8. On the Species of Eusthenopteron found in Russia and the Baltic States.

By

Erik Jarvik.

Introduction.

Hitherto only one species has been described of the Rhipidistid Crossopterygian *Eusthenopteron*. This species, *Eusthenopteron foordi* WHITEAVES, has until quite recently been found only in the Upper Devonian of Scaumenac Bay, Canada. Last year, however, GROSS, with some hesitation, referred to it some fragmentary specimens from the lowermost Upper Devonian of Latvia (1936, pp. 69—73; Abb. 1—5, 8; Abb. 9, figs. 2, 3).

For some time I have been engaged in the Paleozoological Department of the Swedish Riksmuseum on a detailed monograph of *Eusthenopteron foordi*, a monograph based on material from Scaumenac Bay.[1] In the course of this work I found that the Crossopterygians from the Upper Devonian of Juchora at the river Sjass in Russia described and figured by ROHON in 1889 as *Dendrodus biporcatus* OWEN and *Cricodus wenjukowi* ROHON appear to be so closely related to *Eusthenopteron* that they must belong to the latter genus. As shown by TRAQUAIR (1889, p. 490), ROHON's account is in several respects incorrect, and a new description of these excellent specimens therefore seems justified. For that purpose I have borrowed the specimens figured by ROHON in 1889 in pl. I, figs. 1, 3, 5, 9 and 11 from the Leningrad Geological Institute. I have also had an opportunity of studying the Baltic specimens figured by GROSS in 1936 on Abb. 9, figs. 2, 3. Further preparation and cleaning of these specimens, and the use of xylol and strong illumination when studying the object through a binocular microscope, have revealed several new features. The matrix has been removed from the imperfect divisio cranialis anterior,

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[1] Two specimens of *Eusthenopteron foordi* from the same locality have also been studied by Professor STENSIÖ in two grinding-series, which he kindly has allowed me to use.

(GROSS 1936, Abb. 9, fig. 2) and the anterior part of the lower jaw (Abb. 9, fig. 3) so as to allow examination also of the ventral face of the fronto-ethmoidal shield, the vomeres, the parasphenoid, and parts of the inner face of the lower jaw. The ethmosphenoid is too crushed to allow any close examination.

In the subsequent account, the Russian and the Baltic specimens are described under the names of *Eusthenopteron wenjukowi* (ROHON) and *Eusthenopteron säve-söderberghi*[1] n. sp. respectively.

For the sake of brevity, I do not intend to discuss the terminology used in this paper, nor will any reasons be given here for the interpretations of foramina, canals and other anatomical structures. All these matters will be fully considered in my forthcoming monograph on *Eusthenopteron foordi*.

I wish to express my best thanks to the Director of the Paleozoological Department of the Swedish Riksmuseum, Professor E. STENSIÖ, for excellent working facilities, and for placing at my disposal a specimen of *Eusthenopteron foordi* in the possession of the Riksmuseum.

For loan of material I wish to express my gratitude to Professor H. BACKLUND, Keeper of the Paleontological Institution of the Uppsala University; to Professor P. N. PRAVOSLAVLEFF, Staatliche Bubnov-Universität, Leningrad; and to Dr. A. C. STEPHEN, Royal Scottish Museum, Edinburgh. I also wish to express my sincere thanks to Dr. D. OBRUTSHEV, Moscow, for valuable information on Russian Devonian stratigraphy.

I. Remarks on the nomenclature.

As the present paper demonstrated that the Russian Crossopterygians described by ROHON (1889) as *Dendrodus biporcatns* and *Cricodus wenjukowi* actually belong to the same genus as the Crossopterygian known as *Eusthenopteron foordi* WHITEAVES (1881), the question arises whether the generic name *Eusthenopteron* WHITEAVES (1881) should not be dropped in favour of one of the older generic names *Dendrodus* OWEN (1841), *Cricodus* AGASSIZ (1844) or *Polyplocodus* (introduced by PANDER, 1860, p. 28, as a synonym to *Cricodus*, and used by several authors, e. g. by TRAQUAIR, 1895; OBRUTSHEV, 1930, and by GROSS, 1933). The question also arises, whether the generic differences between *Tristichopterus* EGERTON (1861)

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[1] This name was proposed by GROSS (in a Ms.) in honour of Dr. G. SÄVE-SÖDERBERGH, Stockholm, but as the characteristics of the species given by GROSS in that Ms. — based mainly on the incomplete and in several respects incorrect description of *Eusthenopteron foordi* by BRYANT (1919) — according to my investigations were distinguishing also of *E. foordi*, the Baltic species was provisionally included in that species (cf. GROSS 1936, pp. 72—73).

