Diagnosis.—Large rhizodontid fishes, attaining a total length of about 2.5 m. Scales and dermal bones ornamented with ridges generally forming net-works. Independent tubercles rare. Fronto-ethmoidal shield very long, about 2.3 times as long as the parietal shield. Postorbital division of the fronto-ethmoidal shield occupying almost the posterior half of that shield. Parietal shield short and broad, proportionately. Fenestra exonarina anterior situated high up in the lateral side of the snout and visible when the fish is viewed from above. Pineal foramen very small and situated far back, behind the centre of radiation of the frontal and distinctly behind the middle of the postorbital division of the fronto-ethmoidal shield. Pineal fenestra very large, occupying about 0.35—0.57 of the length of the median suture between the frontals. Pineal plates large, sometimes fused into a single plate. Orbital fenestra small—its length less than 0.3 of the length of the parietal shield—and situated very far forwards, opposite the anterior end of the frontal. Posterior supraorbital extends downwards behind the orbital fenestra to meet the jugal and the lachrymal; posterior end of the bone separated from the dermosphenotic by the frontal. External cheek plate long and low, about 3.5 times longer than the parietal shield and about 3.0 times as long as high. Postorbital and jugal excluded from the orbital fenestra, which is bounded by the supraorbito-tectal, the posterior supraorbital and the lachrymal only. Quadratojugal comparatively long and low, about 2.6 times as long as high. Centre of radiation of the quadratojugal and the quadratojugal pit-line situated far behind the middle of the bone. Maxillary attains its greatest height in the anterior half of the bone. Lower jaw comparatively long, about 4.0 times as long as the parietal shield. Opercular and subopercular higher than long. Branchiostegal rays, probably eight in number, extending forwards to or almost to the symphysis. Principal gular plate rather narrow; its centre of radiation and its pit-line situated

distinctly behind the middle of the bone. Sensory canals with long, richly branching tubes. Scales cycloid, with a distinct elongated protuberance, pointed antero-dorsally, on the inner side. Overlapped areas of the scales large.

Remarks.—*Eusthenodon* in many respects agrees well with *Eusthenopteron*, especially with *E?dalglesiensis*, in which the fronto-ethmoidal shield is comparatively long and the pineal foramen is situated distinctly behind the centre of radiation of the frontal. It differs clearly from *Eusthenopteron* and other *Osteolepiformes* inter alia in the following respects: the ornamentation consists of ridges forming distinct net-works, whereas independent tubercles are rare; the fronto-ethmoidal shield, the external cheek plate and the lower jaw are longer proportionately than in any other members of the *Osteolepiformes*; the postorbital division of the fronto-ethmoidal shield occupies almost the posterior half of that shield; the pineal plates and the pineal fenestra are much larger proportionately than in other forms; the pineal foramen is situated distinctly behind the middle of the postorbital region of the fronto-ethmoidal shield; the small orbital fenestra is situated opposite the anterior ends of the frontals; the lachrymal and the posterior supraorbital meet behind the orbital fenestra and exclude the jugal and postorbital from that fenestra, which accordingly is bounded by three bones only; the maxillary is highest about at the suture between the lachrymal and the jugal.

Genotype: *Eusthenodon wängsjöi* n.sp.

***Eusthenodon wängsjöi* n. sp.**

(Figs. 23, 24, 25 A, 26—29, 30 A, B, 31 A; pls. 9—20).

1931. *Rhizodontidae*. Genus et species indet. — STENSJÖ, pp. 201—202, fig. 93; pl. 33:2; pl. 35:10.

The species is named after Dr. GUSTAV WÄNGSJÖ, Uppsala, who has collected many of the best specimens.

Diagnosis.—The diagnosis is the same as that of the genus.

Type-specimen.—The holotype is specimen No. P. 1476 (figs. 23 A, 27; pls. 9, 10; pl. 11:2) from the horizon at 1174 m. in Sederholms Bjerg (cf. pp. 6—8). The holotype consists of an almost complete flattened skull of moderate size, which after negative preparation presents inter alia more or less complete impressions of the external faces of the cranial roof, the external cheek plate, the lower jaw, the branchiostegal rays and the principal gular. Parts of the palate are shown as well.

Material.—In addition to the holotype only the following specimens in the comprehensive material of Upper Devonian crossopterygians from East Greenland at my disposal will, for the time being, be included in this species: No. 101 (pl. 17:1; STENSJÖ 1931, pl. 33:2), part of cranial

roof, Celsius Bjerg; No. 162 (STENSIÖ 1931, pl. 35:10), detached scale, Celsius Bjerg; No. P. 1473 (pl. 12:3; pls. 15, 16), comparatively small, nearly complete skull, Sederholms Bjerg; No. P. 1474 (fig. 28), posterior part of the external cheek plate, Celsius Bjerg, s. slope; No. P. 1475 (fig. 24), parietal shield, Celsius Bjerg, s. slope; Nos. P. 1477 (pl. 17:2; pl. 18) and P. 1478 (pls. 13, 14), two large skulls from the same locality as the holotype; Nos. P. 1479 (pl. 11:1; pl. 12:1) and P. 1480 (pls. 19, 20), two large skulls, Smith Woodward's Bjerg; No. P. 1481 (pl. 12:2), posterior part of the cranial roof, opercular, cleithrum, etc.; No. P. 1482 (pl. 12:4), impression of the parasphenoid, Remigolepisryg; No. P. 1483 (pl. 17:3), imperfect impression of the ventral side, Sederholms Bjerg. Detached scales are found together with several of the specimens.

Geographical distribution and geological age.—The Remigolepis Series in Gauss Halvö and Ymers Ö, East Greenland. Upper Devonian (probably uppermost Famennian or lowermost Strunian; cf. JARVIK 1950b, p. 15).

Description.

Eusthenodon in most respects agrees well with *Eusthenopteron* (JARVIK 1937; 1944a; 1950c) and other *Osteolepiformes* (JARVIK 1948a; 1949; 1950a; 1950b; 1950c) and a complete description will not be given.

Skull.

In most specimens the skull is comparatively large. In the holotype the parietal shield, the fronto-ethmoidal shield and the external cheek plate measure ca. 56, 129 and 195 mm., respectively, in length and the total length of the skull, including the opercular apparatus, may be estimated to have been about 270 mm. The holotype is thus much larger than most of the *Osteolepiformes* I have recently described (1948a, etc.) and of about the same size as *Eusthenopteron wenjukowi* (JARVIK 1937, p. 90) and the largest of the specimens of *Eusthenopteron foordi* at my disposal. However, several of the skulls are much larger. The parietal

Fig. 23. *Eusthenodon wängsjöi* n.g., n.sp. Sketches of the cranial roof or part of it in various specimens, showing variations in size and in the pattern of the dermal bones. A, No. P. 1476 (holotype; pls. 9, 10); B, No. P. 1478 (pls. 13, 14); C, No. P. 1480 (pls. 19, 20); D, No. 101 (pl. 17:1); E, No. P. 1473 (pl. 15). All specimens 2/5. D, dermosphenotic; Ext.l, Ext.m, lateral and median extrascapulars; Fr, frontal; It, intertemporal; Na, nasal; NRP, naso-rostro-premaxillary; Pa, parietal; Pin.pl, pineal plates; Ptr_{an}, anterior median postrostral; Ptr_m, space, probably for one or more middle postrostrals; Ptr_p, posterior median postrostral; R.l, lateral rostral;

So-Te, supraorbitotectal; St, supratemporal; Te.a, anterior tectal. fe.exa, fenestra exonarina anterior; f.pin, pineal foramen; ioc, infraorbital sensory canal; pl.Fr., frontal pit-line; pl.po.Pa, posterior oblique parietal pit-line; pl.St, supratemporal pit-line; pl.tr.Pa, transverse parietal pit-line; soc, supraorbital sensory canal.

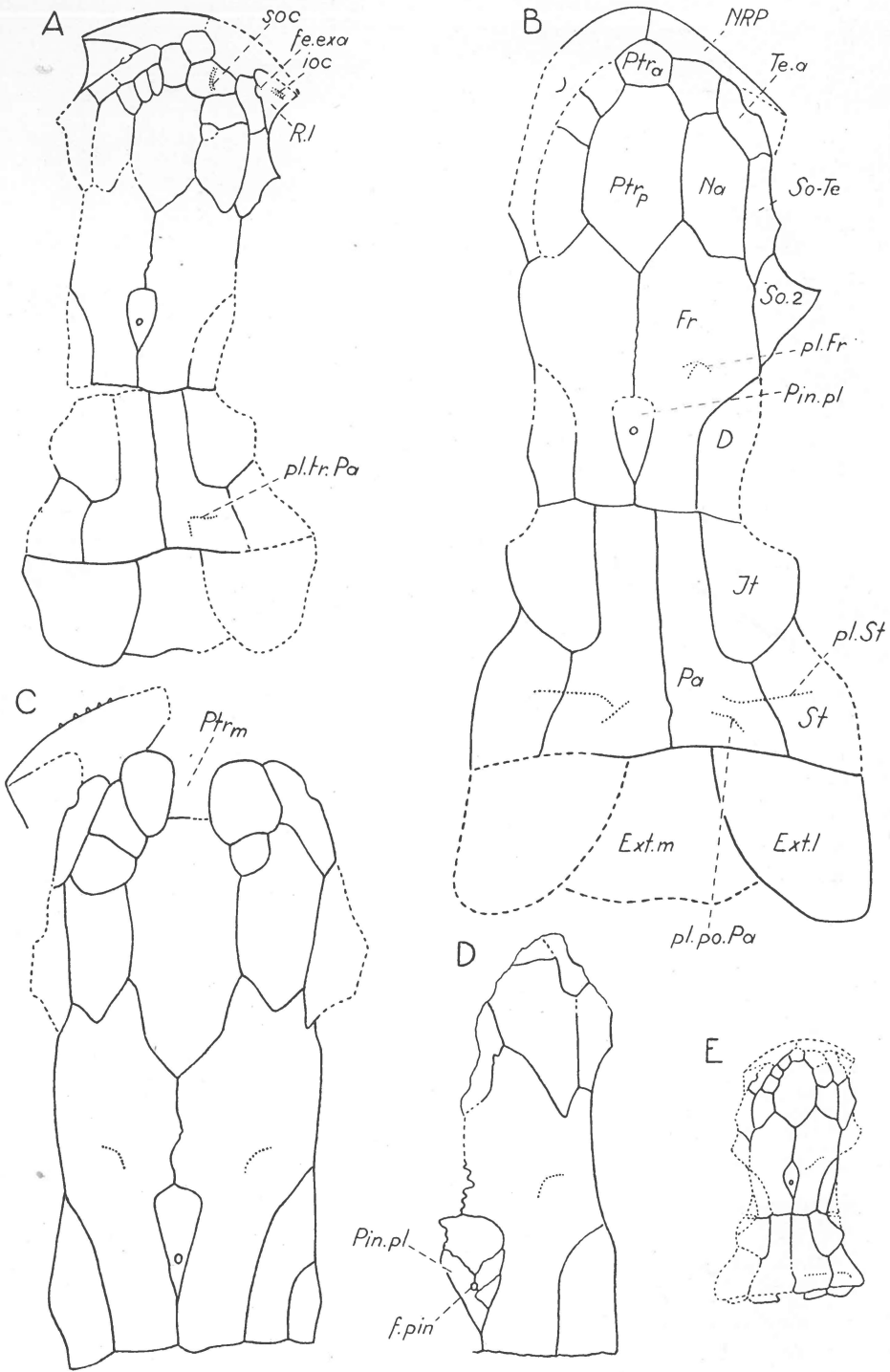


Fig. 23.

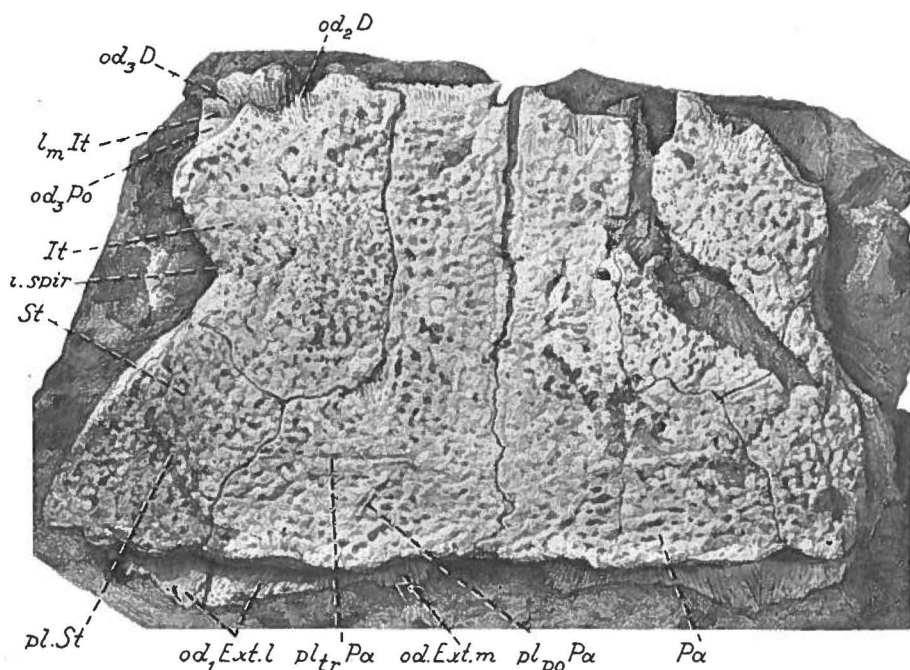


Fig. 24. *Eusthenodon wängsjöi* n.g., n.sp. Parietal shield in dorsal aspect, showing overlapped areas (cf. JARVIK 1944a, fig. 7C). Specimen No. P. 1475. From the southern slope of Celsius Bjerg, Ymers O. 3/4.

It, intertemporal; *Pa*, parietal; *St*, supratemporal.

lmIt, middle lamina of intertemporal, overlapping posterior end of dermosphenotic; *i.spir*, spiracular notch; *od1Ext.m*, area of parietal shield overlapped by median extrascapular; *od1Ext.l*, area of parietal shield overlapped by lateral extrascapular; *od2D*, *od3D*, dorsal and ventral areas of intertemporal overlapped by dermosphenotic; *od3Po*, area of intertemporal overlapped by dermosphenotic; *pl.po.Pa*, posterior oblique parietal pit-line; *pl.St*, supratemporal pit-line; *pl.tr.Pa*, transverse parietal pit-line.

shield shown in fig. 24 thus measures about 84 mm. in length and in No. P. 1480 (pls. 19, 20) the fronto-ethmoidal shield is ca. 220 and the external cheek plate ca. 340 mm. long, whereas in No. P. 1477 (pl. 18) the latter attains a length of no less than ca. 360 mm. The skull in No. P. 1477 was thus almost twice as long as in the holotype and attained a length of nearly half a meter. Since the length of the skull in the *Osteolepiformes* generally is contained ca. 4.5—5 times in the body length, the total length of the fish may be estimated to have been ca. 2.25—2.50 m., whereas the holotype probably attained a length of ca. 1.20—1.35 m. One of the skulls, No. P. 1473 (fig. 23 E), is comparatively small and measures only about 130 mm. in length.

Ornamentation (see figs. 24, 28, 31 A and the plates).—The ornamentation of the dermal bones of the skull both in the small and the

large specimens consists mainly of tubercles united into anastomosing ridges, generally forming net-works (cf. *Acanthostega*, p. 73; fig. 31 B). It differs clearly from that in *Eusthenopteron foordi* and other species of that genus (JARVIK 1937, figs, 3, 10, 14, 17; 1944a; 1944b) in which real net-works are rarely formed and the ornamentation generally consists of short ridges of a few incompletely fused tubercles or of free tubercles.

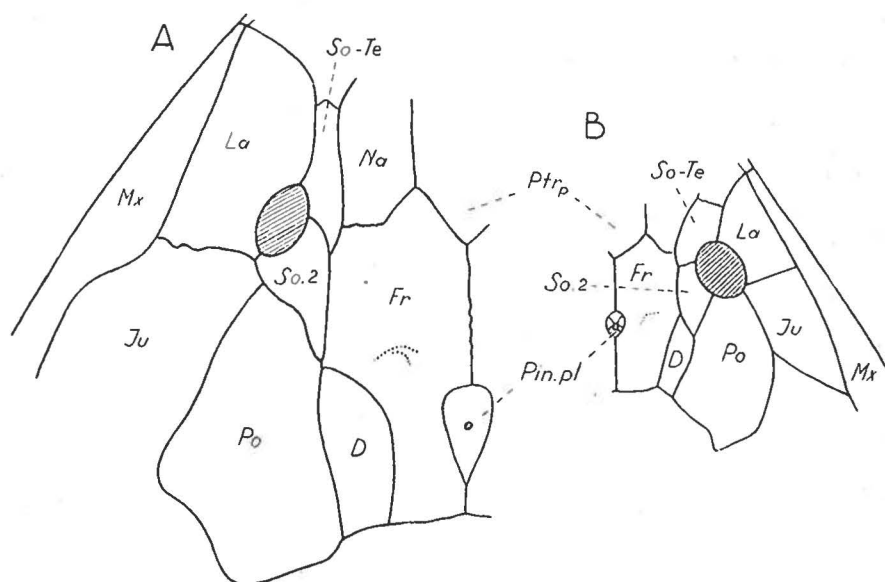


Fig. 25. Parts of the fronto-ethmoidal shield and the external cheek plate, showing mainly the orbital fenestra and the surrounding dermal bones. A, *Eusthenodon wängsjöi* n.g., n.sp. Specimen No. P. 1478 (fig. 23 B, pl. 14). 3/7. B, *Eusthenopteron foordi*. Mainly after specimen No. 1897. 51. 204. Figured by JARVIK (1944a, fig. 10 A, B). 1/2.

D, dermosphenotic; Fr, frontal; Ju, jugal; La, lachrymal; Mx, maxillary; Na, nasal; Pin.pl, pineal plates; Po, postorbital; Ptrp, posterior median postrostral; So.2, posterior supraorbital; So-Te, supraorbito-tectal.

The cranial roof (figs. 23, 24, 25 A, 26; pls. 9, 10; pl. 11:1; pl. 12:1; pls. 13, 14; pl. 15:1—3; pl. 17:1; pl. 18:1; pls. 19, 20).—The fronto-ethmoidal shield is comparatively long and narrow. Its breadth is at the orbital notch about 0.50 and most posteriorly about 0.40 of its length and it is no less than about 2.3 times as long as the parietal shield. It is thus distinctly longer proportionately than in *Eusthenopteron? dalgleisiensis* (JARVIK 1950c), which has the longest fronto-ethmoidal shield, proportionately, among the *Osteolepiformes* previously known, the corresponding ratio being about 2.0. The parietal shield is short and broad. Most anteriorly it is about as broad as long, whereas at the spiracular

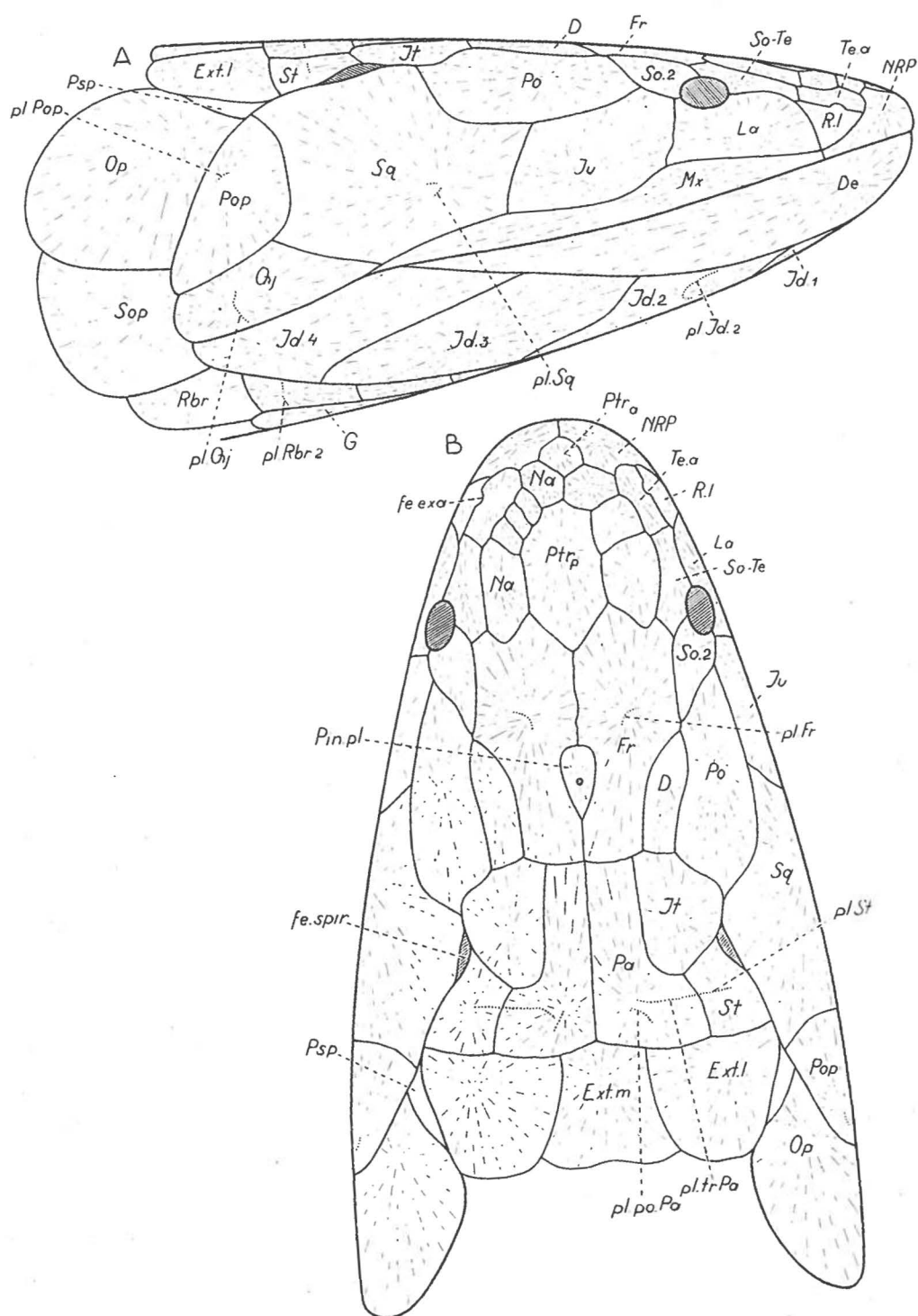


Fig. 26 A—B.

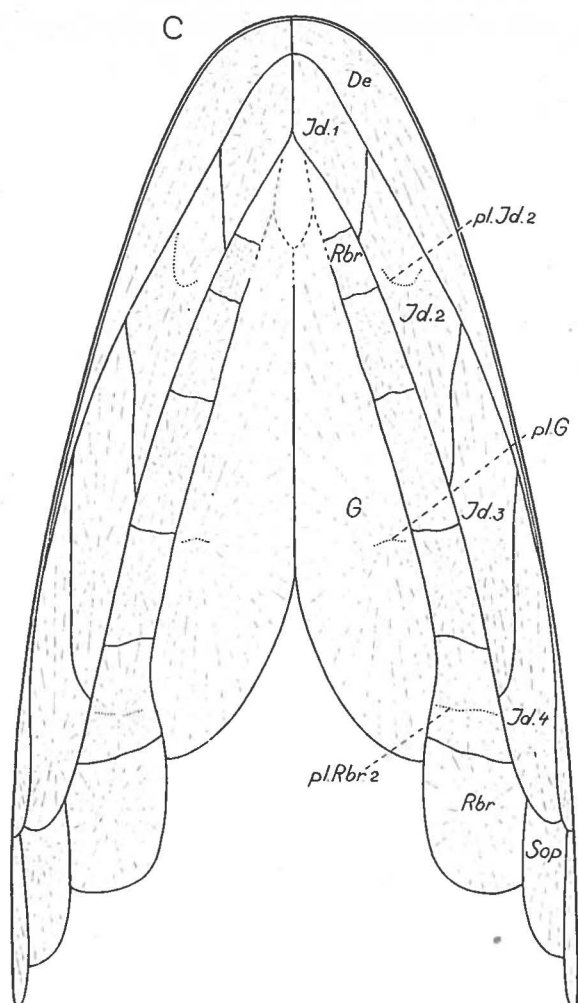


Fig. 26 C.

Fig. 26. *Eusthenodon wängsjöi* n.g., n.sp. Restorations of the skull in, A, lateral, B, dorsal, and C, ventral aspects. Mainly after the holotype. 1/2.

D, dermosphenotic; De, dentary; *Ext.l*, *Ext.m*, lateral and median extrascapulars; *Fr*, frontal; *G*, principal gular plate; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentaries 1, 2, 3, and 4; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *NRP*, naso-rostro-premaxillary; *Op*, opercular; *Pa*, parietal; *Pin.pl*, pineal plates, *Po*, postorbital; *Pop*, preopercular; *Psp*, space, probably occupied by postspiracular plate; *Ptr_a*, *Ptr_p*, anterior and posterior postrostrals; *Qj*, quadratojugal; *Rbr*, branchiostegal rays; *R.l*, lateral rostral; *Sop*, subopercular; *So-Te*, supraorbito-tectal; *So.2*, posterior supraorbital; *Sq*, squamosal; *St*, supratemporal; *Te.a*, anterior tectal. *fe.exa*, fenestra exonarina anterior; *fe.spir*, spiracular fenestra; *pl.Fr*, frontal pit-line; *pl.G*, pit-line of principal gular; *pl.Pop*, preopercular pit-line; *pl.po.Pa*, posterior oblique parietal pit-line; *pl.Qj*, quadratojugal pit-line; *pl.Rbr.2*, pit-line of branchiostegal ray 2; *pl.Sq*, squamosal pit-line; *pl.St*, supratemporal pit-line; *pl.tr.Pa*, transverse parietal pit-line; *pl.Id.2*, vertical pit-line of infradentary 2.

notch it is ca. 1.20 and at the postero-lateral corner ca. 1.70 times broader than it is long.

The dermal bones of the snout are fairly well shown in several specimens and the sutures are generally distinct. The nasal series (*Na*), which as usual consists of about seven elements fused in various combinations, in some specimens meets the corresponding series of the other side between the anterior and posterior median postrostrals (*Ptr_a*, *Ptr_p*), as it sometimes does in *Osteolepis* (JARVIK 1948a, figs. 14, 15). No middle postrostrals have been found, but apparently such bones were developed in No. P. 1480 (*Ptr_m*, fig. 23C). The fenestra exonarina anterior (*fe.exa*) is situated high up in the side of the snout and is visible when the skull is viewed from above.

The posterior supraorbital (*So.2*), which is generally detached or missing, in several respects differs from the corresponding bone in other *Osteolepiformes*. It is three-sided and extends far downwards behind the orbital fenestra (*fe.o*) as it does sometimes in *Eusthenopteron foordi* (JARVIK 1944a, p. 12, fig. 5) but contrary to conditions in that form (fig. 25B) and other *Osteolepiformes* known in this respect it extends so far ventrally as to meet the lachrymal. Consequently it excludes both the postorbital and the jugal from the orbital fenestra and is joined to both these bones with fairly long sutures. Another remarkable feature is that posteriorly, where it is pointed, the bone ends a little in front of the dermosphenotic. In consequence of this the frontal (*Fr*), which like the dermosphenotic (*D*) is comparatively long and narrow, laterally meets the postorbital in a short suture.

The pineal foramen (*f.pin*) is a diminutive opening, whereas the pineal fenestra and the pineal plates (*Pin.pl*) are unusually large. The latter opening, which extends backwards almost to the posterior margin of the frontal¹⁾, thus occupies no less than about 0.35—0.57 of the median suture between the frontals, whereas for example in *Eusthenopteron* this ratio is only about 0.15. In several specimens, inter alia in the holotype, there seems to be a single pineal plate pierced by the pineal foramen, but sometimes (fig. 23; pl. 15:1, 2; pl. 17:1) this plate is divided into several smaller plates and apparently there is a relatively large anterior median plate, a small posterior median plate and two pairs of lateral plates as in *Eusthenopteron foordi*. The pineal foramen (and the pineal fenestra) is situated very far back, far behind the transverse line running through the postorbital corner and distinctly behind the centra of radiation of the frontals. It is thus situated somewhat as in the nearly contemporaneous Scottish rhizodontids (*Eusthenopteron* cf. *traquairi* and *E?dalglesi-*

¹⁾ In a new skull-roof from Smith-Woodwards Bjerg collected in 1951 the pineal fenestra and the pineal plates are large and reach the posterior margin of the fronto-ethmoidal shield.

ensis, JARVIK 1950c, figs. 8, 9), but contrary to conditions in these forms and in all other *Osteolepiformes* known in this respect as well, it lies distinctly behind the middle of the postorbital division of the fronto-ethmoidal shield (cf. JARVIK 1948a, p. 35, fig. 12), which is very long and occupies almost the whole posterior half of the fronto-ethmoidal shield.

The dermal bones of the parietal shield (*Pa*, *It*, *St*) are comparatively short and broad. The overlapped areas (see fig. 24) are almost

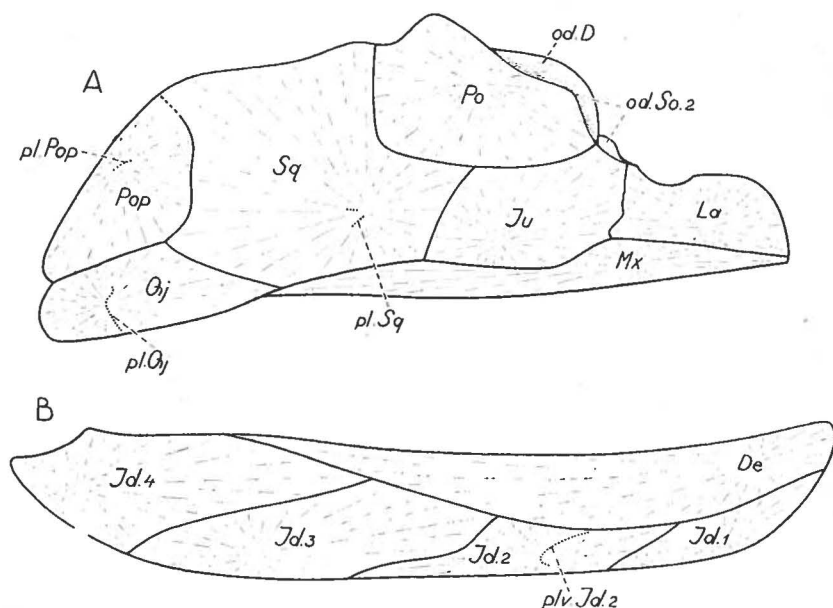


Fig. 27. *Eusthenodon wängsjöi* n.g., n.sp. Restorations of, A, the external cheek plate and, B, the lower jaw in external aspects. Mainly after the holotype. 1/2. *De*, dentary; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentaries 1, 2, 3, and 4; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Po*, postorbital; *Pop*, preopercular; *Qj*, quadratojugal; *Sq*, squamosal.

od.D, area overlapped by the dermosphenotic and frontal; *od.So.2*, area overlapped by posterior supraorbital; *pl.Pop*, preopercular pit-line; *pl.Qj*, quadratojugal pit-line; *pl.Sq*, squamosal pit-line; *plv.Jd.2*, vertical pit-line of infradentary 2.

exactly as in *Eusthenopteron foordi* (JARVIK 1944a, fig. 7C). No extratemporal has been found (cf. p. 64). The extrascapular series of bones (*Ext.l*, *Ext.m*) is as usual.

The external cheek plate (figs. 25A, 26A, B, 27A, 28; pls. 9, 10; pl. 11:1; pl. 12:1; pls. 13, 14; pl. 15:1—3; pl. 16:4; pls. 18—20).—The external cheek plate is about 3.5 times as long as the parietal shield and about 3.0 times as long as high and is thus comparatively long and low. The lachrymal (*La*) is somewhat as in *Eusthenopteron* but is comparatively high in its posterior part, where it extends dorsally to meet the posterior supraorbital in a short suture behind the orbital fenestra.

The jugal (*Ju*), as in *Gyroptychius agassizi* (JARVIK 1948a, fig. 71), does not reach the orbital fenestra, but contrary to conditions in that form and other *Osteolepiformes* it meets the posterior supraorbital in a distinct suture. The fact that the postorbital (*Po*) is excluded from the orbital fenestra is unparalleled in the *Osteolepiformes* as well. In other respects the postorbital agrees with that in *Eusthenopteron*, and as in that form it extends backwards to or almost to the spiracular fenestra (*fe.spir*). Also the squamosal (*Sq*) and the preopercular (*Pop*) are much as in that genus. The quadratojugal (*Qj*) is comparatively long and low, about 2.6 times as long as high. The maxillary (*Mx*) is remarkable in that it attains its greatest height in the anterior half of the bone, close behind the centre of radiation. In this respect *Eusthenodon* differs from all other *Osteolepiformes* but agrees with the contemporaneous stegocephalians (*Acanthostega*, fig. 34; *Ichthyostega*, fig. 35).

The orbital fenestra (*fe.o*, figs. 25A, 26; pls. 9, 10; pl. 11:1; pl. 12:1; pls. 13, 14; pl. 15:2, 3; pl. 16:4; pl. 18:1), which is bounded by three bones only viz. the lachrymal, the posterior supraorbital, and the supraorbito-tectal, is small and is situated very far forwards. It thus lies opposite and partly further forwards than the most anterior part of the frontal and its length is only about 0.12 and 0.27, respectively, of the length of the fronto-ethmoidal and parietal shields, whereas in *Eusthenopteron foordi* the corresponding ratios are about 0.25 and 0.40 (cf. JARVIK 1950c, p. 19).

The lower jaw (figs. 26A, C, 27B; pls. 10, 11; pl. 12:3; pl. 15:4; pl. 16:1, 4; pl. 17:3).—The lower jaw decreases in height anteriorly and is comparatively low in its anterior part and in this and many other respects it is suggestive of the lower jaw in the contemporaneous stegocephalians. It is almost 4 times as long as the parietal shield and thus longer proportionately than in *Eusthenopteron*. The external side is covered by the normal set of bones (*De*, *Id.1*, *Id.2*, *Id.3*, *Id.4*) and dorsally there are three coronoids (*Co.1*, *Co.2*, *Co.3*). The hindmost coronoid is extended into a pointed posterior process situated laterally to the anterior part of the dorsal margin of the adductor fossa and medially to the dentary. The prearticular (*Prart*) at the anterior end and in front of said fossa is bent laterally (*la.l*) in its dorsal part and forms the roof of the most medial part of the cavity of the jaw.

Opercular and gular bones (fig. 26; pl. 10; pl. 11:1; pl. 12:1, 2; pl. 15:3; pl. 16:1; pl. 17:3).—The opercular (*Op*), which is rarely preserved, is higher than long and on the whole suggestive of that in *Eusthenopteron foordi*. Along the dorsal margin there is a distinct depressed area (*od.Psp*; pl. 12:2), but whether this area was overlapped by the postspiracular plate as the very similar area in *Eusthenopteron* or by the lateral extrascapular as in the osteolepids (cf. JARVIK 1948a, pp. 61—

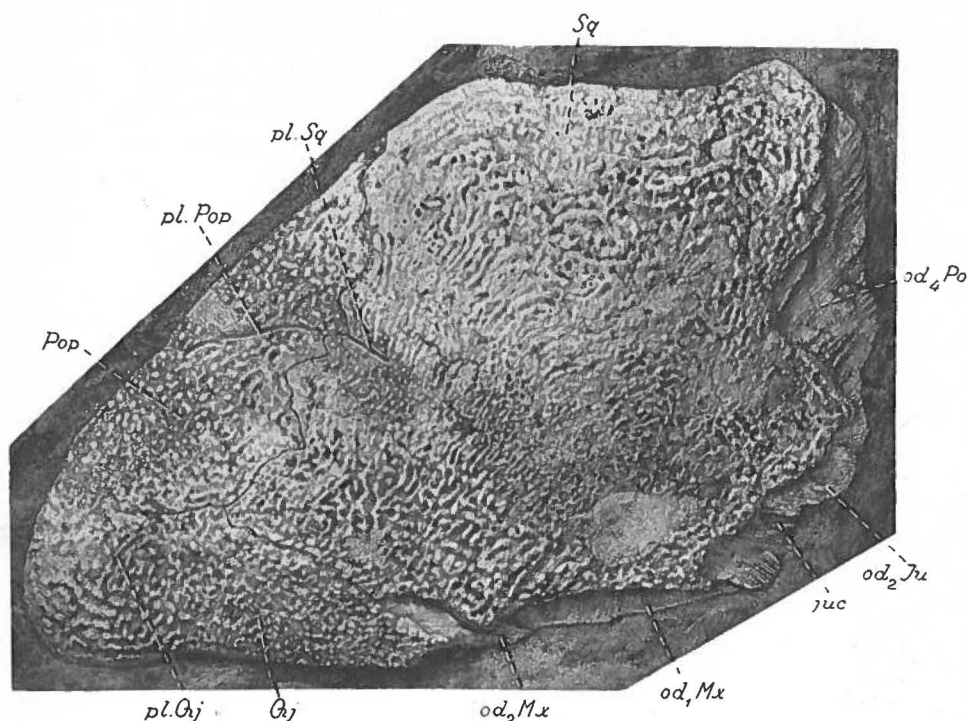


Fig. 28. *Eusthenodon wängsjöi* n.g., n.sp. Posterior part of external cheek plate in outer view, showing overlapped areas (cf. *Eusthenopteron*, JARVIK 1944a, fig. 9A). Specimen No. P. 1474. From the same locality as the specimen shown in fig. 24. 2/3.

Pop, preopercular; *Qj*, quadratojugal; *Sq*, squamosal.

juc, jugal sensory canal; *od1Mx*, area of squamosal overlapped by maxillary; *od2Ju*, area of squamosal overlapped by jugal; *od2Mx*, area of quadratojugal overlapped by maxillary; *od4Po*, area of squamosal overlapped by postorbital; *pl.Pop*, preopercular pit-line; *pl.Qj*, quadratojugal pit-line; *pl.Sq*, squamosal pit-line.

62, 95) could not be established with certainty. However, since no extra-temporal seems to be developed, the former alternative appears to be more likely. The subopercular (*Sop*), judging from the conditions in No. P. 1473, is fairly high. The branchiostegal rays (*Rbr*, fig. 26) are shown in the holotype (pl. 10) and in No. P. 1483 (pl. 17:3), but in both specimens the most anterior ray or rays are missing and whether they extend forwards to the symphysis as they do e.g. in *Eusthenopteron foordi* remains uncertain. They are seven or more probably eight in number. The principal gular plate (*G*) is incomplete anteriorly in all specimens in which it is preserved, but apparently it is narrow but fairly short, as compared with the length of the lower jaw, as it is in *Eusthenopteron foordi*. The median gular plate is unknown.

The palate (fig. 29; pl. 11:1; pl. 12:4; pl. 16:1—3).—The dermal bones of the palate, which are incompletely displayed, are on the whole

developed as in *Eusthenopteron* and other *Osteolepiformes* (JARVIK 1944a; 1950c). The vomer (*Vo*), which is provided with a ventral tooth-bearing lamina (*la.Vo*) and a posterior process, forms the posterior boundary of the fossa apicalis (*fo.ap*), but no details are known. Quite as in *Ichthyostega* (fig. 36) but contrary to conditions in *Eusthenopteron*, the dermo-

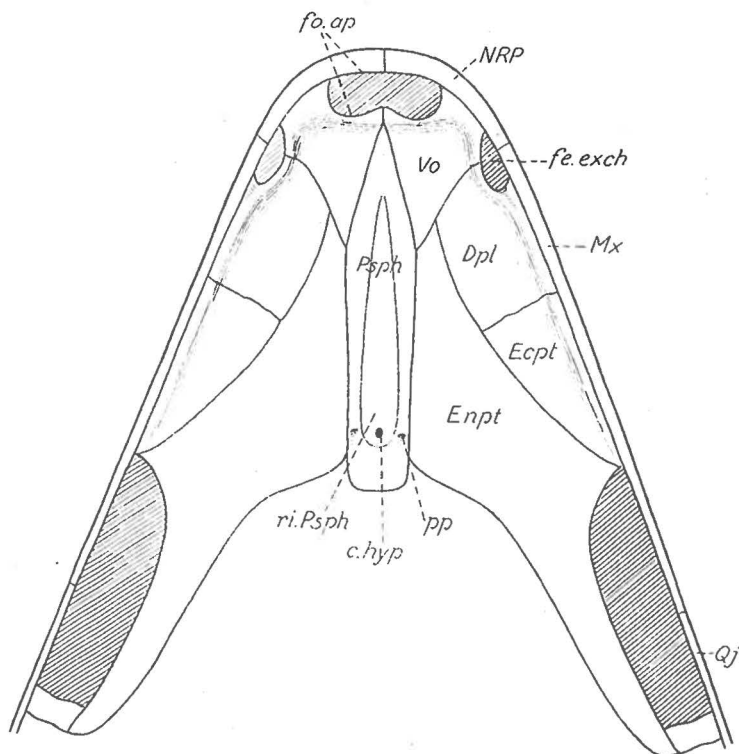


Fig. 29. *Eusthenodon wängsjöi* n.g., n.sp. Sketch of the dermal bones of the palate in ventral aspect. Teeth omitted. Mainly after specimen No. P. 1473 (pl. 16). 1/1. *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *NRP*, naso-rostro-premaxillary; *Psph*, parasphenoid; *Qj*, quadratojugal; *Vo*, vomer. *c.hyp*, canal for ventral tube of hypophysis; *fe.exch*, fenestra exchoanalis; *fo.ap*, fossa apicalis; *pp*, posteriorly directed pit of parasphenoid; *ri.Psph*, ventral tooth-bearing ridge of parasphenoid.

palatine (*Dpl*) extends slightly forwards laterally to the fenestra exchoanalis (*fe.exch*). The parasphenoid (*Psph*) agrees well with that in *Eusthenopteron foordi*, and as in that form its tooth-bearing portion, which is rounded posteriorly, is pierced by a canal (*c.hyp*) for the hypophysis. On each side of the posterior end of this portion or a little farther back there is a canal-like pit (*pp*.) opening more or less backwards.

Dentition.—The tusks of the upper and lower jaws may attain a considerable size. The largest tusks in the material, which are incom-

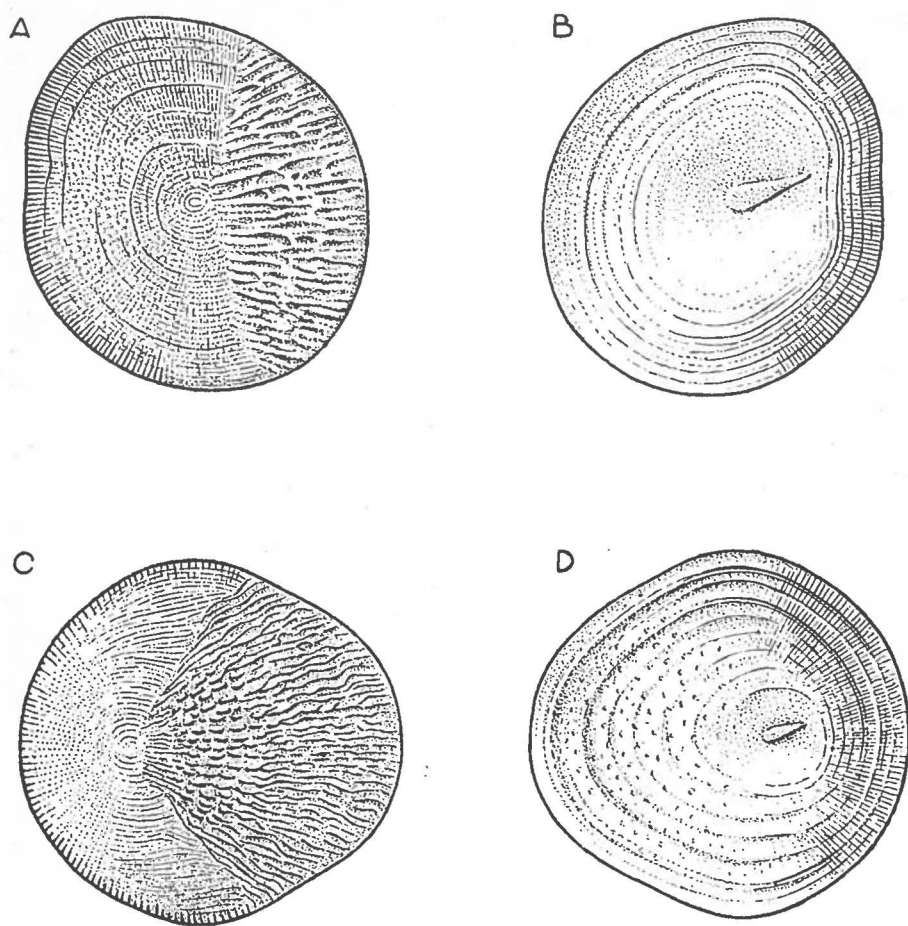


Fig. 30. Restorations of scales in external and internal aspects. *A, B, Eusthenodon wängsjöi* n.g., n.sp. Mainly after specimens Nos. P. 1477 and P. 1481. Ca. 3/2. *C, D, Eusthenopteron foordi*. *C*, from JARVIK (1950a, fig. 33E). *D*, mainly after unregistered specimen, Edinburgh (same specimen as in fig. 9D). Ca. 5/1.

plete, may be estimated to have been at least 50 mm. long, but proportionately they are not larger than in *Eusthenopteron* and in other respects as well the dentition as far as known is as in that genus (JARVIK 1944a, pp. 37—38).

Sensory canals and pit-lines.—The sensory canals (*ioc*, etc.; figs. 23, 28; pls. 9, 10; pl. 15:1, 2; pl. 18:1), which are only partly disclosed, are developed as usual. The tubes are long and richly branching, sometimes entering adjoining non-canal bones (quadratojugal, maxillary, etc.; cf. JARVIK 1944a, fig. 17). The following pit-lines have been found (figs. 23—28; pls. 9, 10; pl. 12:1; pl. 14; pl. 15:1; pl. 17:1, 3; pl. 18:1;

pl. 20): the frontal (*pl.Fr*), the supratemporal (*pl.St*), the transverse parietal (*pl.tr.Pa*), the anterior oblique parietal (*pl.po.Pa*), the squamosal (*pl.Sq*), the preopercular (*pl.Pop*), and the quadratojugal (*pl.Qj*) pit-lines, the vertical pit-line of infradentary 2 (*plv.Id.2*), and the pit-lines of the second branchiostegal ray (*pl.Rbr.2*) and the principal gular (*pl.G*).

The postcranial skeleton.

The postcranial skeleton is very imperfectly shown and is represented mainly by detached scales. Small parts of the squamation together with inconsiderable remains of the pectoral fin (*pv*) are shown in Nos. P. 1479 (pl. 11:1) and P. 1481, and in the latter specimen, in addition, an almost complete cleithrum very suggestive of that in *Eusthenopteron* (JARVIK 1944b) is preserved.

The scales (fig. 30A, B; pl. 17:2) resemble those in *Eusthenopteron foordi* (fig. 30C, D) but the overlapped portion is comparatively large and the ornamentation, as in the dermal bones, consists mainly of ridges forming net-works. The inner side presents a distinct elongated protuberance (*pt.Sc*). As is evidenced by the material of *Eusthenopteron foordi* at my disposal the pointed end of this protuberance is directed anteriorly and somewhat upwards. As pointed out by WOODWARD (1891, p. 341, 349, pl. 16:2) this protuberance, which presumably represents a vestige of the ridge on the inner side of the scales in the osteolepids (JARVIK 1948a, fig. 28), seems to be characteristic of the rhizodontid scale.

Labyrinthodontia. Ichthyostegalia.

Family Acanthostegidae n. fam.

Genus Acanthostega n. g.

The name of the genus refers to the spine-like posterior process of the tabular.

Diagnosis.—Primitive labyrinthodont stegocephalians of moderate size (skull about 135 mm. in length in the specimens known). Ornamentation consists of ridges, forming net-works, and of more or less independent tubercles. Cheeks long, forming the most posterior part of the skull-roof and firmly connected with the exoskeletal roof of the neural endocranium. Orbital fenestra situated in the middle of the skull and fairly large. Posterior margin of the skull-roof with distinct otic notch, long tabular process, deep tabular notch, and distinctly convex between the tabular notches as seen in dorsal aspect. Internasal and anterior tectal probably developed. Nasal in contact with the lachrymal. Prefrontal meets the jugal. Postfrontal long and narrow. Parietal joined with the postorbital in a distinct lateral suture. Independent intertemporal lacking. Supra-

temporal situated laterally to the posterior part of the parietal. Postparietal paired and comparatively long. Tabular with a low vertical lamina along the medial margin of the tabular notch; its centre of radiation is situated farther forwards than the centre of the squamosal and postparietal. Jugal large. Postorbital small. Squamosal joined with the tabular in a long suture in front of the otic notch. Preopercular present. Maxillary bent medially in its anterior part in the fashion characteristic of the ichthyostegids. Fenestra exonarina anterior probably situated on the ventral side of the snout, close to the tooth-bearing margin. Sensory lines at least partly enclosed in narrow canals in the dermal bones, opening outwards with short tubes.

Remarks.—The new family *Acanthostegidae*, which is still imperfectly known, differs from the family *Ichthyostegidae* SÄVE-SÖDERBERGH (1932 b) chiefly in the development of the posterior parts of the skull-roof. The main differences are as follows: The supratemporal in the acanthostegids is chiefly situated laterally to the parietal and it meets the postparietal in a short postero-medial suture only; in the ichthyostegids (figs. 32, 35; SÄVE-SÖDERBERGH 1932b) it extends backwards at least to the transverse line running through the centre of radiation of the postparietal and has a long median suture with that bone. The postparietal is paired in the acanthostegids and the posterior margin of the skull-roof formed by this bone and the adjoining parts of the tabular is distinctly convex as seen in dorsal aspect, whereas in the ichthyostegids the postparietal is unpaired and the corresponding margin strongly convex. The tabular is radically different both as to structure and position (see pp. 78—80).

Genotype: *Acanthostega gunnari* n.sp.

Acanthostega gunnari n. sp.

(Figs. 31 B, 33, 34; pl. 21).

The species is named in honour of the late professor GUNNAR SÄVE-SÖDERBERGH, Uppsala.