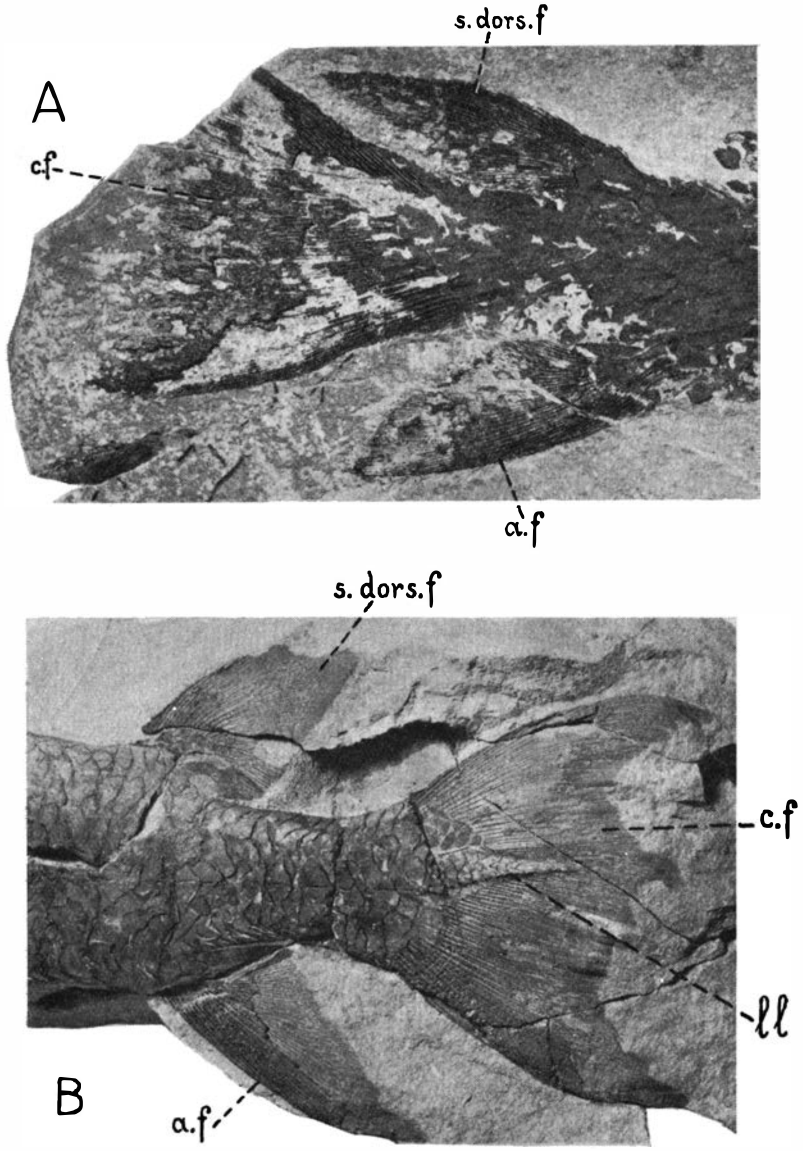

Fig. 1. A, *Tristichopterus alatus* EGERTON. Imperfect caudal region. Specimen 1900, 68/6 in the Royal Scottish Museum, Edinburgh. Natural size. B, *Eusthenopteron foordi* WHITEAVES. Caudal region. Specimen P. 222 a in the Riksmuseum, Stockholm. Half nat. size. Figured by HOLMGREN 1928, p. 324, fig. 3. *a. f*, anal fin; *c. f*, caudal fin; *ll*, lateral line canal of trunk; *s.dors.f* second dorsal fin.

and *Eusthenopteron* are not important enough to justify the retention of the latter generic name.

Of the generic differences between *Tristichopterus* and *Eusthenopteron* given by WHITEAVES (1881, p. 32; 1883, pp. 161—162; 1889, pp. 79—

89), and summarized by him (1889, pp. 89—90) in four points, only points 3 and 4 hold good according to TRAQUAIR (1890, p. 17).

Point 3 applies to the caudal fin, which is considered to be externally almost symmetrical in *Eusthenopteron* but asymmetrical in *Tristichopterus*. In the latter genus (fig. 2) the part of the caudal fin situated above the axis is considerably smaller (occupying about 1/3 of the vertical height of the caudal fin) than the part situated below that axis. In *Eusthenopteron*, on the other hand, the dorsal and ventral lobes are said to be almost equally developed, but — as pointed out by STENSIÖ (1925, p. 2), GRAHAM-SMITH[1] (1936, p. 598) and also indicated in HUSSAKOF's figure (1912, fig. 2) — the dorsal lobe is slightly smaller than the ventral (in WHITEAVES' restoration, 1889, pl. VI, the dorsal lobe is made larger than the ventral, which is certainly incorrect). More precisely, the part of the caudal fin above the axis in *Eusthenopteron foordi* (as I have been able to ascertain on a very well preserved tail of that species, fig. 1 B) constitutes about 3/7 of the vertical height of the caudal fin. The caudal fin of *Eusthenopteron* is thus not externally symmetrical, and the difference in caudal fin development between *Eusthenopteron* and *Tristichopterus* is only one of degree, and of but small value generically.

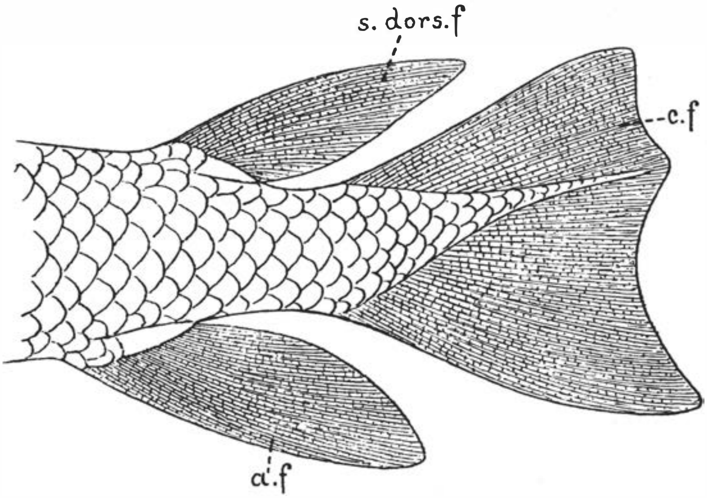

Fig. 2. *Tristichopterus alatus* EGERTON. Restoration of the caudal region. Natural size. From WATSON 1935; slightly altered. *a.f*, anal fin; *c.f*, caudal fin; *s.dors.f*, second dorsal fin.

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[1] As may be seen on my figure 1 B, the main lateral line of the body continues in *Eusthenopteron foordi* to the extreme posterior tip of the body, piercing a row of scales situated latero-ventrally on the axis of the caudal fin. It thus extends further back than shown on GRAHAM-SMITH's figure 15. The ending of the main lateral line in *Osteolepis macrolepidotus* and *Tristichopterus alatus* shown on his figures 13 and 14 still requires confirmation.

In WATSON's recent restoration of *Tristichopterus alatus* (1935, p. 165, fig. 33) the second dorsal and the anal fin are close to the origin of the caudal fin, whereas in *Eusthenopteron* they are separated from this by a fairly long, narrow portion of the tail (fig. 1 B). Several specimens of *Tristichopterus alatus* examined by me, from Deerness on the Mainland of the Orkneys (collected by SÄVE-SÖDERBERGH in 1934), from Caithness (specimens 1900 68/8, 1900 68/6 in the R. Scottish Museum, Edinburgh), as well as the type specimens figured by EGERTON (1861, pl. 4 and 5) from John o'Groats in Caithness, however, show a position and shape of the second dorsal and the anal fin very similar to that found in *Eusthenopteron foordi* (figs. 1 A, 1 B, 2).

Point 4 of WHITEAVES refers to the shape of the teeth. The larger teeth are said to be compressed and provided with two cutting edges in *Eusthenopteron*, but of round section in *Tristichopterus*. In my material of *Eusthenopteron foordi* from Scaumenac Bay, however, the shape of the teeth varies greatly. I have found teeth of round section and teeth with two cutting edges in the same specimen. Moreover, there occur in my material straight, bent, pointed, blunt, smooth, and striated teeth, varying in size from the very small diminutive teeth (less than 1 mm) that form an outer series along the oral margin of the maxillary and dentary to the large (up to 2 cm long) tusks of the coronoids, vomeres, dermopalatines and ectopterygoids. The external shape and size of the teeth are thus evidently of no systematic value.