Diagnosis.—The diagnosis is the same as that of the genus.

Type-specimen and material.—The material with certainty pertaining to the genus *Acanthostega* consists of two imperfect skulls¹⁾ both showing mainly the dorsal and right lateral parts of the skull roof in external views. The one of these skulls, No. A. 33 (fig. 33 A; pl. 21:1, 2), chosen as holotype of the new species, was collected by SÄVE-SÖDERBERGH in 1932 in talus of the Remigolepis Series in Wimans Bjerg,

¹⁾ A third specimen (No. A. 170) collected in 1932 in Stensiös Bjerg and consisting of a fragmentary skull roof has recently been detected among the material of dipnoans.

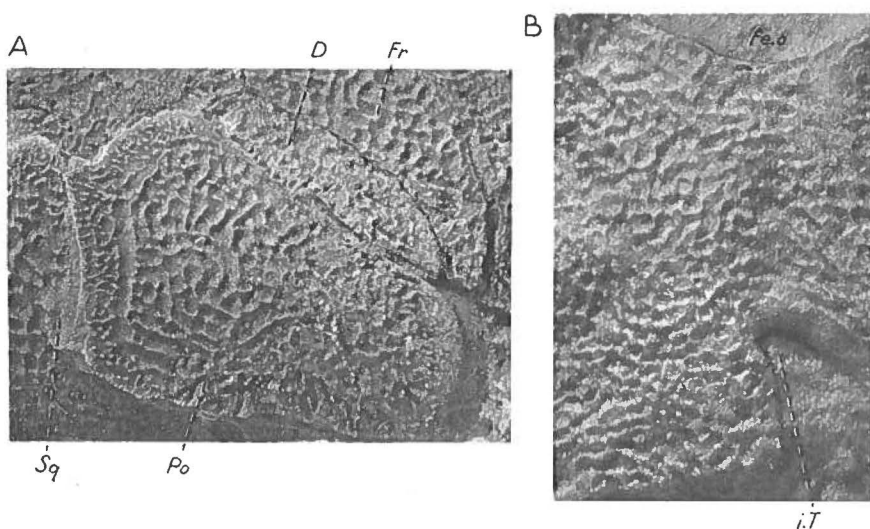


Fig. 31. Parts of the exoskeleton of the skull showing ornamentation. Photographs of casts in plastic material according to the method of STRÄHL (1951). 2/1. *A*, *Eusthenodon wängsjöi* n.g., n.sp. Specimen No. P. 1473. Same specimen as shown in pls. 15, 16. *B*, *Acanthostega gunnari* n.g., n.sp. Specimen No. A. 85. Same specimen as in pl. 21: 3.

D, dermosphenotic; *Fr*, frontal; *Po*, postorbital; *Sg*, squamosal.
fe.o, orbital fenestra; *i.T*, tabular notch.

Gauss Halvø. It is somewhat compressed and in several places more or less thick external portions of the dermal bones have been split off or parts of the dermal bones are completely lacking. The other specimen, No. A. 85 (fig. 33 B; pl. 21:3), preserved mainly as an impression, was found in 1947 in local talus in about the middle part of the Remigolepis Series in the southern slope of Celsius Bjerg, Ymers Ø. In certain respects, e.g. in the shape of the orbital fenestra, it differs distinctly from the holotype and it is doubtful whether it really belongs to this species. It is impossible to decide with certainty whether any of the postcranial material from the Remigolepis Series is referable to this form (cf. pp. 9, 83).

Geographical distribution and geological horizon.—The Remigolepis Series, Gauss Halvø and Ymers Ø, East Greenland. Upper Upper Devonian (cf. p. 56).

Description.

The following brief description is based mainly on the holotype.

The part preserved in the holotype measures about 118 mm. in the median line and backwards to the posterior end of the cheek about 130 mm., and presumably the skull, when complete, was only a few mm. longer. The other skulls are about the same size.

The posterior margin of the skull table (figs. 33, 34; pl. 21), cha-

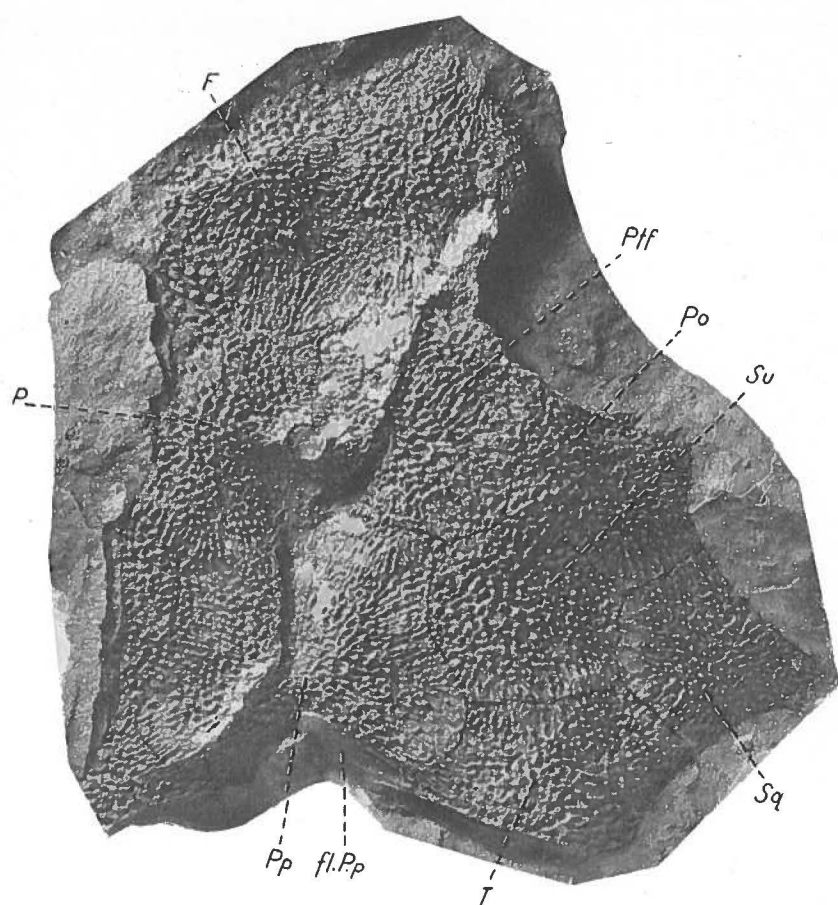


Fig. 32. *Ichthyostega* sp. Imperfect skull roof in dorsal aspect. Photograph of cast in plastic material (cf. fig. 31). Specimen No. A. 99. From the northern side of Celsius Bjerg. 1/1.

F, frontal; *P*, parietal; *Po*, postorbital; *Pp*, postparietal; *Ptf*, postfrontal; *Sq*, squamosal; *Su*, supratemporal; *T*, tabular.

fl.Pp, occipital flange of postparietal.

acterized inter alia by a very deep notch (*i.T*) in the posterior margin of the tabular and a strong posterior tabular process (*pr.T*), differs very much from the corresponding margin of the ichthyostegids (figs. 32, 35, 36), but in other respects the general shape and proportions of the skull roof are about as in those forms. The snout is broad. The fairly plane cheeks meet the table at distinct angles—in the holotype these angles, in the region between the orbital fenestra and the tabular notch, are about 145° in the present state of preservation (cf. SÄVE-SÖDERBERGH 1932 b, pp. 13, 61)—and is firmly joined to the table with sutures. The orbital fenestra (*fe.o*) is on the whole situated as in the ichthy-

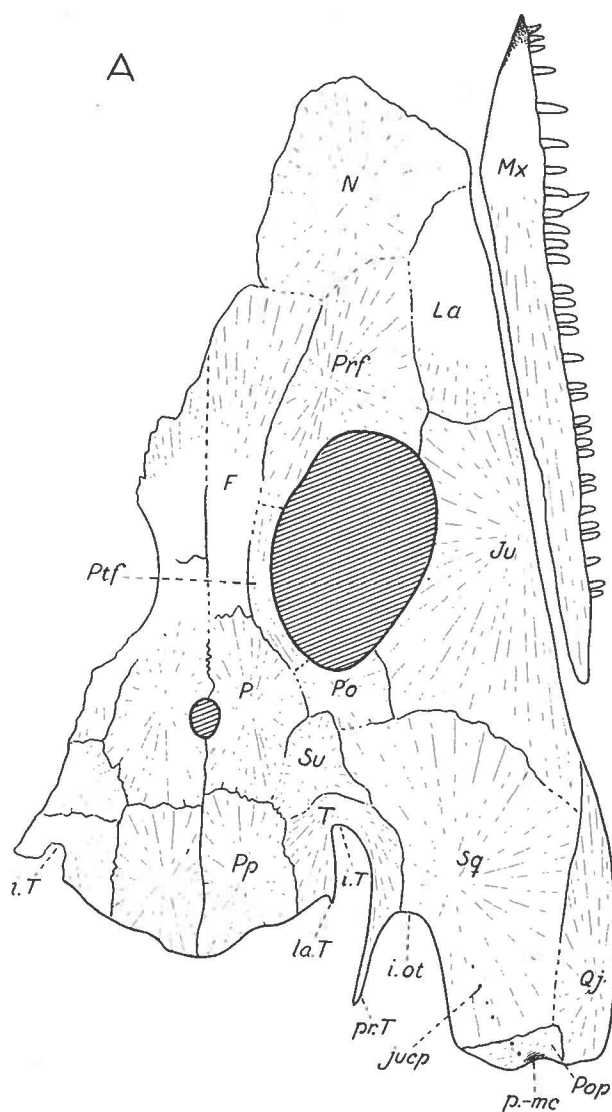


Fig. 33 A.

stegids, but it lies comparatively close to its fellow and is comparatively large, longer even, proportionately, than it is in *Ichthyostegopsis*. In the holotype it is about 1.5 times as long as high, whereas in No. A. 85, in which the postfrontal is missing, it seems to have been less elongated and was probably only about 1.1 times as long as high.

The pineal foramen (*f.pin*), at any rate in the present state of preservation, is fairly large in the holotype. In No. A. 85, in which it is indistinct, it seems to have been a little smaller. In both specimens it lies a little farther back than the centre of radiation of the parietal.

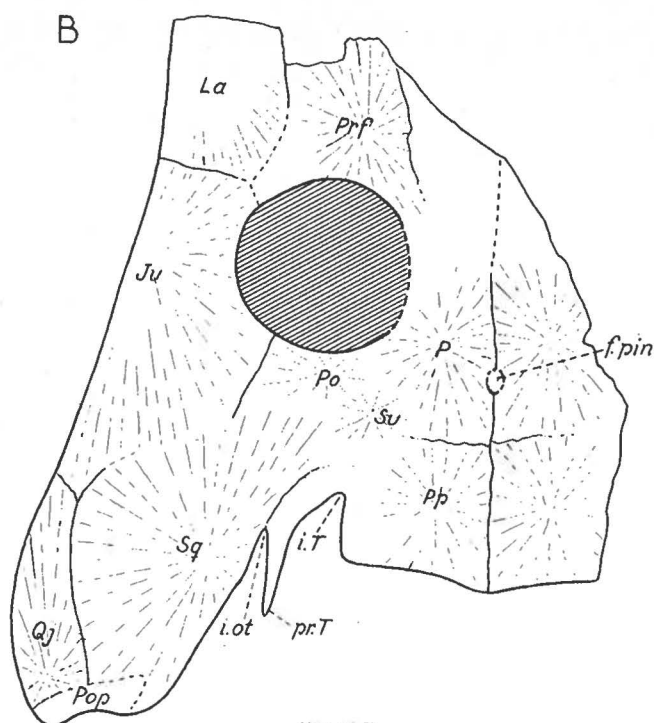


Fig. 33 B.

Fig. 33. *Acanthostega gunnari* n.g., n.sp. Sketches of the parts preserved of the skull roof in, A, the holotype, and B, specimen No. A. 85. Same specimens as shown in pl. 21. 1/1.

F, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *N*, nasal; *P*, parietal; *Po*, postorbital; *Pop*, preopercular; *Pp*, postparietal; *Prf*, prefrontal; *Ptf*, postfrontal; *Qj*, quadratojugal; *Sq*, squamosal; *Su*, supratemporal; *T*, tabular.

f.pin, pineal foramen; *i.ot*, otic notch; *i.T*, tabular notch; *jucp*, pores of jugal sensory canal; *la.T*, posterior end of ventral lamina of tabular; *p.-mc*, preoperculo-mandibular sensory canal; *pr.T*, posterior process of tabular.

The ornamentation of the dermal bones is well shown in No. A. 85 only (fig. 31 B; pl. 21:3). It consists mainly of ridges forming net-works or of more or less free tubercles. In several bones the ridges or rows of tubercles have a distinct radial course. The ornamentation is rather suggestive of that both in the ichthyostegids (fig. 32; cf. SÄVE-SÖDERBERGH 1932 b, pl. 4:2, 3) and in *Eusthenodon* (fig. 31 A).

The centra of radiation of the individual dermal bones of the skull roof are generally very distinct in the holotype, whereas in some places the sutures are more or less difficult to trace. Owing to the fact that the bony tissue of the dermal bones is partly badly damaged and in some places even missing, the sutures actually seen and shown in the drawings are not always those running on the external side. In No. A. 85 only a few of the sutures are discernible.

The dermal bones of the skull roof (figs. 33, 34; pl. 21), those in the posterior part of the table excepted, agree, on the whole, with the corresponding bones in the ichthyostegids (figs. 32, 35) with regard to number, shape and mutual position. The preopercular is developed, whereas an independent intertemporal is lacking.

The premaxillary (*Pmx*) is not preserved. No internasal (*In*) has been observed, but judging from the shape of the antero-medial parts of the nasals it seems likely that such a bone was developed and situated about as in the ichthyostegids. The nasal (*Na*) is a large paired bone about as long as broad, and joined with sutures to the lachrymal, the prefrontal and the frontal. In the region of the antero-lateral part of the nasal the skull roof is imperfect and it is uncertain whether there is an independent anterior tectal (*Tec.a*; anterior antorbital SÄVE-SÖDERBERGH; cf. JARVIK 1942, p. 623) as in the ichthyostegids¹.

The prefrontal (*Prf*) is a large bone suggestive of that in *Ichthyostega*. As in that genus, it meets the jugal postero-laterally and is joined to the lachrymal, the frontal, and the nasal with long sutures. The suture with the postfrontal is indistinct in the material available. Also the frontal (*F*) and the postfrontal (*Ptf*) resemble the corresponding bones in *Ichthyostega*. The suture between the postfrontal and the parietal is indistinct and possibly the postfrontal extends a little more postero-medially than is shown in the figures. The parietal (*P*), which is joined to its fellow with a distinct median suture, laterally meets the postorbital, as in the ichthyostegids.

The dermal bones of the snout and table now described agree well with the corresponding bones in the ichthyostegids, whereas the remaining three bones of the table, the postparietal, the supratemporal, and the tabular, in many respects are very different.

The postparietal (*Pp*) is thus paired as in the majority of stegocephalians. It extends farther back than the adjoining part of the tabular and the posterior margin of the table formed by the postparietals and the medial parts of the tabulars is strongly convex as seen in dorsal view, whereas the corresponding margin in the ichthyostegids (figs. 32, 35) is deeply concave and often somewhat V-shaped.

The bone which I—with some hesitation—have called the supratemporal (*Su*) lies comparatively far anteriorly. It is thus situated laterally to the posterior half of the parietal, on the whole in front of the lateral continuation of the transverse suture between the parietal and the postparietal and relatively far in front of the otic notch. In the ichthyostegids (figs. 32, 35), on the other hand, the major part of the supratemporal, including its centre of radiation, is situated behind the

¹) This bone must not be confused with the septomaxillary (cf. foot-note 1 on p. 80 and JARVIK 1937, pp. 119—122; 1942).

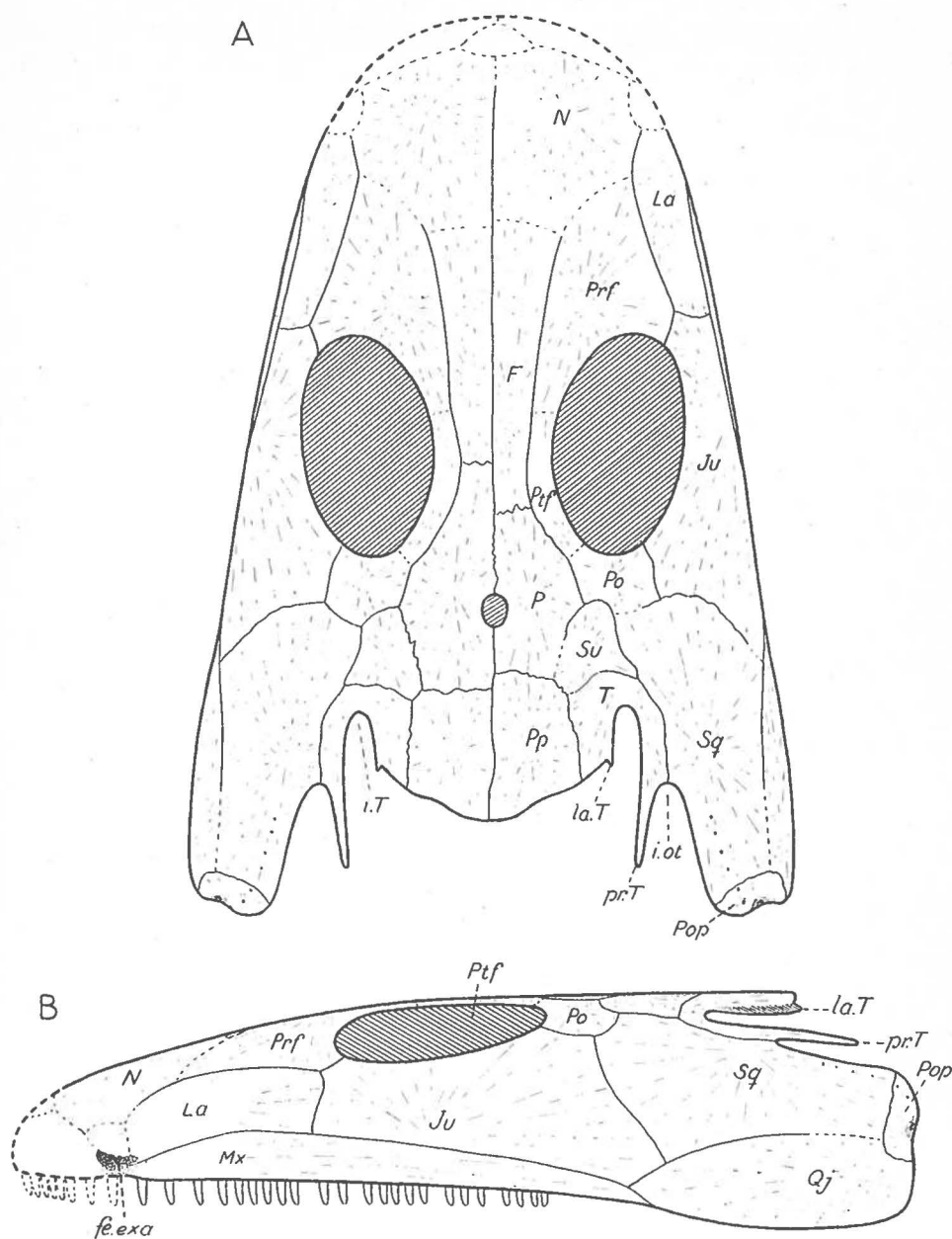


Fig. 34. *Acanthostega gunnari* n.g., n.sp. Restorations of the skull roof in, A, dorsal and, B, lateral aspects. 9/10.

F, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *N*, nasal; *P*, parietal; *Po*, postorbital; *Pop*, preopercular; *Pp*, postparietal; *Prf*, prefrontal; *Pt.f*, postfrontal; *Qj*, quadratojugal; *Sq*, squamosal; *Su*, supratemporal; *T*, tabular.

fe.exa, fenestra exonarina anterior; *i.ot*, otic notch; *i.T*, tabular notch; *la.T*, ventral lamina of tabular; *pr.T*, tabular process.

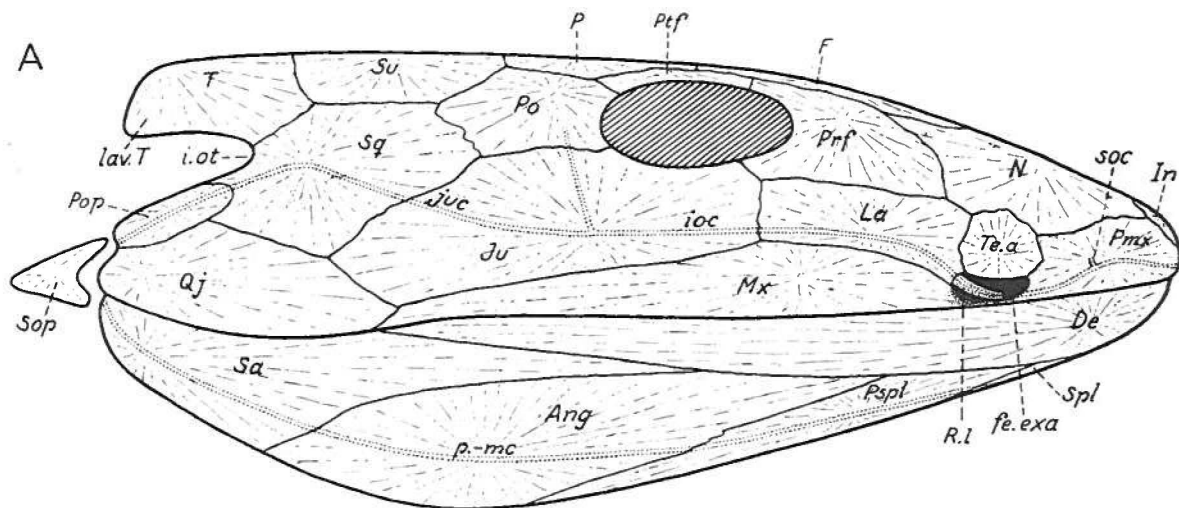


Fig. 35 A.

Fig. 35. *Ichthyostega* sp. Restorations of the skull in, A, lateral and, B, dorsal aspects. Sensory canals in the dorsal parts partly omitted. Mainly after specimens Nos. A. 64, A. 89, A. 138 and A. 148. Ca. 3/4.

Ang, angular (infradentary 3); *De*, dentary; *F*, frontal; *In*, internasal (postrostral); *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *N*, nasal; *P*, parietal; *Pmx*, premaxillary; *Po*, postorbital; *Pop*, preopercular; *Pp*, postparietal; *Prf*, prefrontal; *Pspl*, post-splenial (infradentary 2); *Ptf*, postfrontal; *Qj*, quadratojugal; *R.l*, lateral rostral; *Sa*, supraangular (infradentary 4); *Sop*, subopercular; *Spl*, splenial (infradentary 1); *Sq*, squamosal; *Su*, supratemporal; *T*, tabular; *Te.a*, anterior tectal.

fe.exa, fenestra exarina anterior; *fl.Pp*, occipital flange of postparietal; *ioc*, infra-orbital sensory canal; *i.ot*, otic notch; *juc*, jugal sensory canal; *lav.T*, ventral laminae of tabular; *p.-mc*, preoperculo-mandibular sensory canal; *soc*, supraorbital sensory canal; *stcc*, supratemporal commissural canal.

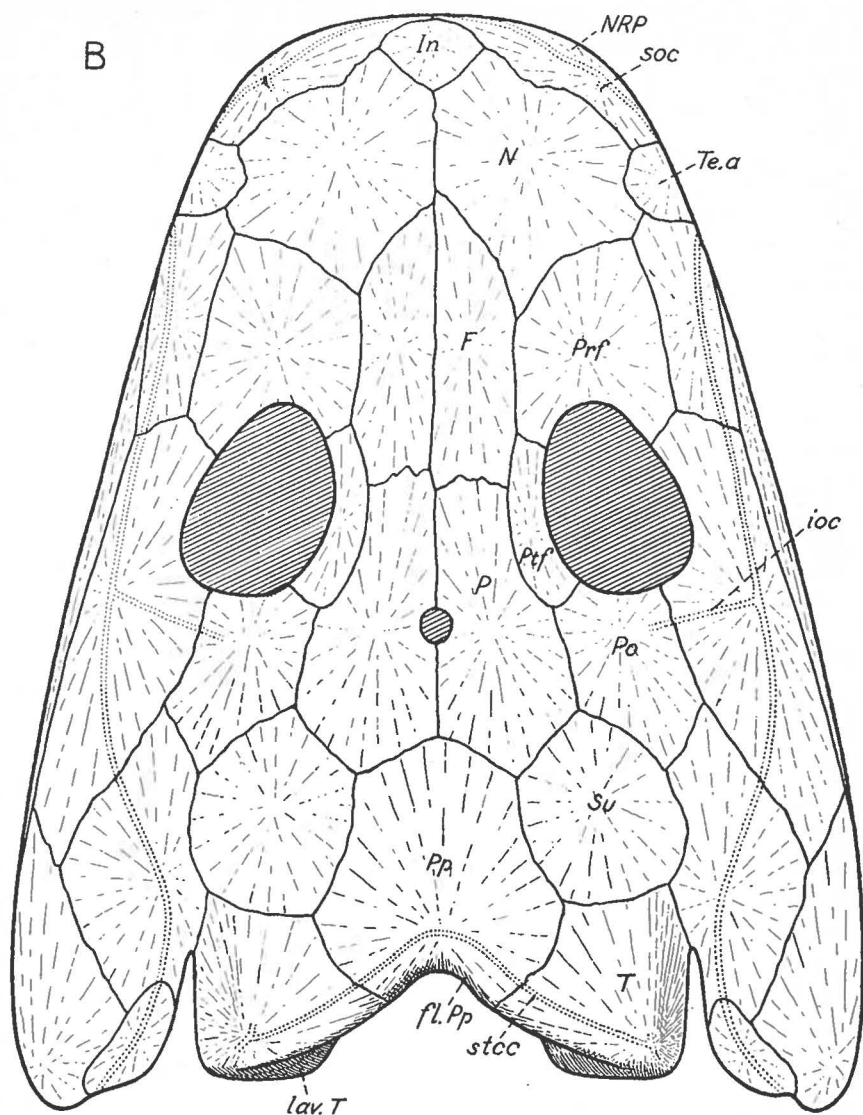


Fig. 35 B.

lateral continuation of the suture between the parietal and postparietal, and it is joined medially to the latter bone with a fairly long suture. Its posterior end lies more or less close in front of the otic notch. Both in *Acanthostega* and in the ichthyostegids the bone anteriorly is widely separated from the postfrontal¹⁾.