The more pronounced vertical asymmetry of the caudal fin in the former genus is thus the only remaining of the original generic differences between *Tristichopterus* and *Eusthenopteron*. But another difference may be added. Measurements on several specimens of *Tristichopterus alatus* (specimens 1875 29/215, 217, 221, 224; 1896 25/2 in the R. Scottish Museum, Edinburgh, and the specimens figured by TRAQUAIR 1875, pl. XXXII) show that the length of the fronto-ethmoidal shield in the median line is about 1.4 of the median length of the parietal shield (for the terms fronto-ethmoidal and parietal shield, see SÄVE-SÖDERBERGH 1933, p. 73), whereas in *Eusthenopteron foordi* (see my forthcoming paper on that species) the same relation is about 1.85. The fronto-ethmoidal shield of *Tristichopterus* is thus relatively shorter than that of *Eusthenopteron*.

The differences so far known between *Tristichopterus* and *Eusthenopteron* may be summarized as follows:

1) About $^1/_3$ of the total height of the caudal fin in *Tristichopterus* is dorsal to the axis, and about $^3/_7$ in *Eusthenopteron*.

2) In *Tristichopterus* the length of the fronto-ethmoidal shield is about 1.4 of the parietal shield, and about 1.85 in *Eusthenopteron*.

Our knowledge of *Tristichopterus alatus* is rather incomplete, and it is probable that on closer investigation other differences than those enumerated above will be revealed. The circumstance that the fronto-ethmoidal shield is relatively shorter in *Tristichopterus* than in *Eusthenopteron* necessarily gives different proportions to the ethmosphenoid, palatoquadrate and dermal bones of the cheek. The difference between *Tristichopterus* and *Eusthenopteron* mentioned in point 2 above thus seems to me important enough to justify for the time being a retention of the genus name *Eusthenopteron.* In this connection it may also be mentioned that the two genera differ in stratigraphical distribution (see the table, pp. 120—121).

To decide whether the genus name *Eusthenopteron* WHITEAVES must be dropped and replaced by one of the generic names *Dendrodus* OWEN, *Cricodus* AGASSIZ, or *Polyplocodus* PANDER, it will be necessary to consider the types of these genera.

The name *Dendrodus* was introduced in 1841 by OWEN (1841, p. 4), who in the first part of his account on *Dendrodus* in The Microscopic Journal described and figured a single tooth from Scaat Craig in Scotland (lowermost Upper Devonain; see the table on pp. 120—121) as *Dendrodus biporcatus* (pp. 4—8, figs. 1 and 2). This tooth is the holotype of the species *Dendrodus biporcatus,* which is the genotype of *Dendrodus.* As this holotype is thus only a detached tooth, which from its histological structure (»dendrodont») can only be said to belong to the family *Holoptychidae,* it is in fact indeterminable as to species. It is consequently impossible to refer other new material to *Dendrodus.* The genus name *Dendrodus* can accordingly be used only for the type tooth from Scaat Craig. WOODWARD (1891, p. 338) and TRAQUAIR (1892, p. 35; 1895, p. 255), however, consider this tooth to belong to *Holoptychius giganteus* AGASSIZ (1845[1]). This can hardly be proved, but it seems at least very likely, that the tooth under discussion belongs to one of the species of *Holoptychius* described from the Scaat Craig locality (see the table below on pp. 120—121). As the genus name *Holoptychius* (= *Holoptychus*) was introduced by AGASSIZ as early as in 1839 (p. 599), and thus has priority of the name *Dendrodus* OWEN (1841), it is, according to the above, doubtful whether the latter name can be retained.

In 1860 PANDER described some teeth and jaw fragments (according to GROSS 1930, p. 20, found in the Middle Devonian of Livonia) under the name of *Dendrodus biporcatus* OWEN. As their »dendrodont» structure described in detail by PANDER cannot be proved to be of any importance for the determination of species, and probably occurs not only in different species but also in different genera, these teeth must be considered indeterminable. On the other hand, the jaw fragments described by PANDER (1860, p. 42; pl. 10, figs. 1 and 2) belong (GROSS 1930, p. 20; 21; 1933,

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[1] The dates of publication of AGASSIZ' papers 1833—44 and 1844—45 are quoted from WOODWARD and SHERBORN, A Catalogue of British Fossil Vertebrata (pp. XXV —XXIX), 1890.

p. 50) to a genus clearly distinguished from *Holoptychius*. Since, according to the above, *Dendrodus* is most probably synonymous with *Holoptychius*, the specimens from the Baltic Middle Devonian described by PANDER as *Dendrodus biporcatus* OWEN, and the specimens referred to that species by GROSS (1930, p. 21; 1933, p. 50), must obviously be given a new generic name.

From the above it is evident that the Crossopterygians from Juchora at Sjass discussed below, and previously described by TRAUTSCHOLD (1880, p. 139) as *Dendrodus* OWEN, and by ROHON (1889, p. 49; Tafel 1, figs. 1 and 9) as *Dendrodus biporcatus* OWEN, cannot either retain the genus name of *Dendrodus* OWEN.