¹⁾ ROMER (1947, p. 90) lays particular stress upon the fact that the supratemporal in the ichthyostegids lacks contact with the postfrontal. However, this condition can hardly be of more importance than e.g. the facts that the nasal and

The tabular (*T*, figs. 33, 34; pl. 21) differs radically from that in the ichthyostegids as regards position and structure. It consists of an almost horizontal plate, with a very deep notch (*i.T*) in the posterior margin and a low inconsiderable vertical lamina (*la.T*) along the medial margin of this notch. Laterally to the notch the horizontal plate is extended into a long pointed posterior process (*pr.T*) forming the dorso-medial boundary of the otic notch (*i.ot*). The vertical lamina projects freely a little behind the adjoining part of the horizontal plate ending posteriorly in a small process. Anteriorly and laterally to the tabular notch there is a rather broad marginal area lacking ornament. This area, which along the posterior part of the lateral side of the notch is distinctly depressed in its most marginal part, continues on to the tabular process, which is quite devoid of ornament and evidently was embedded in soft tissue. Anteriorly the tabular is joined to the supratemporal with an irregular transverse suture situated about opposite the transverse suture between the parietal and the postparietal. Medially it meets the postparietal and laterally it has a very long suture with the squamosal. The centre of radiation of the bone is situated remarkably far forwards. It thus lies close to the anterior margin, laterally to the anterior margin of the postparietal and much further anteriorly than the centre of radiation both of the postparietal and of the squamosal.

In the ichthyostegids (figs. 32, 35, 36; see also SÄVE-SÖDERBERGH 1932b), on the other hand, the centre of radiation of the tabular is situated in the posterior part of the bone and it lies further back than the centre of radiation of the postparietal and squamosal and farther back even than the posterior margin of the postparietal. Other striking differences between acanthostegids and ichthyostegids are that the characteristic tabular notch and the strong posterior process are lacking in the latter. Moreover, the vertical lamina along the medial side of the tabular notch in *Acanthostega* has no equivalent in the ichthyostegids, in which the tabular instead is provided with several strong peculiar descending laminae (*lav.T*), preliminarily described by SÄVE-SÖDERBERGH (1932b). On the whole, the ichthyostegid tabular is a very complicated structure and together with occipital flanges of the postparietal (*fl.Pp*, fig. 36) it covers a considerable part of the occipital face of the neural endocranium in a fashion which is unparalleled in the acanthostegids and, as far as

lachrymal in *Ichthyostega* sometimes lack contact, sometimes meet in a short suture (SÄVE-SÖDERBERGH 1932b), whereas in *Acanthostega* they are joined with a relatively long suture. In this connection it is worth while to mention that the dermal bones in the rhipidistids (fig. 25 B), situated somewhat as the postfrontal and supratemporal in *Acanthostega*, viz. the posterior supraorbital (*So.2*) and the dermosphenotic (*D*), are generally joined with a distinct suture, whereas in *Eusthenodon*, as described above (p. 62, figs. 23, 25 A, 26), they lack contact.

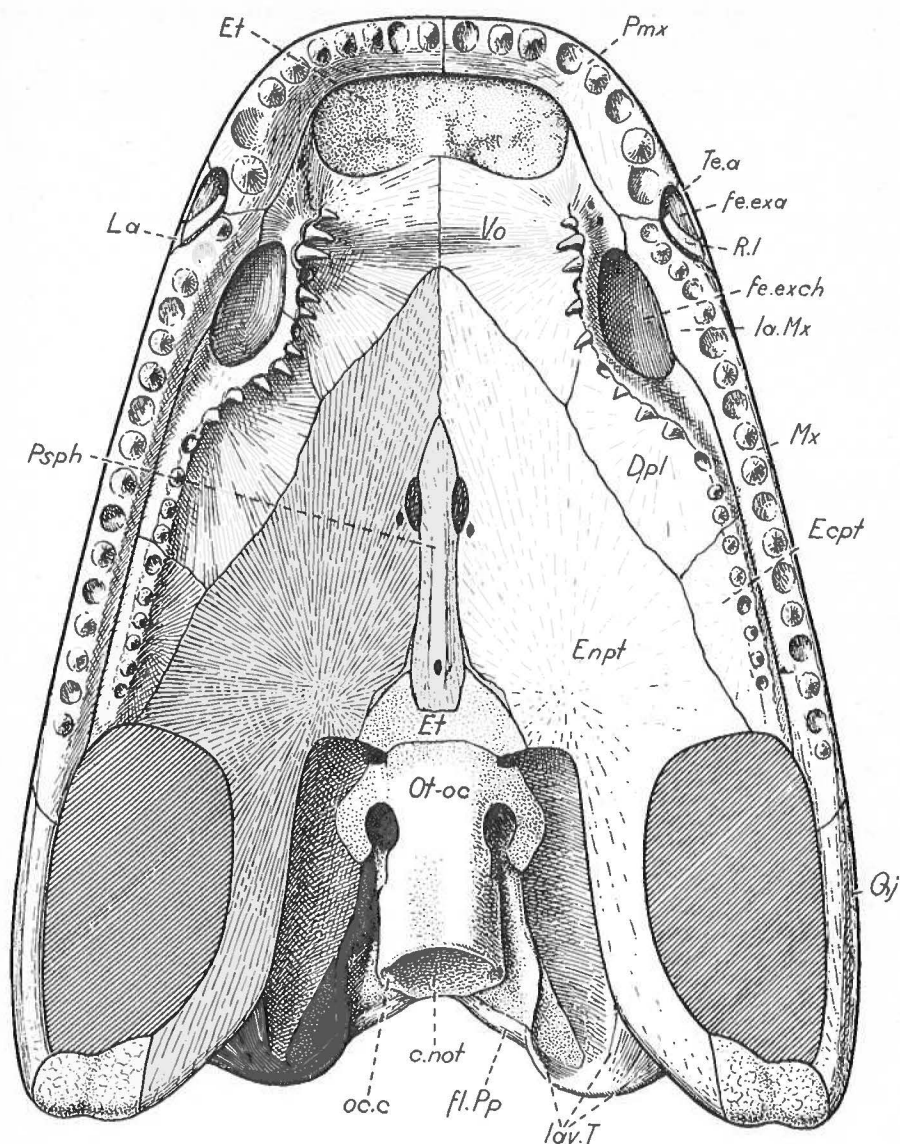


Fig. 36. *Ichthyostega* sp. Restoration of the palate in ventral aspect. Mainly after specimens Nos. A. 55, A. 64, A. 94 and A. 117. Ca. 3/4.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Et*, ethmosphenoid; *La*, lachrymal; *Mx*, maxillary; *Ot-oc*, otico-occipital; *Pmx*, premaxillary; *Psph*, parasphenoid; *Qj*, quadratojugal; *R.l*, lateral rostral; *Te.a*, anterior tectal; *Vo*, vomer. *c.not*, notochordal canal; *fe.exa*, fenestra exonarina anterior; *fe.exch*, fenestra exchoanalis; *fl.Pp*, occipital flange of postparietal; *la.Mx*, palatal lamina of maxillary; *lav.T*, ventral laminae of tabular; *oc.c*, occipital condylus.

may be judged at present, fairly different from the conditions in post-Devonian stegocephalians (cf. WATSON 1919; 1926; 1929; NILSSON 1946, fig. 23; ROMER 1947, figs. 2—4).

The dermal bones of the cheek in *Acanthostega* (figs. 33, 34; pl. 21) agree fairly well with the corresponding bones in the ichthyostegids (figs. 32, 35). The lachrymal (*La*) has a comparatively long suture with the nasal and as in *Ichthyostega*, but contrary to conditions in *Ichthyostegopsis*, it is excluded from the orbital fenestra by the prefrontal and jugal. The jugal (*Ju*) is large as in the ichthyostegids. Its centre of radiation is situated fairly far forwards and lies somewhat in front of the middle of the bone. The postorbital (*Po*) is short and ends posteriorly about opposite the pineal foramen. The squamosal (*Sq*) is a large bone extending farther back than the tabular. Dorsally it is joined to the supratemporal and tabular with long sutures. The preopercular (*Pop*) is shown both in the holotype and in No. A. 85, but the sutures separating it from the squamosal and quadratojugal are partly indistinct. In the posterior margin of the bone there is a shallow notch in which is found the opening of the preoperculo-mandibular sensory canal (*p.-mc*). The quadratojugal (*Qj*) is fairly long and low, being about 3 times as long as high. The maxillary (*Mx*) is well shown in the holotype but is a little detached. It is a long and slender bone very similar to that in the ichthyostegids. As in these forms (see also fig. 36), the anterior part of the maxillary is bent distinctly medially, it bears teeth, it is provided with a strong palatal lamina (*la.Mx*), and, except at the very tip, its external face is ornamented. The very similar development of the anterior part of the maxillary strongly indicates that the fenestra exonarina anterior (*fe.exa*) in *Acanthostega*, quite as in the ichthyostegids, migrated secondarily downwards to be situated on the ventral side of the snout¹).

¹) In connection with this downwards migration of the fenestra exonarina anterior the anterior end of the maxillary secondarily was driven inwards, and, as explained elsewhere (JARVIK 1942, p. 622), it was also to be expected that the lateral rostral, which in the crossopterygian ancestors forms the ventral boundary of the fenestra exonarina anterior, became reduced. That this is so is now confirmed by the new ichthyostegid material at my disposal. In an excellently preserved specimen of *Ichthyostega* (No. A. 64) the lateral rostral (*R.l*, figs. 35, 36) is preserved almost in its natural position. It is highly vestigial, as far as known consisting merely of a thin cylinder of bone, which encloses the infraorbital sensory canal and carries this canal from the lachrymal to the rostral portion of the so-called premaxillary (the latter bone no doubt is a compound bone, as it has proved to be in the *Osteolepiformes*, JARVIK 1942, p. 347, foot-notes 1 and 2; 1944a). The vestigial lateral rostral in *Ichthyostega*, as will be further elucidated in a forthcoming paper, is situated ventromedially to the fenestra exonarina anterior (*fe.exa*), close dorso-laterally to the anterior end of the palatal lamina of the maxillary (*la.Mx*), which as evidenced by several specimens, is joined inside the lateral rostral to the posterior end of the palatal lamina of the premaxillary with a distinct suture. The contact between

Sensory canals.—As in the ichthyostegids (see SÄVE-SÖDERBERGH 1932b) and as in fishes, the sensory lines at least partly run in closed canals in the dermal bones. The sensory canals are narrow as in the ichthyostegids and open outwards by short, probably unbranching tubes. On the whole, they are imperfectly preserved in the material available and have been observed with certainty only in the jugal (*ioc*, pl. 21:3) in No. A. 85, and in the preopercular and the adjoining part of the squamosal (*p.-mc*, *juc*, *jucp*, fig. 33A; pl. 21:1, 2) in the holotype. Openings and canals probably representing pores and sensory canals have been found in other bones as well (nasal, tabular, lachrymal, etc.), but since they are indistinct they have been omitted in the figures.

Dentition.—The maxillary teeth are fairly well preserved in the holotype (pl. 21:1), which in addition presents a comparatively large detached tooth, probably a palatal tusk. The maxillary teeth are fairly straight and of moderate size, about as in *Ichthyostegopsis*.

Remarks.

As may be gathered from the brief description now given and the comparisons with the ichthyostegids, the acanthostegids, as far as the skull roof is concerned, agree with the ichthyostegids in several respects, inter alia the following: The shape and proportions are on the whole similar; the cheeks meet the table at angles and are joined to it with sutures; the squamosal meets the tabular; the dermal bones of the snout, the anterior part of the table and the cheek are on the whole very similar with regard to number, general shape and mutual position; the intertemporal is absent as an independent element; the postfrontal and the supratemporal are widely separated; the postparietal is comparatively long; the preopercular is retained; the sensory lines run in closed canals, which are narrow with short tubes; moreover, the anterior part of the maxillary has become modified in the same fashion as in the ichthyostegids, indicating that the fenestra exonarina anterior migrated secondarily downwards.

However, in spite of these and other resemblances, it is questionable if the acanthostegids really are very closely related to the ichthyostegids.

the maxillary and the premaxillary is thus retained in the Ichthyostegids. It is not known whether there is a true septomaxillary in the ichthyostegids. As demonstrated previously (JARVIK 1937, pp. 119—122; 1942, pp. 527—535, 623—626), the septomaxillary corresponds chiefly to the processus dermintermedius of the lateral rostral in the *Osteolepiformes* and, as is readily seen, it is possible that the reduction of the lateral rostral in the phylogeny of the ichthyostegids led to a secondary subdivision of this bone into a sensory canal bone, that is the bone called lateral rostral in *Ichthyostega*, and a dorsal part, the septomaxillary, situated mainly within the nasal cavity and corresponding to the processus dermintermedius in the *Osteolepiformes*.

The presence of the preopercular, the fact that the sensory lines run in closed canals, the fact that the postparietal is long and probably other similarities in proportions and general shape as well, are no doubt primitive features to be expected in early tetrapods of various groups. The similarities in these respects do not allow us to draw any definite conclusions as to a close relationship between the acanthostegids and the ichthyostegids. Nor do the resemblances in the pattern of the dermal bones, including the absence of the intertemporal and the fact that the contact between the postfrontal and the supratemporal is lacking, provide any conclusive evidence. That this is so is readily seen if we consider, first that the pattern of the dermal bones common to the ichthyostegids and the acanthostegids is characteristic of post-Devonian labyrinthodonts as well (see e. g. WATSON 1919; 1926; 1929; 1940; SÄVE-SÖDERBERGH 1935; CASE 1946; ROMER 1947) and, secondly, the fact that the dermal bones in closely related forms and even on both sides of the same individual may be subject to strong variations as to shape and extent and may sometimes be absent as independent elements (cf. foot-note 1, p. 77 and JARVIK 1948a, pp. 67—85; 1950a, p. 53).

As far as I can see, it is only one feature, viz. the very similar modification of the anterior part of the maxillary, that provides more positive evidence of a very close relationship between the acanthostegids and the ichthyostegids. In this case we are concerned with a distinct specialization, since the anterior part of the maxillary apparently was secondarily pushed medially in connection with the migration downwards of the fenestra exonarina anterior, which in the acanthostegids presumably had a very ventral position quite as in the ichthyostegids. No corresponding specialization is known of either in crossopterygians or, as far as I am aware, in post-Devonian stegocephalians¹).

This distinct specialization and the resemblances in many other respects are contradicted by the very great differences between the acanthostegids and the ichthyostegids with regard to the development and position of the supratemporal, the postparietal and the tabular (see pp. 74—78). Both the ichthyostegids and the acanthostegids obviously became specialized in the posterior part of the table of the skull roof—and conceivably in the underlying parts of the neural endocranium as

¹) It is true that the fenestra exonarina anterior in certain post-Devonian labyrinthodonts, e. g. *Megalocephalus* ("Orthosaurus", WATSON 1926, figs. 6, 7, 9) and *Otocratia* (WATSON 1929, p. 228, fig. 5), is situated comparatively far ventrally, but in all cases it pierces the lateral side of the snout and, as far as it is known, the anterior part of the maxillary never became modified in the fashion characteristic of the acanthostegids and ichthyostegids. As I have repeatedly pointed out (1942, pp. 485, 486; 1948a, p. 36; 1948b, p. 6, foot-note 1; cf. 1937, fig. 18), the fenestra exonarina anterior in *Osteolepiformes* and, it may be added, in other crossopterygians as well, always pierces the lateral side of the snout dorsally to the ventral margin of the cranial roof, which is intact.

well—but they became modified in quite different directions and differ radically from each other in this part of the skull. The ichthyostegid condition, characterized inter alia by the strong development of descending laminae of the postparietal and tabular, does not occur in any of the post-Devonian stegocephalians which ROMER (1947; cf. foot-note on p. 83 and JARVIK 1948b, p. 6) included in the *Ichthyostegalia* or, as far as I can find, in any other post-Devonian labyrinthodonts. Nor is a deep tabular notch corresponding to that characteristic of the acanthostegids to be seen in later forms and the centre of radiation of the tabular never appears to be situated so far forwards as it is in the acanthostegids (see e. g. CASE 1946; ROMER 1947). However, the acanthostegids seem to be less modified in the occiput than are the ichthyostegids, and in certain respects (e. g. the presence of a paired postparietal) they agree more with later forms than do the ichthyostegids¹).

The specializations in the region of the external nostril and in the occiput render it unlikely that neither the acanthostegids nor the ichthyostegids include the direct ancestor of any of the well-known post-Devonian labyrinthodonts (cf. p. 21). On the other hand, the very great differences between the acanthostegids and the ichthyostegids in the posterior part of the skull strongly indicate that in phylogeny the acanthostegids and the ichthyostegids developed independently of each other for a considerable span of time, and it may be questioned, therefore, if it is justifiable to refer the acanthostegids to the *Ichthyostegalia*. However, on account of the similar development of the anterior part of the maxillary, the similar development of the sensory canals, the retention of the preopercular and other resemblances, and since the acanthostegids are still very incompletely known, I have found it most reasonable to include them provisionally in that unit.

The *Ichthyostegalia* SÄVE-SÖDERBERGH (1932) would thus comprise the following families and genera²):

Family *Ichthyostegidae* SÄVE-SÖDERBERGH (1932)

Genus *Ichthyostega* SÄVE-SÖDERBERGH (1932)

Genus *Ichthyostegopsis* SÄVE-SÖDERBERGH (1932)

Family *Acanthostegidae* n. fam.

Genus *Acanthostega* n. g.

¹) In this connection it is worth while to mention that among the postcranial material from the Remigolepis series there is a well preserved detached humerus suggestive of that in *Eryops* and other post-Devonian stegocephalians, but very different from the complicated ichthyostegid humerus (cf. pp. 9, 19). This *Eryops*-like humerus may belong to an acanthostegid.

²) The imperfect exoskeletal cranial roof preliminarily described by WESTOL (1938) as *Elpistostege* and the post-Devonian labyrinthodonts *Otocratia*, *Erpetosaurus*, and *Colosteus* which ROMER (1945, 1947) included in the *Ichthyostegalia* cannot at present be referred to this group (see foot-notes on pp. 77, 82 and JARVIK 1948 b).

IV. SUMMARY

1. The skeleton of the tail of the ichthyostegid stegocephalians, which are the oldest known tetrapods (Upper Upper Devonian, East Greenland), has been described (pp. 11—21; figs. 2—7). Contrary to conditions in all other tetrapods the tail is provided with a distinct median fin supported by endoskeletal fin-supports (radials) and dermal fin-rays (lepidotrichia), quite as in fishes. The fin is incompletely divided into an elongated dorsal fin and a heterocercal caudal fin. The tail is covered by vestigial scales.

2. As regards the structure of the tail and in many other respects (cf. Nos. 4, 5, 7, 8, 9) the ichthyostegids are fish-like or intermediate between fishes and tetrapods. However, the limbs and their girdles are developed fundamentally as in primitive post-Devonian tetrapods and the ichthyostegids are to be regarded as true tetrapods.

3. The skeleton of the limbs, which will be described in detail in a forthcoming paper, is comparatively stout and some of the bones, particularly the humerus, present a very complicated structure. The toes are five in number (the fingers are unknown). Each half of the pelvis consists of a single pelvic bone. The iliac portion is extended into a strong posterior process and on its inner side there is a distinct articular area, conceivably for a sacral rib.

4. Two vestigial dermal bones, the subopercular (foot-note 1 on p. 21) and the lateral rostral (foot-note 1 on p. 80), previously unknown in tetrapods, have been recognized in the ichthyostegid skull (figs. 35, 36). The subopercular is suggestive of the subopercular in the *Osteolepiformes*. The lateral rostral consists of a thin bone cylinder carrying the infra-orbital sensory canal from the lachrymal to the rostral portion of the premaxillary. It is situated fundamentally as in the *Osteolepiformes*, and together with the maxillary and premaxillary, which meet inside the bone, it separates the fenestra exonarina anterior from the fenestra exochoanalis.

5. The neural endocranium, which is well ossified even in the ethmoidal region, as far as may be judged at present, consists in the ichthyostegids of but two ossifications, separated by a distinct transverse suture

running close behind the region of the hypophysis (fig. 36). The anterior ossification apparently corresponds to the ethmosphenoid in the *Osteolepiformes*, whereas the posterior one represents the otico-occipital. The latter contains a long wide notochordal canal, closely resembling that in the *Osteolepiformes*. The parasphenoid is narrow, it ends posteriorly close behind the region of the hypophysis and is pierced by a canal for the ventral tube of the hypophysis, exactly as in the *Osteolepiformes* (foot-note on p. 36).

6. The vertebral column, the ribs, and the median endoskeletal fin-supports in *Eusthenopteron foordi* have been described (pp. 26—36, figs. 9—12; 13C—E; pl. 7). Each vertebra consists of two dorsal elements, the interdorsal and the basidorsal or neural arch, and one ventral element, provisionally termed the ventral vertebral arch. The latter conceivably is compound and consists of the basiventral of one segment, which has fused with the interventral of the segment following next behind. The interdorsal is notched for the ventral and dorsal roots of the spinal nerve. The ribs, which were previously unknown in the *Osteolepiformes*, are of the dorsal type and articulate with the ventral vertebral arch and conceivably with the neural arch as well.

7. The vertebral column in the ichthyostegids (pp. 36—40, figs. 6, 13A, B, 14, 15), both in the trunk and in the tail, closely resembles that in *Eusthenopteron*. The two-headed postsacral ribs are suggestive of the ribs in *Eusthenopteron*.

8. The median fin-supports in the ichthyostegids are developed fundamentally as in the caudal fin in *Eusthenopteron*. The dermal fin-rays resemble the elongated basal segments of the fin-rays in *Eusthenopteron* and some other fishes and the histological structure is similar.

9. The close agreement as to the structure of the vertebral column and other resemblances strongly confirm the assumption that the ichthyostegids are closely related to the *Osteolepiformes* and evolved from primitive members of that group. In the phyletic development from the primitive osteolepiform to the ichthyostegid stage of evolution the main changes in the skeleton of the tail may be assumed to have been as follows: the second dorsal fin became elongated and fused incompletely with the dorsal lobe of the caudal fin; the distal thin and jointed parts of the lepidotrichia became completely reduced and the scales became vestigial. In the main anterior part of the ventral lobe of the caudal fin, which supported the tail, the lepidotrichia disappeared entirely and the radials became slightly modified (pp. 48—49).

10. The vertebral column in early *Dipnoi* (pp. 40—48, figs. 16—21; pl. 8) contains solid amphicoelous vertebral centra, comparable to those in selachians and many actinopterygians, but unparalleled in *Eusthenopteron* and the ichthyostegids. The great differences in the vertebral

column between early *Dipnoi* and *Eusthenopteron* and the fact that the ribs in the dipnoans are ventral ribs, strongly contradict the assumption that the *Dipnoi* are closely related to the *Osteolepiformes* (foot-note, p. 40).

11. A new stegocephalian genus, *Acanthostega*, originating from the same geological strata as the ichthyostegids, has been described and has been referred to a new family, the *Acanthostegidae*, provisionally included in the *Ichthyostegalia* SÄVE-SÖDERBERGH.

12. The acanthostegids agree fundamentally with the ichthyostegids as to the structure of the lateral and anterior parts of the skull roof. As in the ichthyostegids the intertemporal is lacking, the preopercular is retained, the sensory lines run in narrow canals in the dermal bones, and the anterior part of the maxillary has been modified in connection with a downward migration of the fenestra exonarina anterior.

13. The acanthostegids differ considerably from the ichthyostegids in the development and position of the supratemporal, the postparietal and, particularly, the tabular. Both the acanthostegids and the ichthyostegids are specialized in the occiput, but in quite different directions, which suggests that in phylogeny they developed independently of each other for a considerable time.

14. In no post-Devonian stegocephalians or other early tetrapods does the region of the fenestra exonarina anterior seem to have become specialized in the fashion characteristic of both the ichthyostegids and the acanthostegids. Nor does the posterior part of the skull table appear to have been modified in any later forms either in the ichthyostegid or in the acanthostegid fashion. These conditions strongly indicate that both the ichthyostegids and the acanthostegids are blind offshots of the early labyrinthodont stem.

15. A new large rhizodontid, *Eusthenodon wängsjöi*, also from the same geological strata as the ichthyostegids, has been described.

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PLATES

The specimens shown in plates 1—6 and 8—21 originate from the Remigolepis Series in Gauss Halvø and Ymers Ø, East Greenland, and were collected during Dr. LAUGE KOCH's Greenland expeditions in 1929, 1932, 1933, 1936, 1947, 1948, 1949. The specimen shown in pl. 7 is from Scaumenac Bay, Canada. If not otherwise stated the fossils have been photographed in a dry condition. All photographs have been slightly retouched.

Plate 1.

Ichthyostega sp.

Figs. 1, 2. Incomplete tail with counterpart. Specimen No. A. 69. From Smith Woodward's Bjerg. 1/1.

Dfrb, dermal fin-ray; *N.a*, neural arch (basidorsal); *Rd*, dorsal radial; *Rv*, ventral radial; *V.a*, ventral vertebral (haemal) arch; *U*, urostyle.

cdf, dorsal lobe of caudal fin; *c.h*, haemal canal; *hsp*, haemal spine; *nsp*, neural spine.

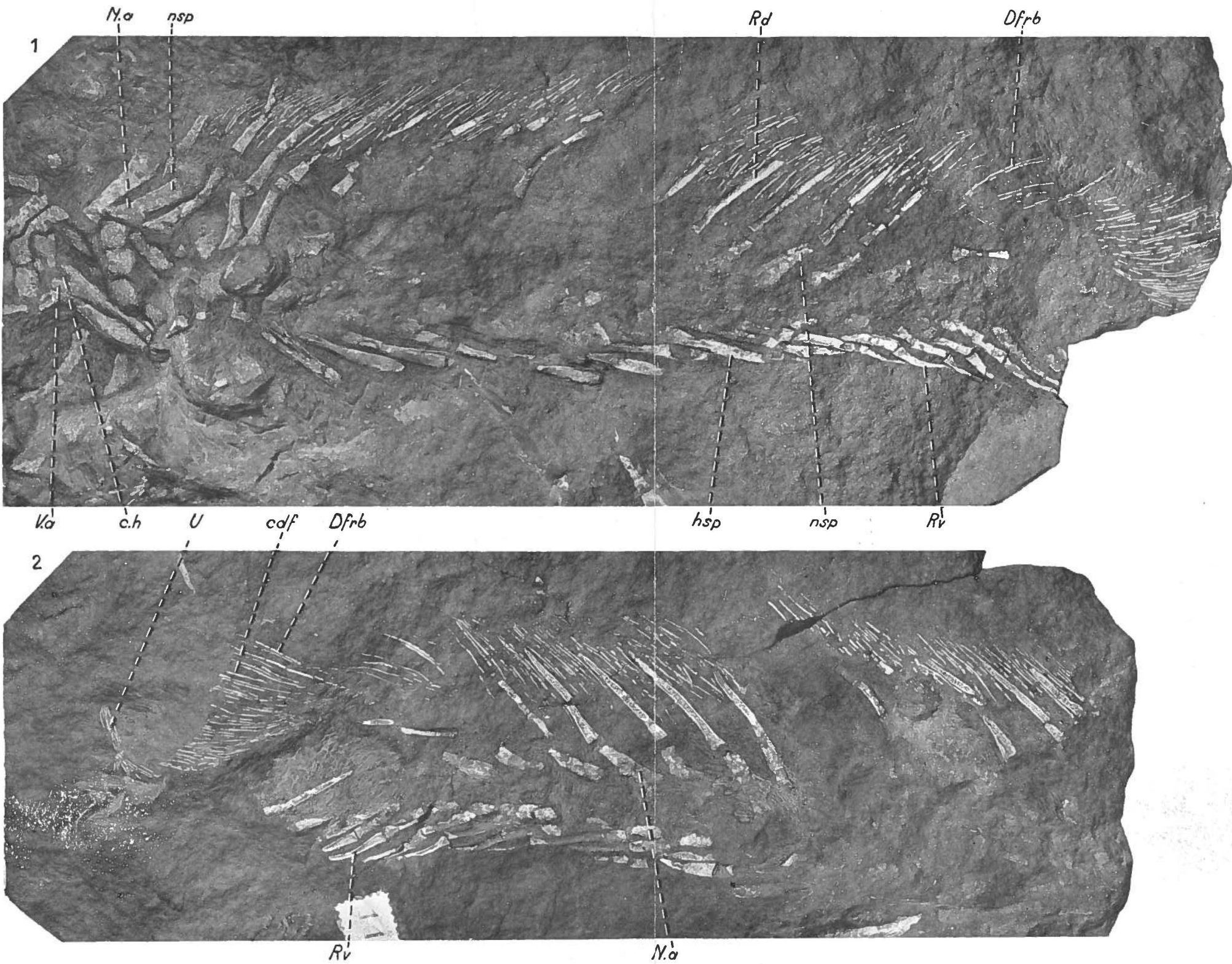


Plate 2.

Ichthyostega sp.

Ventral side of the left hind limb, part of the left pelvic bone in medial aspect, and imperfect tail. Specimen No. A. 109. Same specimen as in text-figures 2B, 5A, and pls. 3 and 4. From the northern slope of Celsius Bjerg. 1/1.

Fe, femur; *Fi*, fibula; *Fib*, fibulare; *I*, intermedium; *Pb.l*, left pelvic bone; *R.ps*, postsacral rib; *Ti*, tibia; *U*, urostyle; *V.a*, ventral vertebral arch.

pr.Pb, posterior process of pelvic bone.

I, first toe.



Plate 3.

Ichthyostega sp.

Figs. 1, 2. Imperfect tail with counterpart. Specimen No. A. 109. Same specimen as in pls. 2 and 4. 6/5.

Dfrb, dermal fin-ray; *Ido*, interdorsal; *N.a*, neural arch (basidorsal); *Rd*, dorsal radial; *R.ps*, postsacral rib; *Rv*, ventral radial; *Sc*, scale; *U*, urostyle; *V.a*, ventral vertebral (haemal) arch.

cdf, dorsal lobe of caudal fin; *c.h*, haemal canal; *c.li*, canal for dorsal ligament; *c.n.c*, neural canal; *df*, dorsal fin; *hsp*, haemal spine; *nsp*, neural spine.

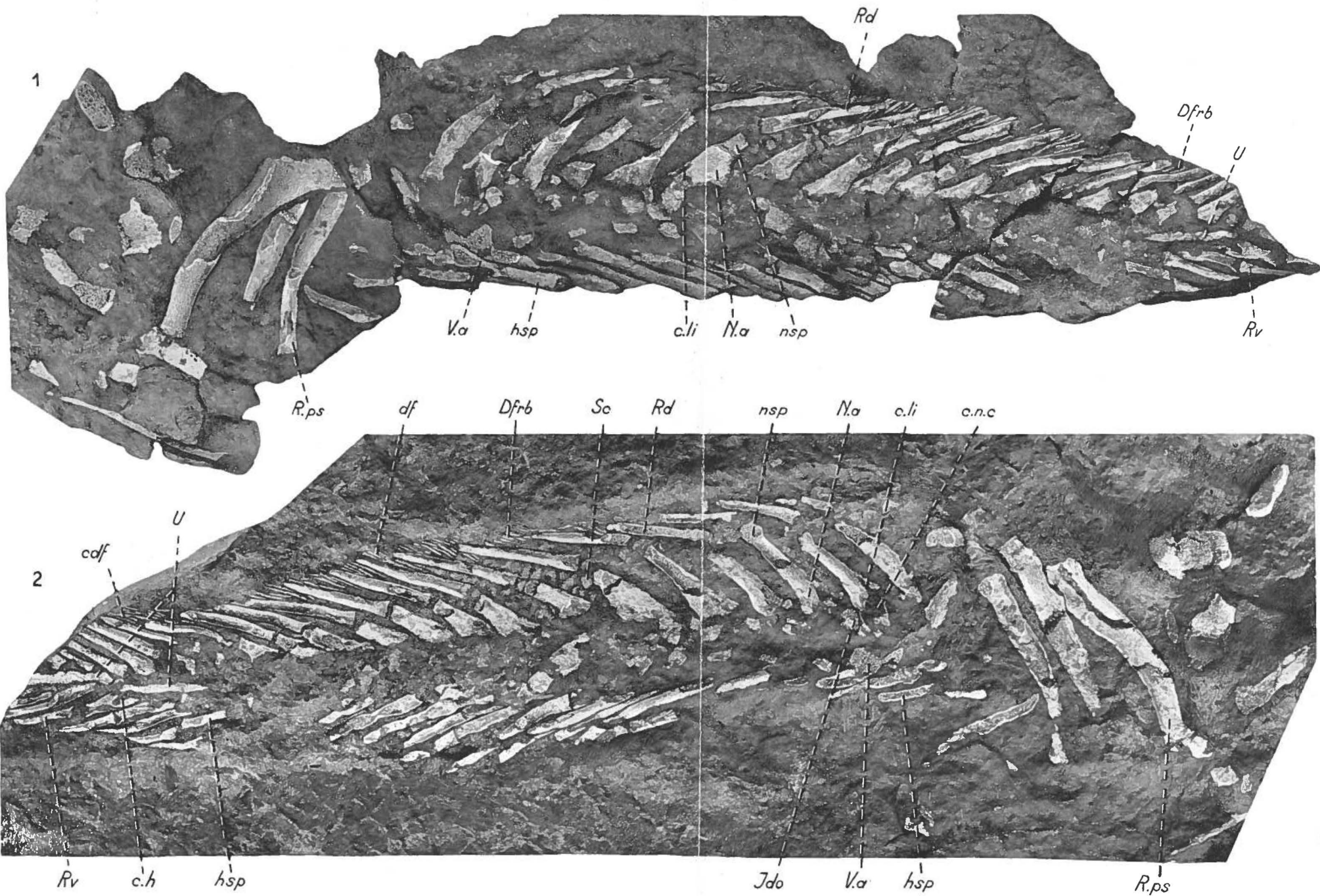


Plate 4.

Ichthyostega sp.

Posterior part of the specimen shown in pls. 2 and 3. 9/4.

Dfrb, dermal fin-ray; *N.a.*, neural arch; *Rd*, dorsal radial; *Rd + nsp*, dorsal radial fused with neural spine; *Rv*, ventral radial; *Rv + hsp*, ventral radial fused with haemal spine; *Sc*, scale; *U*, urostyle; *V.a.*, ventral vertebral (haemal) arch.

c.not, canal in urostyle for the posterior part of the notochord; *c.h.*, haemal canal; *hsp*, haemal spine; *nsp*, neural spine.



Plate 5.

Ichthyostega sp.

Figs. 1, 2. Almost complete tail with counterpart. Specimen No. A. 156. From the horizon at 1174 m. in Sederholms Bjerg. 1/1.

Dfrb, dermal fin-ray; *Ido*, interdorsal; *N.a*, neural arch; *Rd*, dorsal radial; *Rd + nsp*, dorsal radial fused with neural spine; *Rv*, ventral radial; *Rv + hsp*, ventral radial fused with haemal spine; *U*, urostyle; *V.a*, ventral vertebral (haemal) arch.

cdf, dorsal lobe of caudal fin; *c.h*, haemal canal; *cvf*, ventral lobe of caudal fin; *df*, dorsal fin; *hsp*, haemal spine; *nsp*, neural spine.

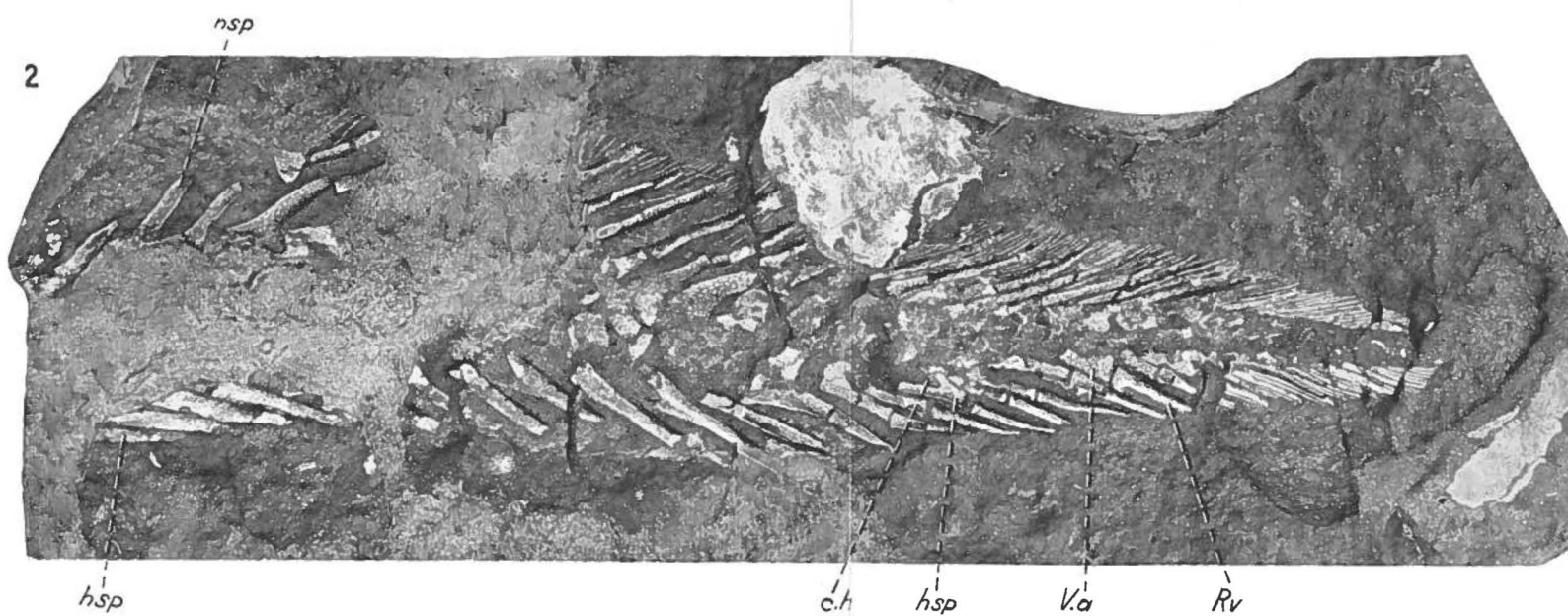
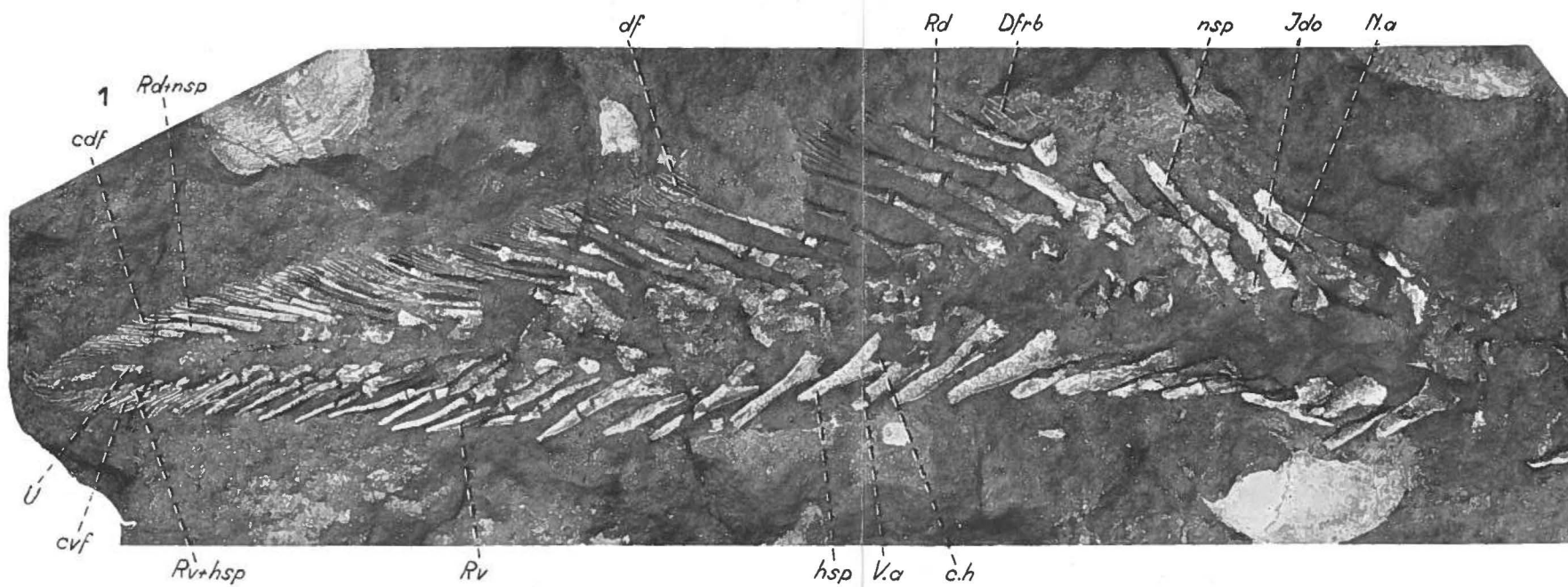


Plate 6.

Ichthyostega sp.

Figs. 1, 2. Almost complete tail with counterpart. Specimen No. A. 157. From the horizon at 1174 m. in Sederholms Bjerg. 4/3.

Dfrb, dermal fin-ray; *N.a*, neural arch; *Rd*, dorsal radial; *Rv*, ventral radial; *U*, urostyle; *V.a*, ventral vertebral arch.

cdl, dorsal lobe of caudal fin; *cvl*, ventral lobe of caudal fin; *df*, dorsal fin; *hsp*, haemal spine; *nsp*, neural spine.

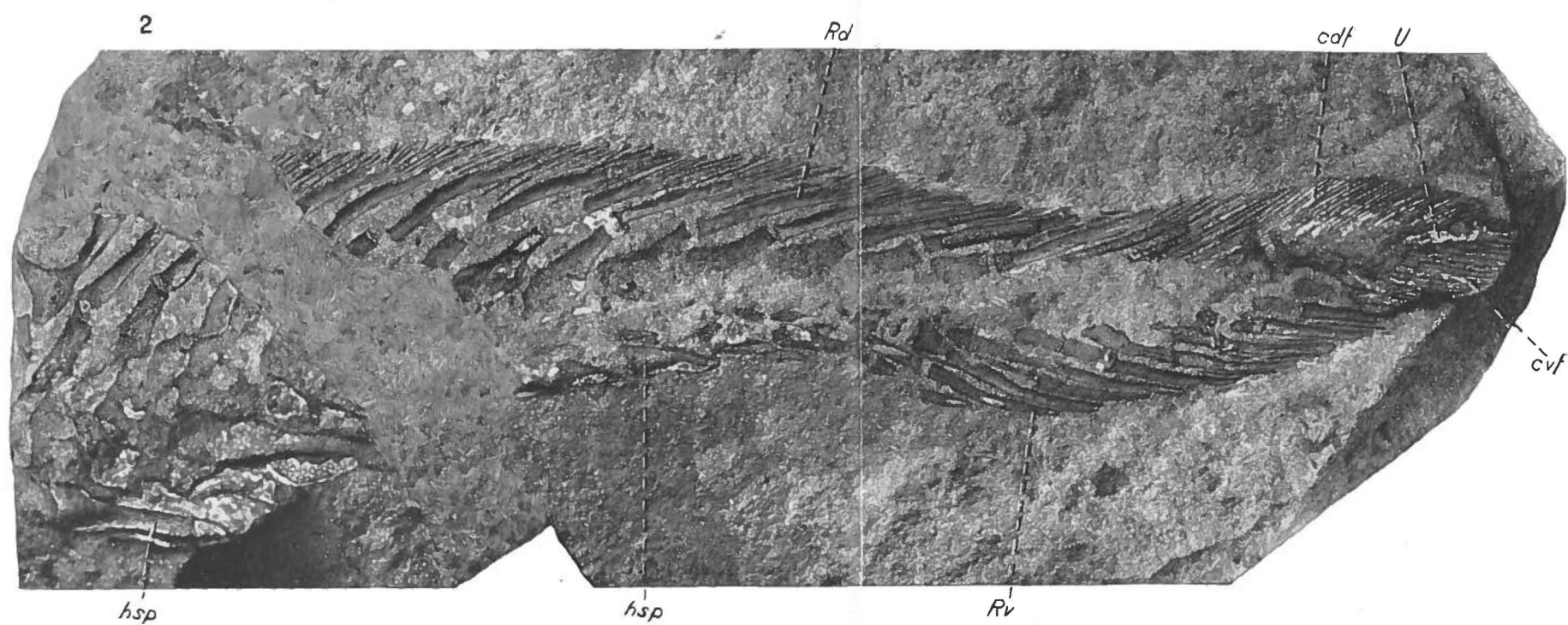
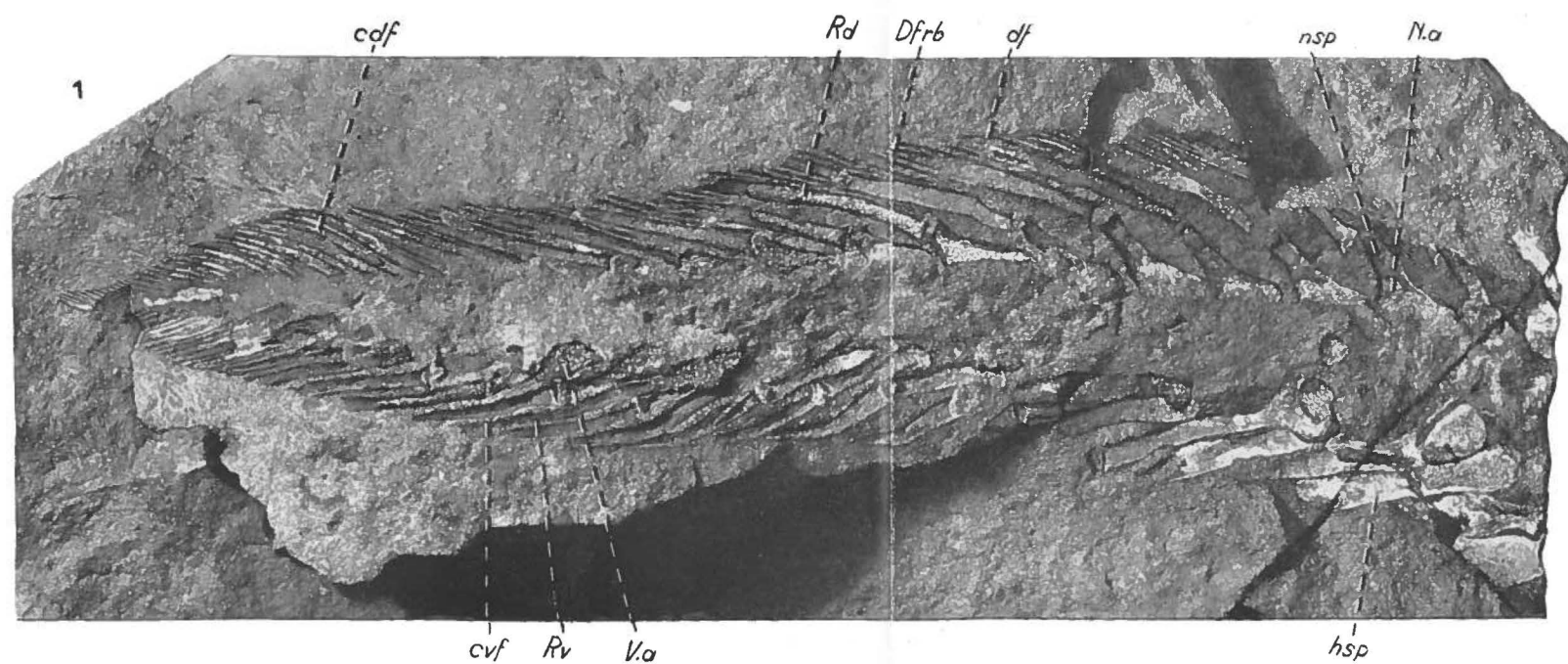


Plate 7.

Eusthenopteron foordi WHITEAVES.

- Fig. 1. Posterior part of almost complete, well preserved specimen in lateral view. Specimen No. P. 222 in the possession of the Paleozoological Department of the Swedish Museum of Natural History, Stockholm. Same specimen as in text-figure 9A—C; see also JARVIK 1937 (fig. 1B), 1944a (fig. 1), 1944b (figs. 5, 6B), 1948a (fig. 2). From Scaumenac Bay, Canada. 5/6.
- Fig. 2. Same specimen as in fig. 1. Part of the squamation removed to show the vertebral column and the supports of the median fins. 5/6.

Dfrb, elongated proximal segment of dermal fin-ray; *Ido*, interdorsal; *N.a*, neural arch; *R*, rib; *Rdd*, *Rdm*, *Rdp*, distal, middle, and proximal series of dorsal radials; *Rd + nsp*, dorsal radial fused with neural spine; *Rv*, ventral radial; *Rvd*, *Rvm*, *Rvp*, distal, middle, and proximal series of ventral radials; *Rv + hsp* ventral radial fused with haemal spine; *V.a*, ventral vertebral arch.

af, anal fin; *bs.af*, basal scute of ditto; *bs.f.df*, basal scute of first dorsal fin; *bs.s.df*, basal scute of second dorsal fin; *cdf*, dorsal lobe of caudal fin; *cvf*, ventral lobe of caudal fin; *f.df*, first dorsal fin; *hsp*, haemal spine; *msc*, main sensory canal; *nsp*, neural spine; *od.N.a*, area of ventral vertebral arch overlapped by neural arch; *pr.a*, anterior paired process of neural arch; *pr.d*, anterior unpaired process of neural arch; *pr.p*, posterior paired process of neural arch; *pr.pv*, postero-ventral process of ventral vertebral arch; *pvf*, pelvic fin; *s.df*, second dorsal fin.

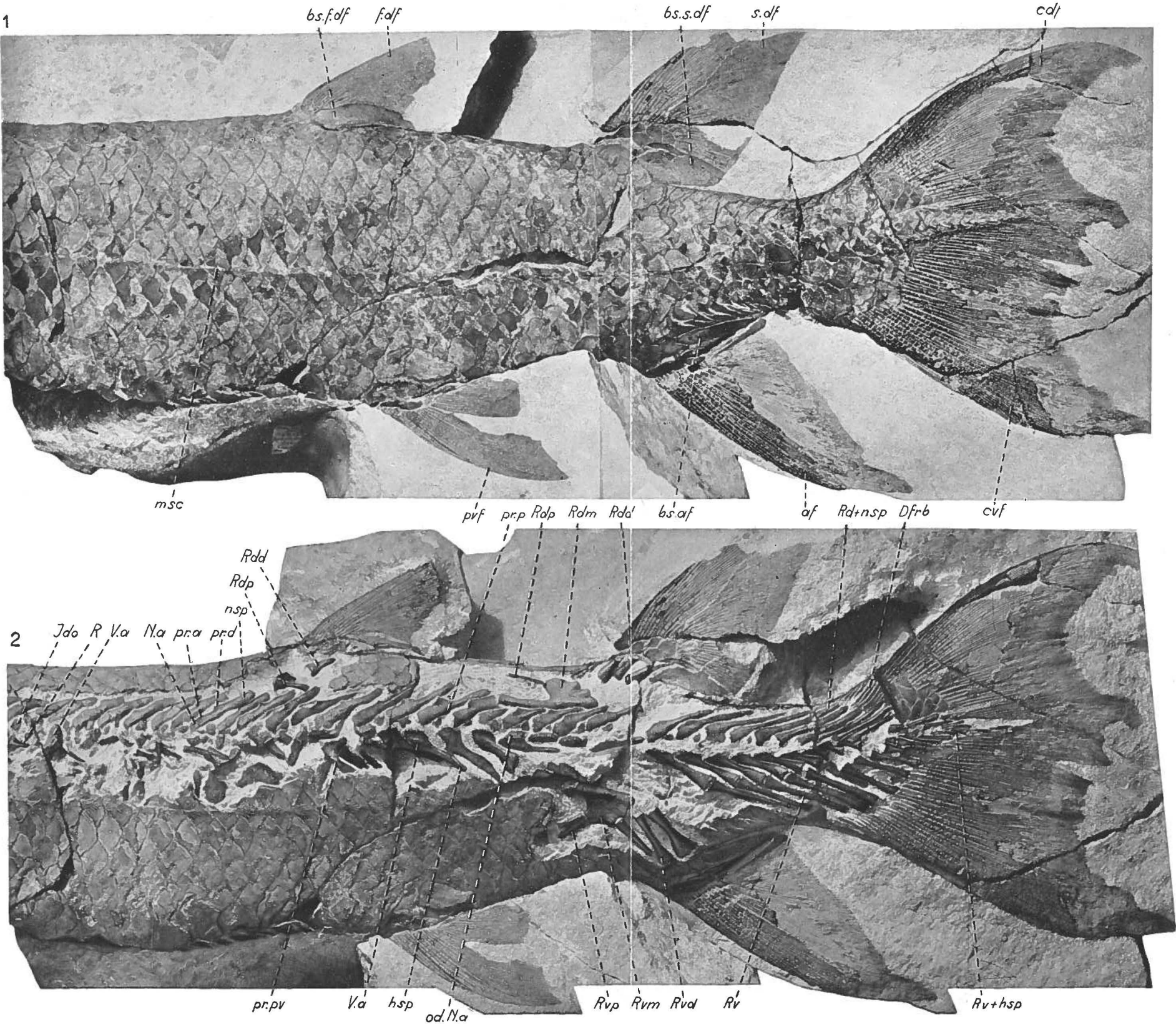


Plate 8.

Vertebral centra of two undetermined dipnoans from the Remigolepis Series, Gauss Halvø, East Greenland.

Figs. 1—6. Form B. Specimen No. P. 1484. From Stensiøs Bjerg.

Fig. 1 Anterior portion of the vertebral column in ventral aspect. 5/2.

Fig. 2 About the same portion as in fig. 1. The posterior part of the column removed. 5/2.

Fig. 3 The removed part of the vertebral column seen from the right lateral side. 5/2.

Fig. 4. Vertebral centrum in posterior aspect. 5/2.

Fig. 5. The second and third vertebral centra, from behind, of the part of the vertebral column shown in fig. 3 in dorso-lateral aspect. Photographed in xylol. 5/1.

Fig. 6. Vertebral centrum in transverse section. Photographed in xylol. 10/1.

Figs. 7—8. Form A. Vertebral centrum in side and end views. Photography of cast in latex. Specimen No. P. 1485. From Nathorsts Bjerg. 5/3.

Fig. 9. Form A. Vertebral centrum in end view. Specimen No. P. 1486. From Nathorsts Bjerg. 5/3.

d.dl, dorso-lateral depression; *d.vl*, ventro-lateral depression; *gr.ao*, groove, probably for the dorsal aorta; *gr.n.c*, groove forming the ventral part of the neural canal; *c.not*, notochordal canal; *re.d.a*, *re.v.a*, deep pits housing proximal cartilaginous portions of dorsal and ventral arcualia.

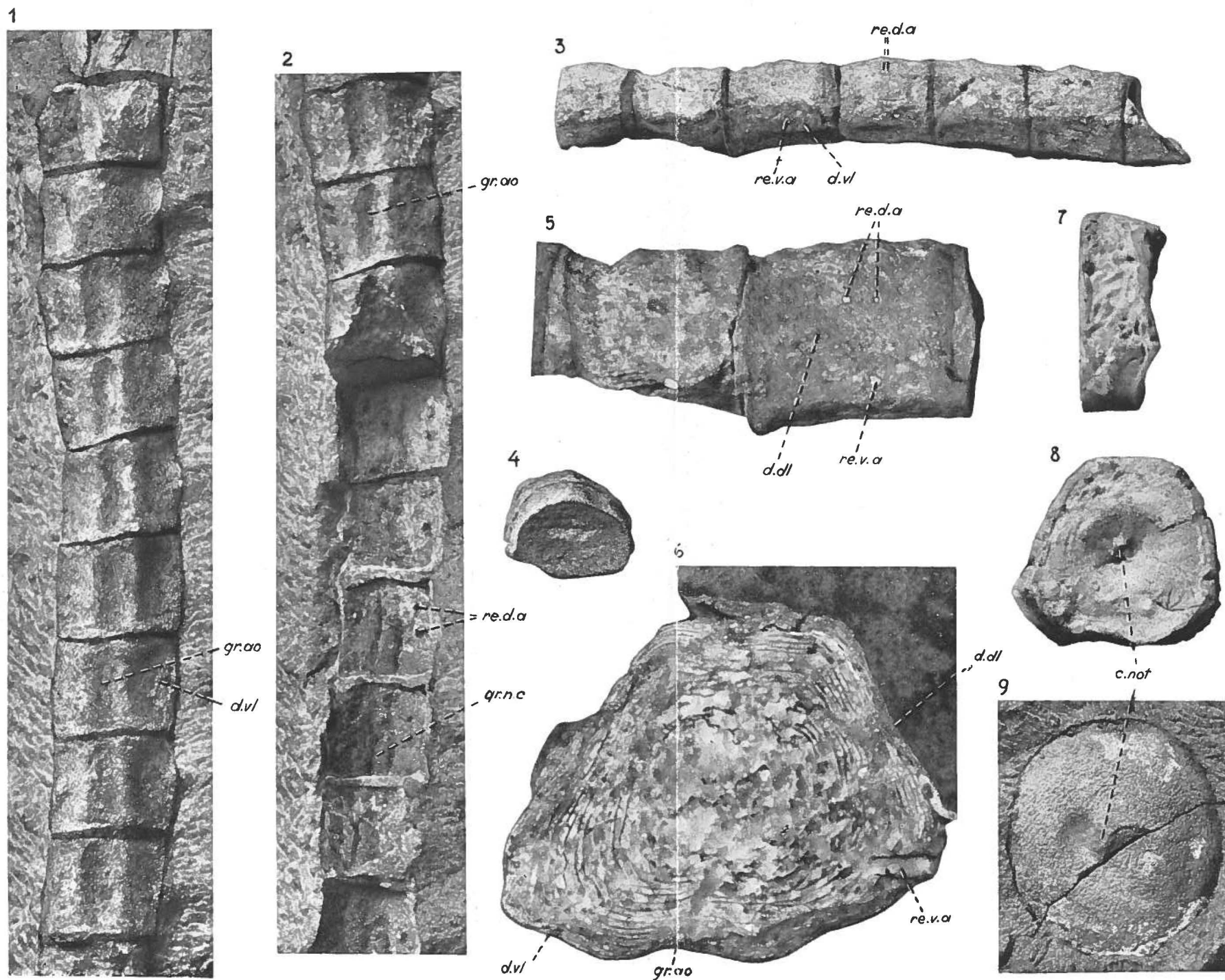


Plate 9.

Eusthenodon wängsjöi n.g., n.sp.

Holotype. Flattened imperfect skull. Impressions of the external faces of the cranial roof and the adjoining parts of the right external cheek plate. Specimen No. P. 1476. Same specimen as in pl. 10 and pl. 11:2. From the horizon at 1174 m. in Sederholms Bjerg. 1/1.

Ext.l, *Ext.m*, lateral and median extrascapulars; *Fr*, frontal; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *NRP*, naso-rostro-premaxillary; *Pa*, parietal; *Pin.pl*, pineal plate; *Po*, postorbital; *Ptr_a*, anterior median postrostral; *Ptr_p*, posterior median postrostral; *R.l*, lateral rostral; *So-Te*, supraorbito-tectal; *Sq*, squamosal; *St*, supratemporal; *Te.a*, anterior tectal.

fe.exa, fenestra exonarina anterior; *fe.o*, orbital fenestra; *ioc*, infraorbital sensory canal; *od.So.2*, areas of postorbital and jugal overlapped by posterior supraorbital; *pl.po.Pa*, posterior oblique parietal pit-line.

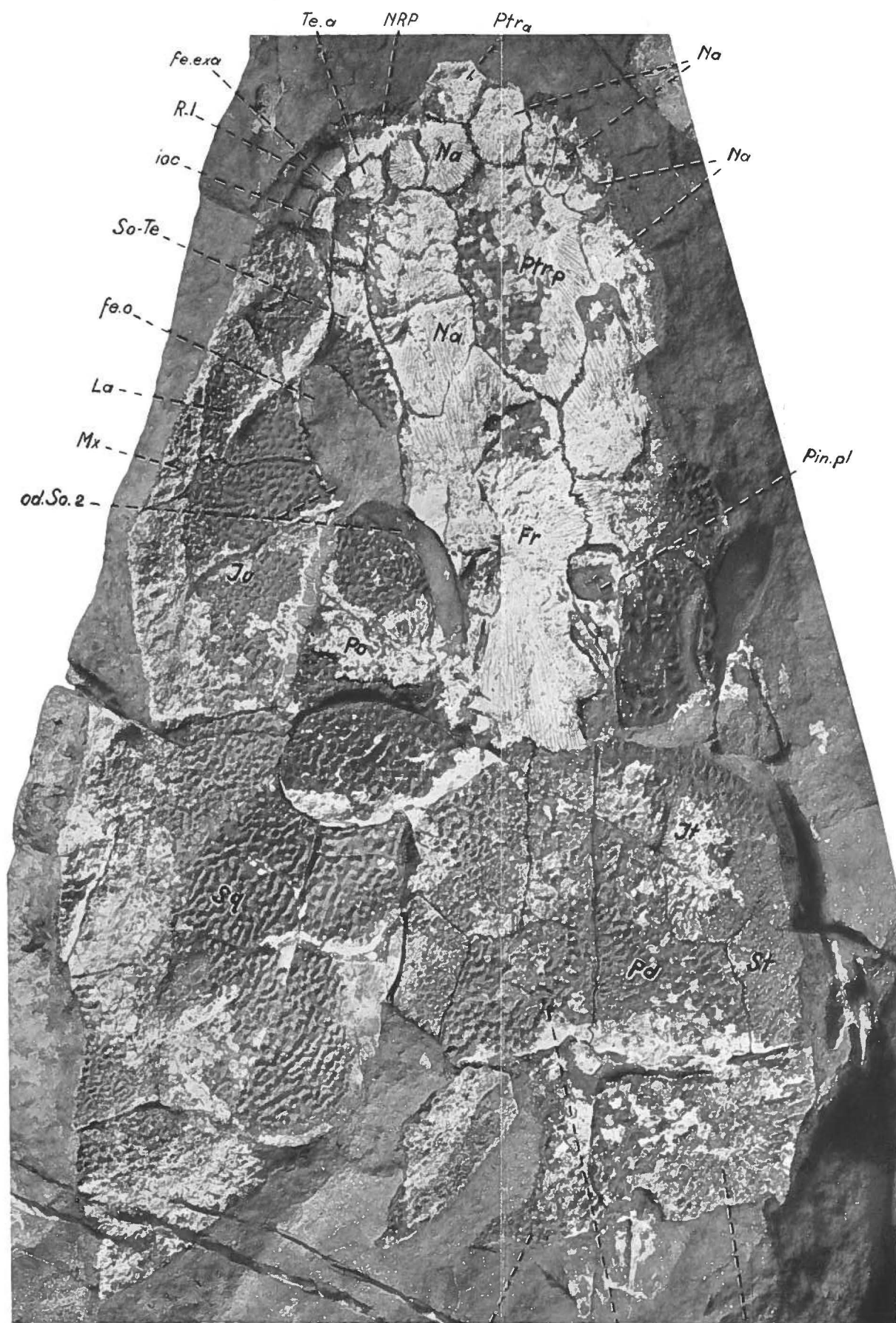


Plate 10.

Eusthenodon wängsjöi n.g., n.sp.

Holotype. Impressions of the external faces of the left and ventral sides of imperfect skull. Specimen No. P. 1476. Same specimen as in pl. 9 and pl. 11:2. 1/1.

De, dentary; *G*, principal gular plate; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentary 1, 2, 3, and 4; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *NRP*, naso-rostro-premaxillary; *Po*, postorbital; *Pop*, preopercular; *Qj*, quadratojugal; *Rbr*, branchiostegal rays; *R.l.* lateral rostral; *So-Te*, supraorbito-ectal; *Sq*, squamosal; *Te.a*, anterior tectal. *fe.exa*, fenestra exonarina anterior; *fe.o*, orbital fenestra; *pl.G*, pit-line of principal gular plate; *pl.Pop*, preopercular pit-line; *pl.Qj*, quadratojugal pit-line; *pl.Rbr.2*, pit-line of branchiostegal ray 2; *pl.Sq*, squamosal pit-line; *plv.Id.2*, vertical pit-line of infradentary 2.

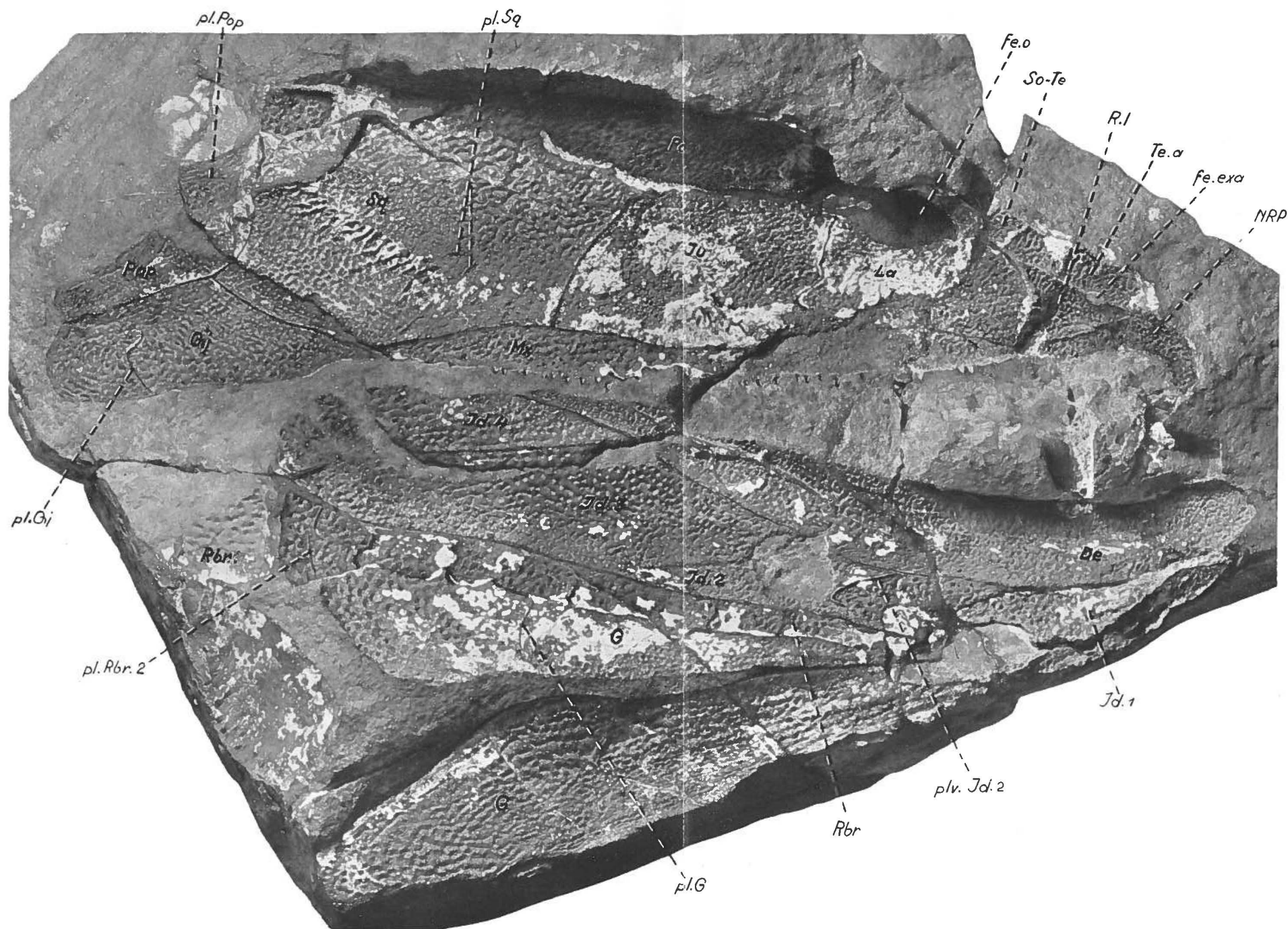


Plate 11.

Eusthenodon wängsjöi n.g., n.sp.

Fig. 1. Compressed imperfect skull in lateral aspect. Specimen No. P. 1479. Same specimen as in pl. 12. 1. From Smith Woodward Bjerg. 3/5.

Fig. 2. *Holotype*. Imperfect lower jaw in lateral aspect. The lateral parts largely lacking so that the inner face of the prearticular is exposed. Same specimen as in pls. 9, 10. 1/1.

Co.1, coronoid 1; *De*, dentary; *Enpt*, entopterygoid; *Ext.l*, *Ext.m*, lateral and median extrascapulars; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Na*, nasal; *NRP*, nasorostror-premaxillary; *Op*, opercular; *Pa*, parietal; *Po*, postorbital; *Prart*, prearticular; *So-Te*, supraorbital-tectal; *So.2*, posterior supraorbital; *Sq*, squamosal; *St*, supratemporal.

cot, teeth of coronoid; *fe.o*, orbital fenestra; *fe.spir*, spiracular fenestra; *la.l*, lateral lamina of prearticular; *pf*, pectoral fin; *prartt*, teeth of prearticular; *t.Co.1*, tusk of coronoid 1; *t.De*, tusk of dentary; *t.Dpl*, tusk of dermopalatine; *t.Vo*, tusk of vomer.

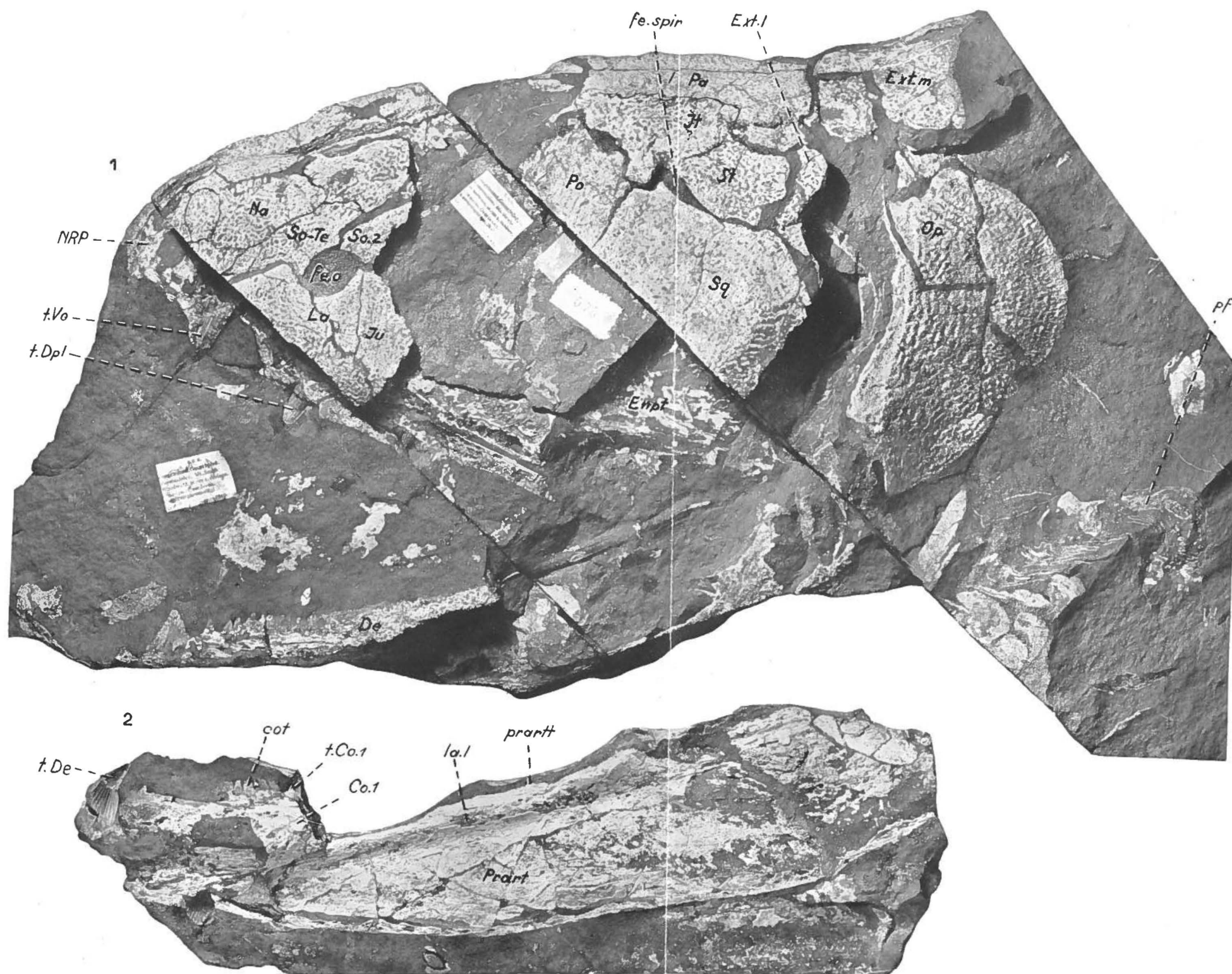


Plate 12.

Eusthenodon wängsjöi n.g., n.sp.

- Fig. 1. Compressed, imperfect skull in dorsal aspect. Specimen No. P. 1479. Same specimen as in pl. 11:1. 3/5.
- Fig. 2. Right opercular. Impression of external side. Specimen No. P. 1481. From the southern slope of Celsius Bjerg. 1/1.
- Fig. 3. Imperfect left lower jaw in dorsal view. Impressions of the inner sides of the dermal bones. Specimen No. P. 1473. Same specimen as in pls. 15, 16. 3/1.
- Fig. 4. Impression of external face of parasphenoid in dorsal view. Specimen No. P. 1482. From Remigolepisryg. 3/2.

Co.2, *Co.3*, coronoids 2, and 3; *De*, dentary; *Ext.l*, *Ext.m*, lateral and median extra-scapulars; *Fr*, frontal; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Na*, nasals; *Op*, opercular; *Pa*, parietal; *Prart*, prearticular; *Psph*, parasphenoid; *So-Te*, supra-orbito-tectal; *St*, supratemporal.

c.hyp, canal for ventral tube of hypophysis; *fe.o*, orbital fenestra; *fo.add*, adductor fossa; *i.spir*, spiracular notch; *la.l*, lateral lamina of prearticular; *od.Pop*, area of opercular overlapped by preopercular; *od.Psp*, area of opercular, probably overlapped by postspiracular plate; *pp*, posteriorly directed pit of parasphenoid; *pl.St*, supratemporal pit-line; *pr.Co.3*, posterior process of coronoid 3; *ri.Psph*, median tooth-bearing ridge of parasphenoid.

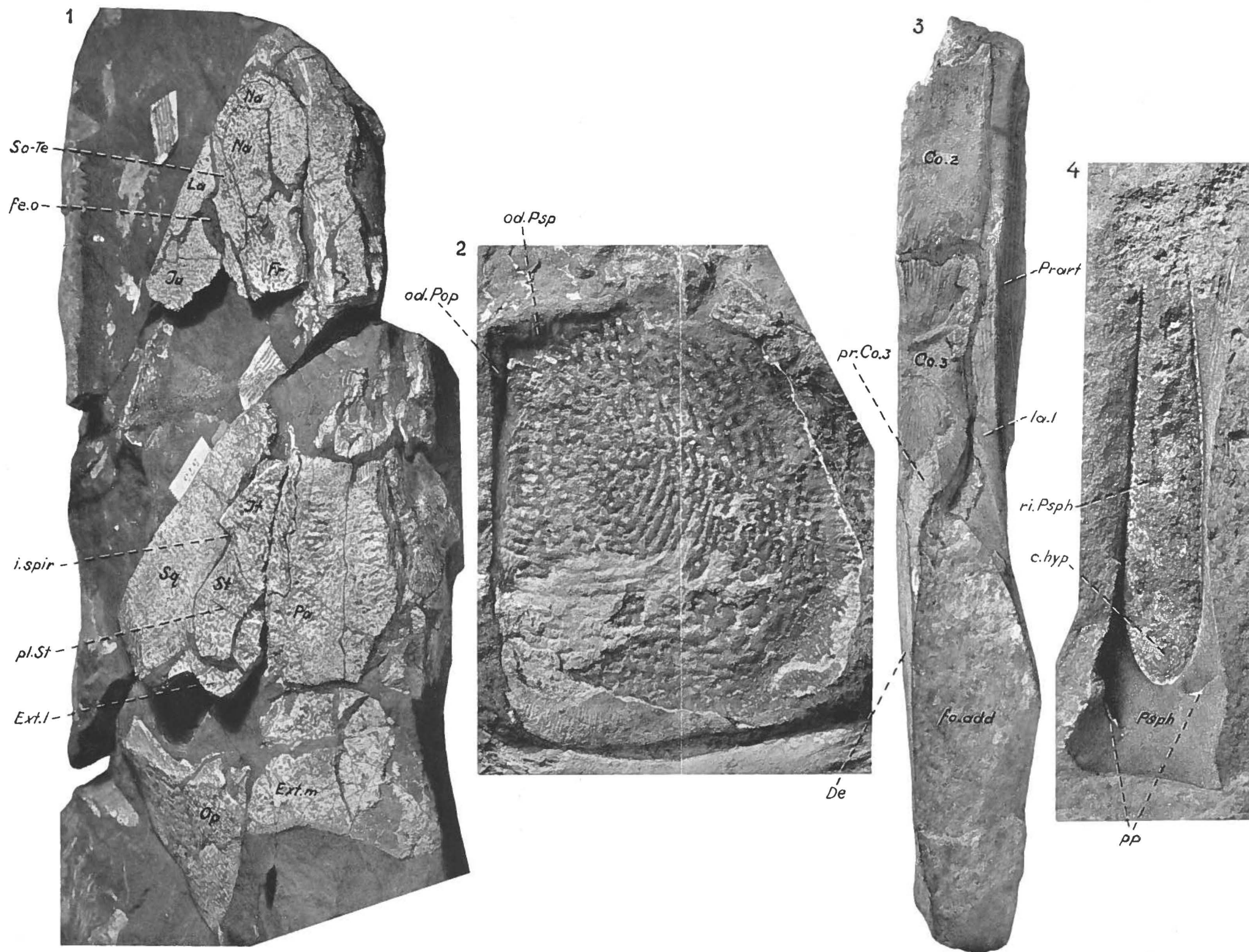


Plate 13.

Eusthenodon wängsjöi n.g., n.sp.

Imperfect, flattened skull in dorsal aspect. Impressions of the inner faces of the dermal bones of the cranial roof and the external cheek plates. Specimen No. P. 1478.

Counterpart in pl. 14. From the horizon at 1174 m. in Sederholms Bjerg. 3/5.

D, dermosphenotic; *Fr*, frontal; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *NRP*, naso-rostro-premaxillary; *Pa*, parietal; *Po*, post-orbital; *Pop*, preopercular; *Ptr_p*, posterior median postrostral; *Qj*, quadratojugal; *R.l*, lateral rostral; *So-Te*, supraorbito-tectal; *Sq*, squamosal; *St*, supratemporal;

Te.a, anterior tectal.

fe.exa, fenestra exonarina anterior; *fe.o*, orbital fenestra.

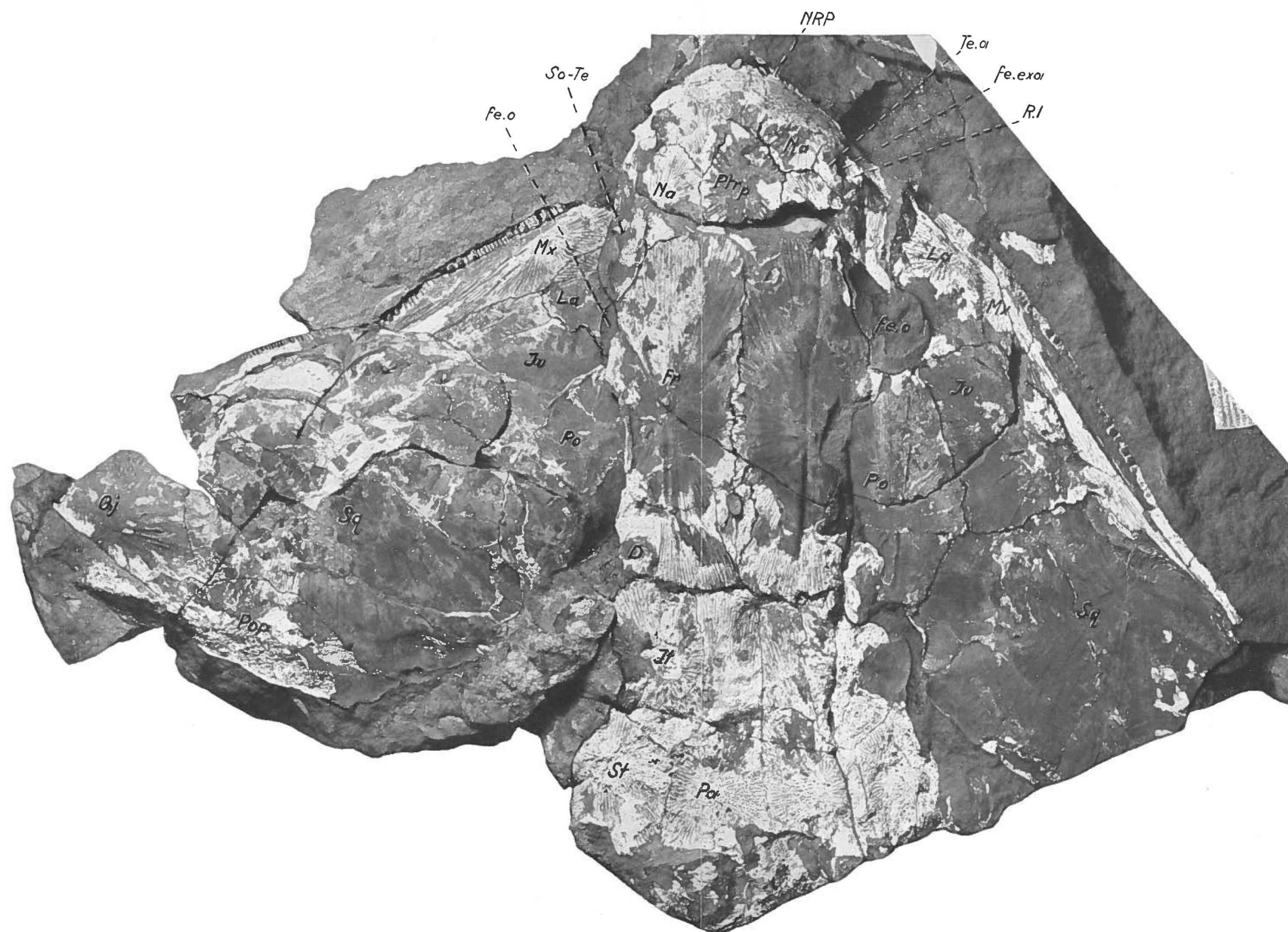


Plate 14.

Eusthenodon wängsjöi n.g., n.sp.

Flattened imperfect skull. Impressions of the external faces of the dermal bones of the cranial roof and the right external cheek plate. Specimen No. P. 1478. Counterpart of the specimen shown in pl. 13. 3/5.

D, dermosphenotic; *Ext.l*, *Ext.m*, lateral and median extrascapulars; *Fr*, frontal; *It*, intertemporal; *Ju*, jugal; *Mx*, maxillary; *Na*, nasals; *NRP*, naso-rostro-premaxillary; *Pa*, parietal; *Pin.pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular; *Ptr_p*, posterior median postrostral; *So-Te*, supraorbito-tectal; *So.2*, posterior supra-orbital; *Sq*, squamosal; *Te.a*, anterior tectal.

fe.exa, fenestra exonarina anterior; *fe.o*, orbital fenestra; *f.pin*, pineal foramen; *pl.Fr*, frontal pit-line; *pl.po.Pa*, posterior oblique parietal pit-line; *pl.Sq*, squamosal pit-line; *pl.St*, supratemporal pit-line; *pl.tr.Pa*, transverse parietal pit-line.

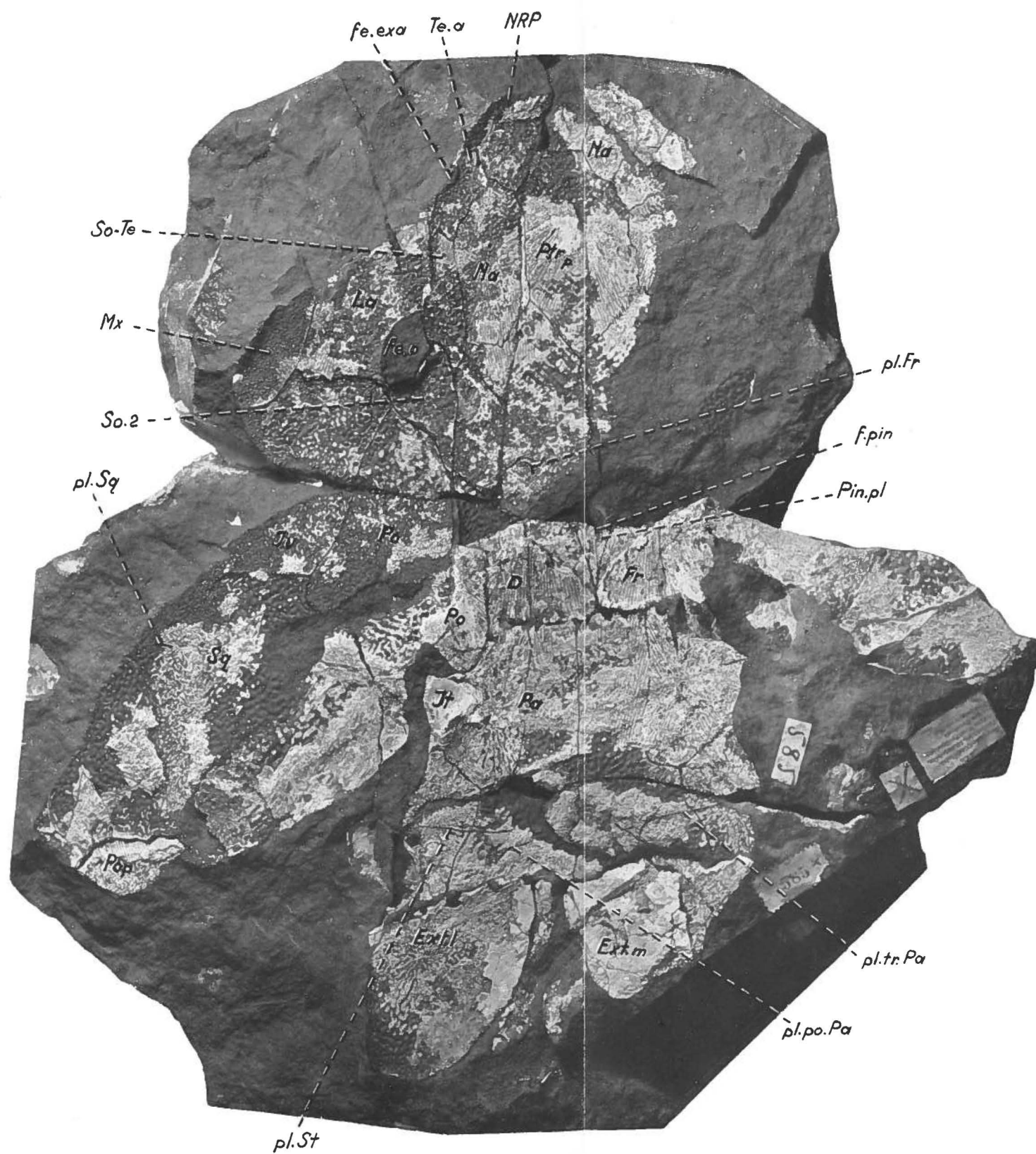


Plate 15.

Eusthenodon wängsjöi n.g., n.sp.

Imperfect skull of small individual. Specimen No. P. 1473. Same specimen as in text-fig. 31 A and pls. 12:3 and 16. From Sederholms Bjerg.

Fig. 1. Impression of the external face of the dorsal parts of the skull in ventral aspect. 5/4.

Fig. 2. Ditto in ventro-medial aspect. 5/4.

Fig. 3. Skull in dorsal aspect. Impressions of inner faces of the dermal bones. Counterpart in figs. 1 and 2. 5/4.

Fig. 4. Lower jaw in medial aspect. Same as in pl. 12:3. 3/1.

Co.2, *Co.3*, coronoids 2 and 3; *D*, dermosphenotic; *Fr*, frontal; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Na*, nasals; *Pin.pl*, pineal plate; *Pa*, parietal; *Po*, post-orbital; *Pop*, preopercular; *Prart*, prearticular; *Ptr_p*, posterior median postrostral; *Qj*, quadratojugal; *Sop*, subopercular; *So-Te*, supraorbito-tectal; *So.2*, posterior supraorbital; *Sq*, squamosal; *St*, supratemporal; *Te.a*, anterior tectal.

fe.o, orbital fenestra; *f.pin*, pineal foramen; *ioc*, infraorbital sensory canal; *juc*, jugal sensory canal; *la.l*, lateral lamina of prearticular; *pl.Fr*, frontal pit-line; *pl.po.Pa*, posterior oblique parietal pit-line; *pl.St*, supratemporal pit-line; *pl.tr.Pa*, transverse parietal pit-line.

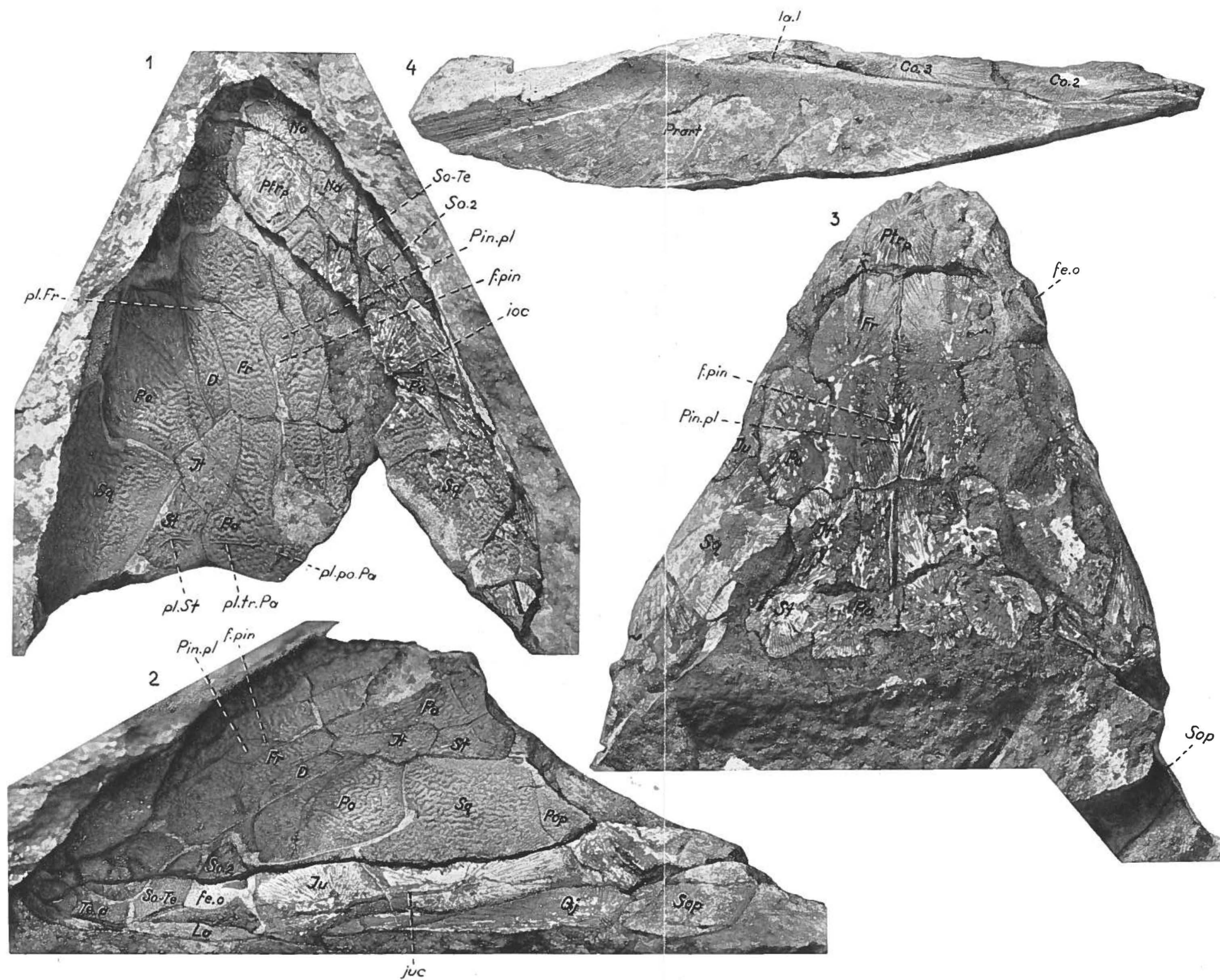


Plate 16.

Eusthenodon wängsjöi n.g., n.sp.

Same skull as in plate 15.

- Fig. 1. The preserved part of the skull in ventral aspect. Impressions of the inner faces of the dermal bones. 5/4.
- Fig. 2. The same as in fig. 1. Ventral parts removed, showing impressions of the dorsal faces of the dermal bones of the palate. 5/4.
- Fig. 3. Impressions of the ventral faces of the posterior part of the parasphenoid and adjoining parts of the entopterygoids. 5/4.
- Fig. 4. The same as in fig. 1 in lateral aspect. 5/4.

Co.1, coronoid 1; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *G*, principal gular plate; *Id.2*, *Id.3*, *Id.4*, infradentary 2, 3, and 4; *Ju*, jugal; *Po*, postorbital; *Pop*, preopercular; *Psph*, parasphenoid; *Qj*, quadratojugal; *Rbr.1*, hindmost branchiostegal ray; *Sop*, subopercular; *Sq*, squamosal; *Vo*, vomer.

c.hyp, canal for ventral tube of hypophysis; *fe.exch*, fenestra exchochialis; *fe.o*, orbital fenestra; *la.Vo*, ventral tooth-bearing lamina of vomer; *pp*, posteriorly directed pit of parasphenoid; *ri.Psph*, median tooth-bearing ridge of parasphenoid; *t.Vo*, tusks of vomer.

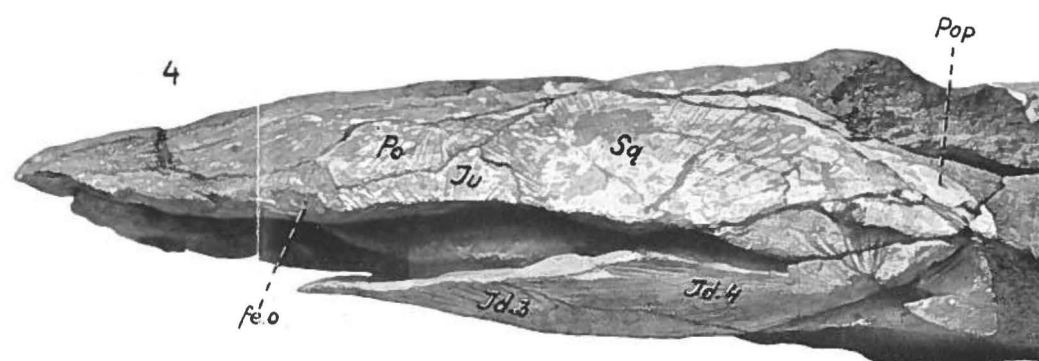
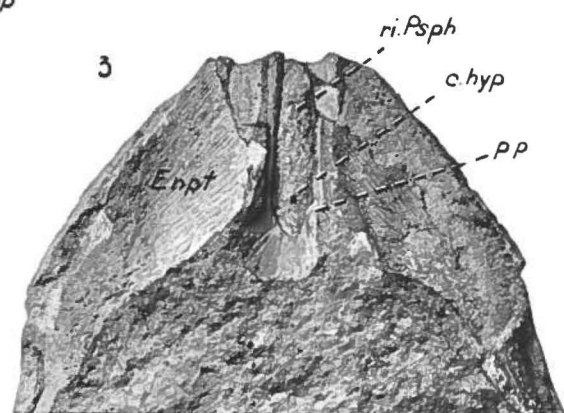
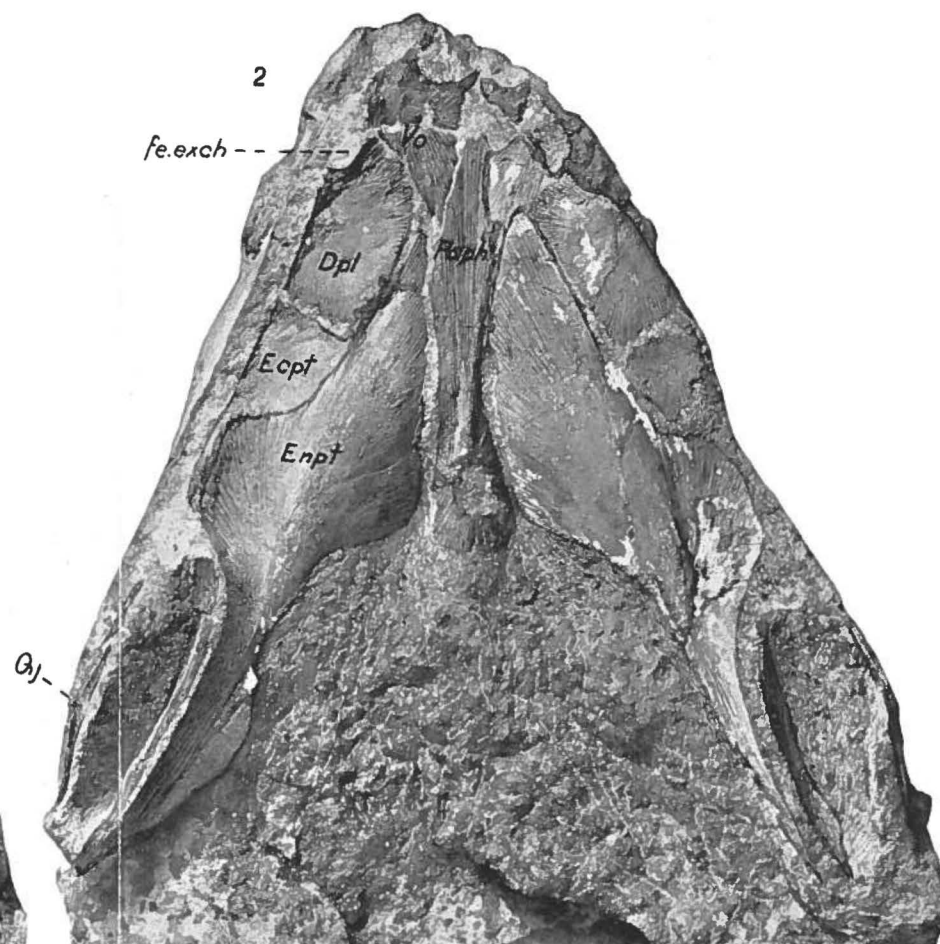
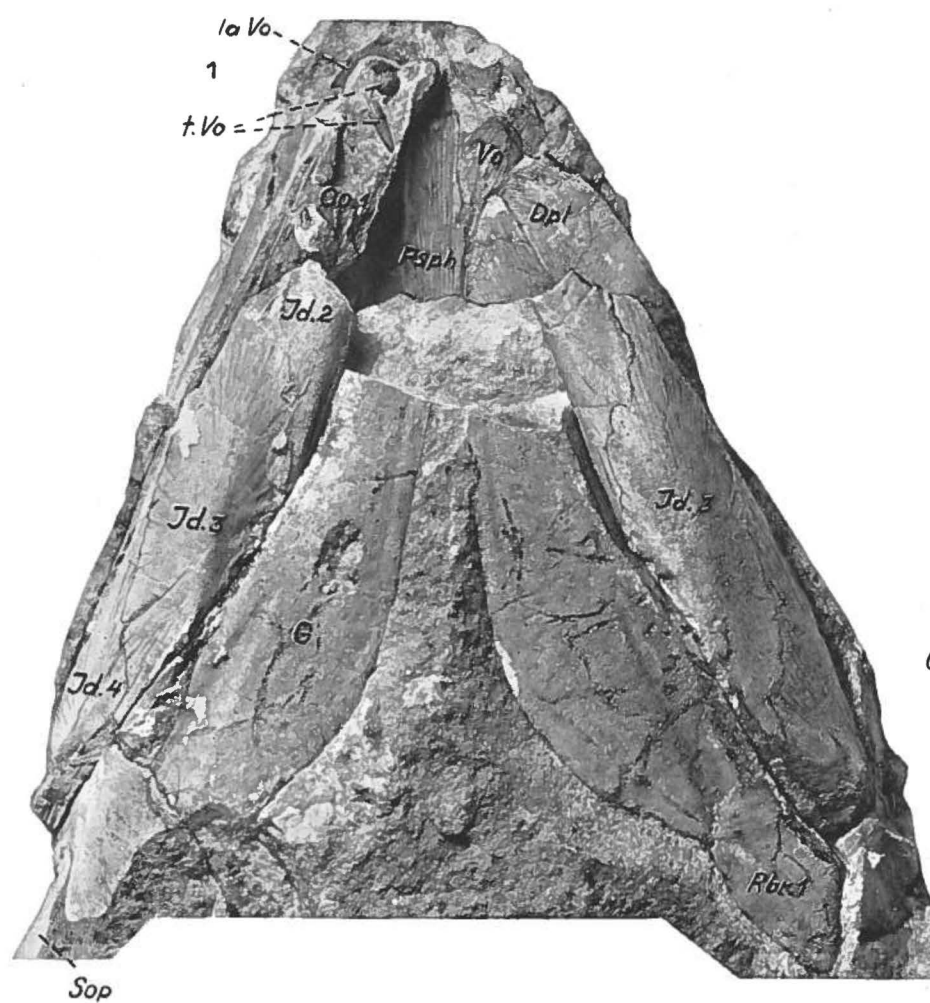


Plate 17.

Eusthenodon wängsjöi n.g., n.sp.

Fig. 1. Part of cranial roof. Impression of external side. Specimen No. 101. From Celsius Bjerg. Figured by STENSIÖ (1931, pl. 33:2). 5/4.

Fig. 2. Imperfect scale in inner aspect. Specimen No. P. 1477. Same specimen as in pl. 18. 3/1.

Fig. 3. Imperfect ventral side of skull. Impression of external side. Specimen No. P. 1483. From Sederholms Bjerg. 8/9.

D, dermosphenotic; *De*, dentary; *Fr*, frontal; *G*, principal gular plate; *Id.2*, *Id.3*, *Id.4*, infradentary 2, 3, and 4; *Na*, nasal; *Pin.pl*, pineal plates; *Ptr_p*, posterior median postrostral; *Rbr.1*, *Rbr.3*, *Rbr.4*, *Rbr.5*, branchiostegal rays; *So-Te*, supraorbitotectal.

f.pin, pineal foramen; *pl.Fr*, frontal pit-line; *pl.G*, pit-line of principal gular plate; *pl.Rbr.2*, pit-line of second branchiostegal ray; *plv.Id.2*, vertical pit-line of infradentary 2; *pt.Sc*, protuberance on inner face of scale.

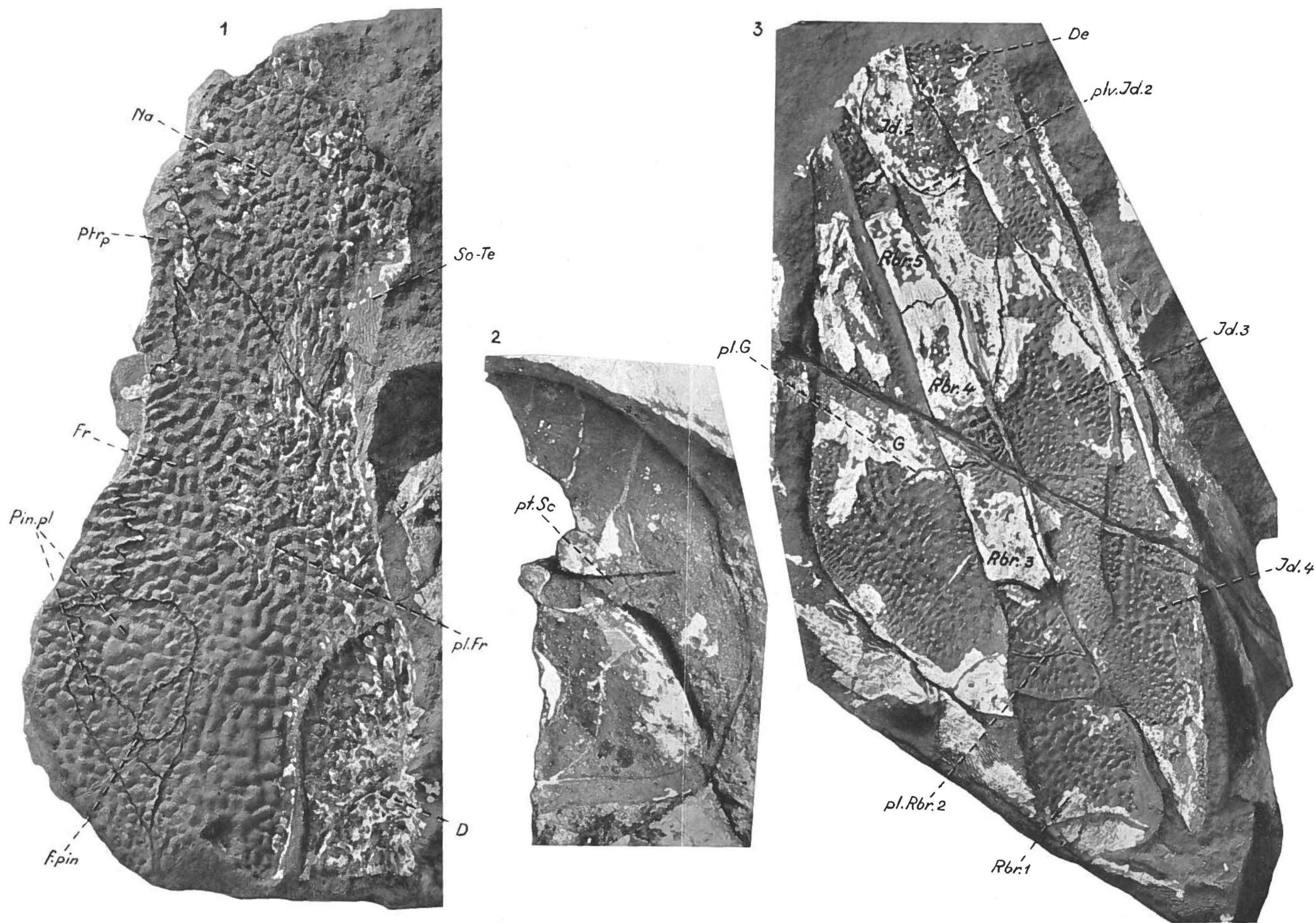


Plate 18.

Eusthenodon wängsjöi n.g., n.sp.

Fig. 1. Right external cheek plate and adjoining anterior parts of cranial roof. Impression of external side. Specimen No. P. 1477. From the horizon at 1174 m. in Sederholms Bjerg. 3/5.

Fig. 2. Counterpart of ditto. Impression of inner side. 3/5.

Fr, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *Po*, postorbital; *Pop*, preopercular; *Ptr_p*, posterior median postrostral; *Qj*, quadratojugal; *So-Te*, supraorbito-tectal; *So.2*, posterior supraorbital; *Sq*, squamosal.

fe.o, orbital fenestra; *juc*, jugal sensory canal; *pl.Fr*, frontal pit-line; *pl.Pop*, preopercular pit-line; *pl.Qj*, quadratojugal pit-line; *p.-mc* preoperculo-mandibular sensory canal; *soc*, supraorbital sensory canal.

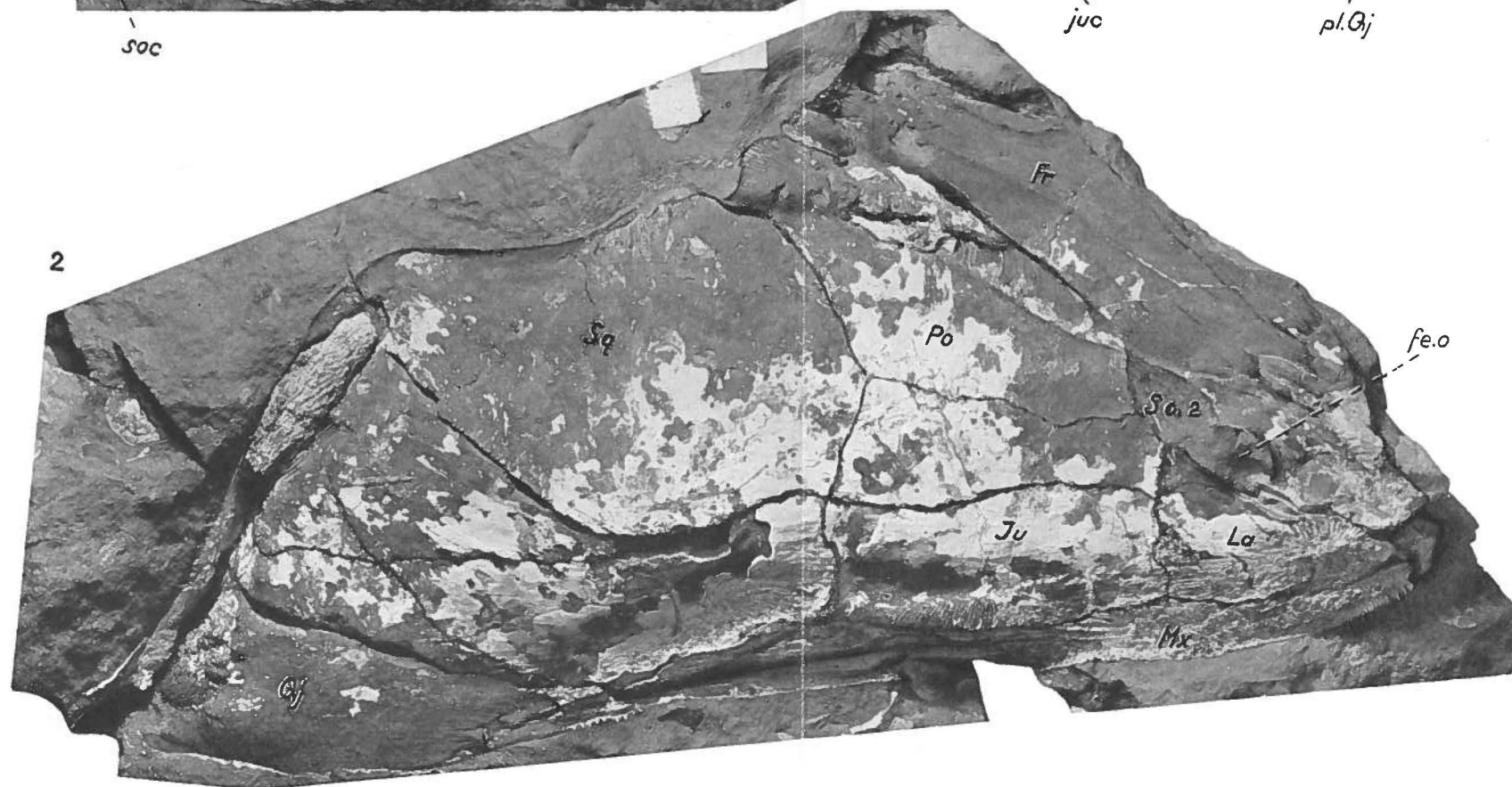
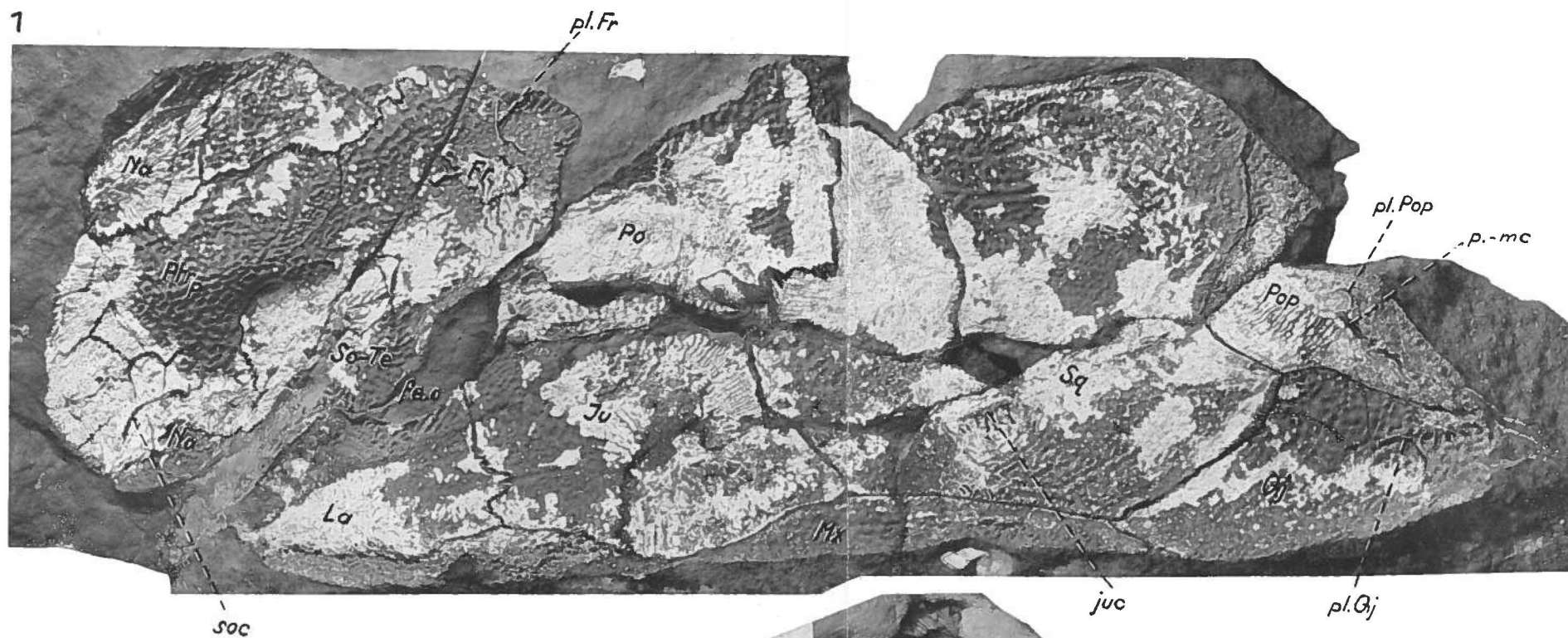


Plate 19.

Eusthenodon wängsjöi n.g., n.sp.

Imperfect, flattened skull in dorsal aspect. Specimen No. P. 1480. Same specimen as in pl. 20. From Smith Woodward's Bjerg. 3/5.

D, dermosphenotic; *Fr*, frontal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *NRP*, naso-rostrum-premaxillary; *Pin.pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular;

Ptr_p, posterior median postrostral; *So-Te*, supraorbital-tectal; *Sq*, squamosal.

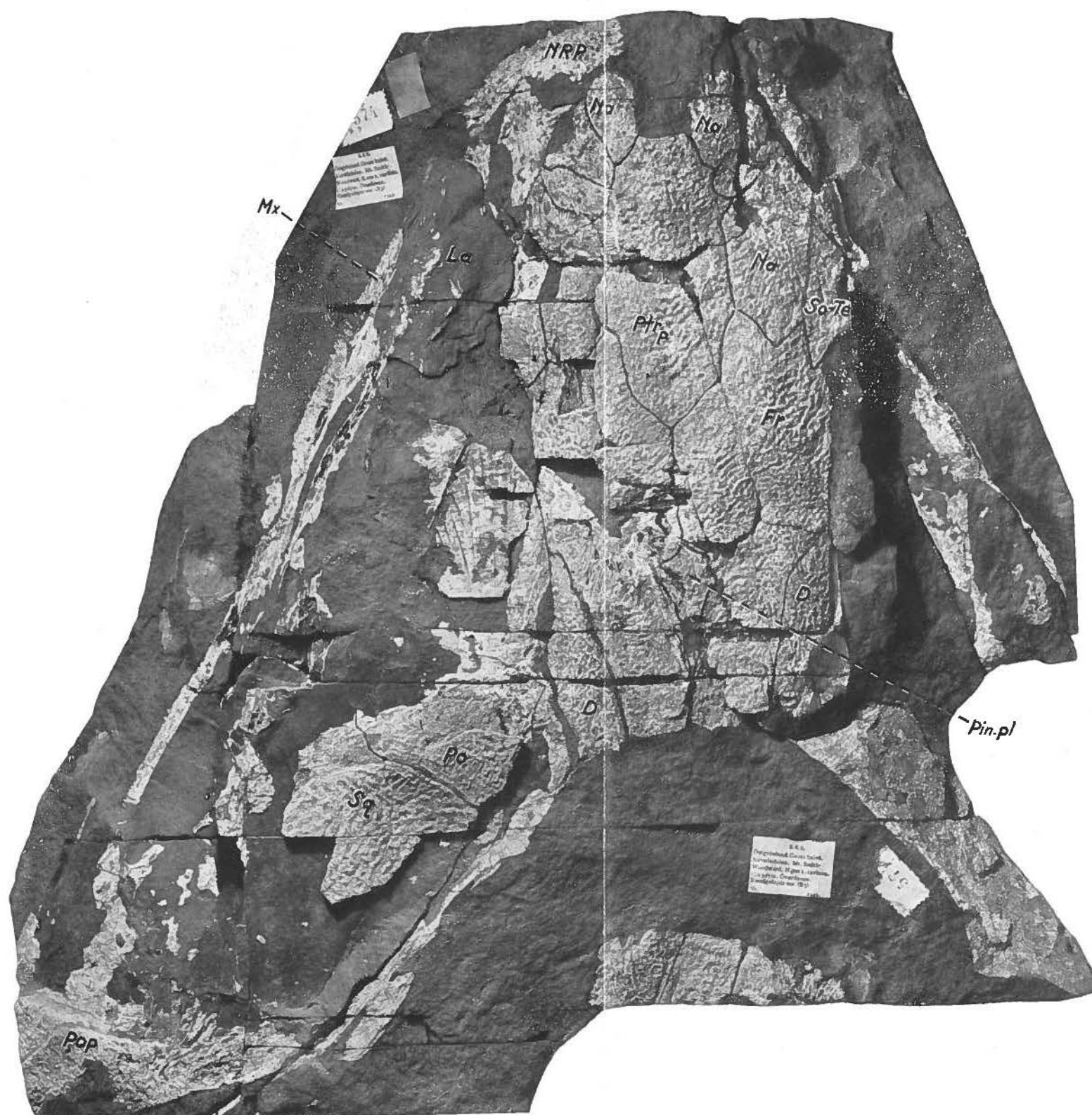


Plate 20.

Eusthenodon wängsjöi n.g., n.sp.

Counterpart of the specimen shown in pl. 19. 3/5.

D, dermosphenotic; *Fr*, frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *NRP*, naso-rostro-premaxillary; *Pin.pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular; *Ptr_p*, posterior median postrostral; *Qj*, quadratojugal; *R.l*, lateral rostral; *Sq*, squamosal; *Te.a*, anterior tectal.

fe.exa, fenestra exonarina anterior; *pl.Fr*, frontal pit-line.

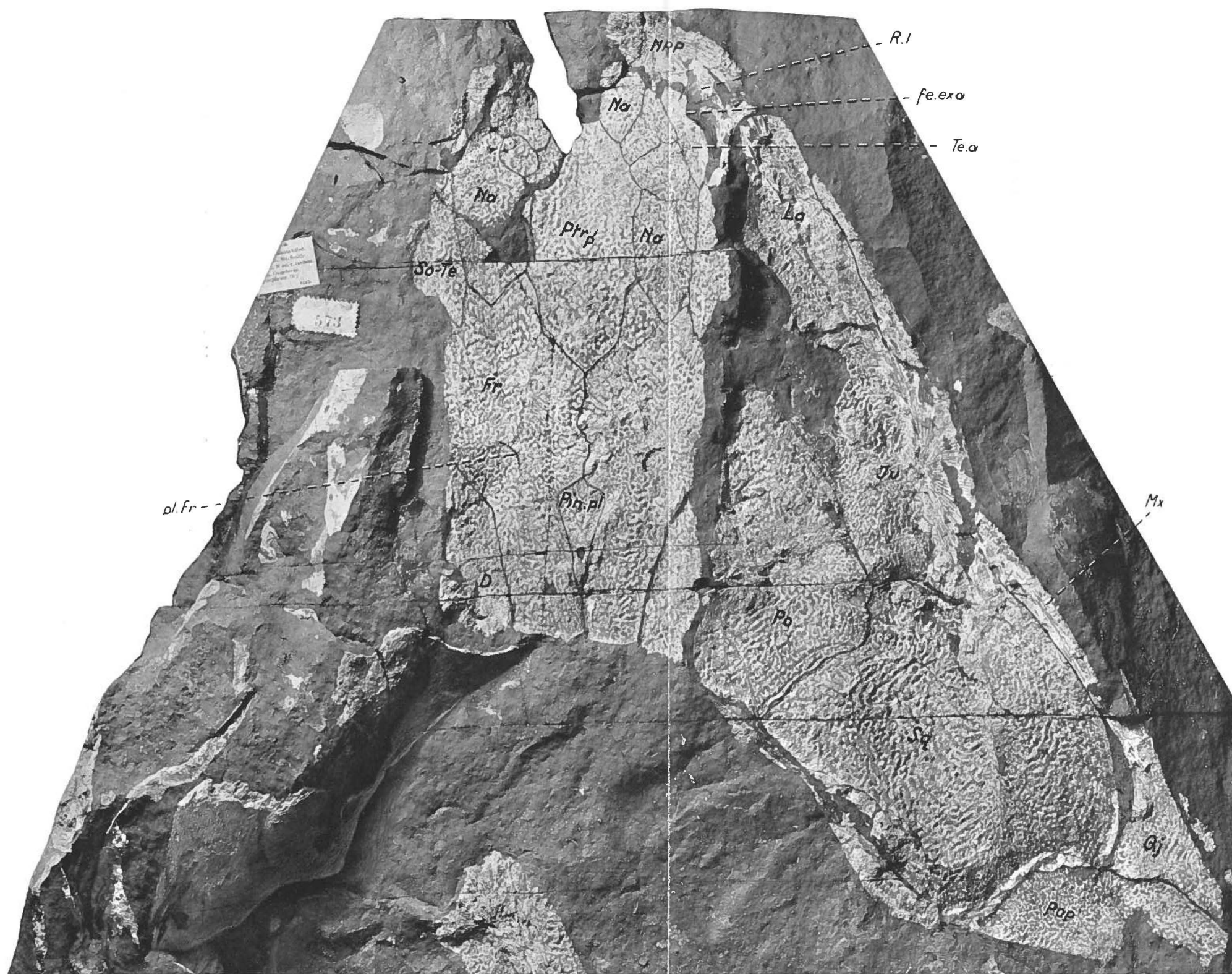


Plate 21.

Acanthostega gunnari n.g., n.sp.

Fig. 1. *Holotype*. Imperfect skull in dorsal aspect. Specimen No. A. 33. From Wimans Bjerg. 3/2.

Fig. 2. *Holotype*. Posterior part of the skull shown in fig. 1 in lateral aspect. 3/2.

Fig. 3. Imperfect skull roof. Impression of external side. Specimen No. A. 85. From Celsius Bjerg. Same specimen as in text-fig. 31 B. 3/2.

F, frontal; *Ju*, jugal; *La*, lachrymal, *Mx*, maxillary; *N*, nasal, *P*, parietal; *Po*, postorbital; *Pop*, preopercular; *Pp*, postparietal; *Prf*, prefrontal; *Ptf*, postfrontal; *Qj*, quadratojugal; *Sq*, suamosal; *Su*, supratemporal; *T*, tabular.

fe.o, orbital fenestra; *f.pin*, pineal foramen; *ioc*, infraorbital sensory canal; *i.ot*, otic notch; *i.T*, tabular notch; *juc*, jugal sensory canal; *jucp*, pores of jugal sensory canal; *la.Mx*, palatal lamina of maxillary; *la.T*, ventral lamina of tabular; *p.-mc*, preoperculo-mandibular sensory canal; *pr.T*, tabular process.