The genus name *Cricodus* was introduced in 1844 by AGASSIZ (1833—1844, tom. 2, part 2, p. 156; pl. H, figs. 9—12), for two detached teeth, one from Scotland, and one from Riga. On page 162 (printed in 1844; WOODWARD and SHERBORN 1890, p. xxv) he mentions the species *Cricodus incurvus* (from Morayshire and Riga), and AGASSIZ obviously employed that species name for the two teeth mentioned already in 1844 (cf. AGASSIZ, 1844—1845, p. 88). One of these two teeth must therefore be considered the holotype of *Cricodus incurvus,* which is the genotype of *Cricodus,* but the tooth figured by AGASSIZ in 1845 (1844—1845, Pl. 28, figs. 4—5) cannot, as stated by TRAQUAIR (1892, p. 35), be so regarded. The fact that, according to TRAQUAIR (1892, p. 35), this latter tooth is of »dendrodont» structure has thus nothing to do with the retention of the genus name *Cricodus* (cf. GROSS 1933, p. 53). The two detached teeth figured by AGASSIZ in 1844, one of which is the type of the genus *Cricodus,* are both indeterminable, however, and — as the genus Cricodus thus cannot be defined — no additional material can therefore be referred to it.

The genus name *Polyplocodus* was introduced by PANDER (1860, p. 28) as a synonym of *Cricodus*. Such alteration of a generic name is not permissible according to the rules of nomenclature (Internationelle regeln etc. . . . 1927[1], p. 10, Art. 25). On the other hand, PANDER has by no means proved that the detached teeth described by him (1860, p. 29, 37, 84, Tab. F. G. L, figs. 1—5) as *Polyplocodus incurvus* (originating according to GROSS; 1930, p. 28, from the Middle Old Red of Livonia) belong to the same species as the type specimen of *Cricodus incurvus* AGASSIZ. The teeth described by PANDER as *Polyplocodus* are moreover indeterminable. They show only a tooth structure which was probably common to several genera of the Rhizodontids.

From the account given above it may be gathered that the generic

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[1] Internationale Regeln der Zoologischen Nomenklatur. Stand vom September 1927 (Congress zu Budapest). 2. Auflage. Frankfurt a. Main, Senckenb. Naturf. Ges., 1928.

names *Dendrodus, Cricodus* and *Polyplocodus* should be avoided. They were all introduced for indeterminable teeth or tooth fragments, and are therefore indefinable. No new material can consequently be referred to them.

II. Description of the material.

Genus Eusthenopteron WHITEAVES (1881).

The history of this genus will be dealt with by the author in a later monograph on *Eusthenopteron foordi.* A new and complete diagnosis of the genus will then also be given.

Remarks on the species. The two species of Rhipidistid Crossopterygians described in the present paper are still imperfectly known, but as far as can be judged at present they agree in all essentials so well with *Eusthenopteron foordi* WHITEAVES, which is the only hitherto known species of the genus *Eusthenopteron,* that they no doubt must belong to that genus. One of these species, *Eusthenopteron säve-söderberghi* n. sp., was shown by GROSS (1936) to belong to this genus, whereas the other, *E. wenjukowi* (ROHON) formerly was referred to the genera *Dendrodus* OWEN, *Cricodus* AGASSIZ and *Polyplocodus* PANDER. As shown above, however, these genera are so ill-defined that no additional material can be referred to them.

1. Eusthenopteron säve-söderberghi[1] n. sp.

(Figs. 3 A; 4—9.)

1936. *Eusthenopteron foordi,* GROSS, p. 69; Abb. 1—5, 8, 9, figs. 2, 3.

Diagnosis. The following diagnosis can at present be given of *E. säve-söderberghi:* — Fish of average size. Total length of the head probably about 95 mm, and of the fronto-ethmoidal shield about 60 mm. Nasal series meet the posterior supraorbital in a short suture. Posterior supraorbital probably longer than the supraorbito-antorbital. Pineal plates fairly large. Two large anterior pineal plates separated by a median suture. Vomeres do not meet in the median line behind the posterior opening of the intervomerine canal. Head ornamented by fairly close-set tubercles and ridges.

Material. — The material at my disposal consists of two specimens from the Paleontological Inst. of Uppsala, both of which have been described and figured by GROSS (1936). One of these two specimens consists of the posterior $^4/_5$ of the divisio cranialis anterior[2], which has been

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[1] See foot-note on page 66.

[2] The name divisio cranialis anterior here designates the anterior cranial complex in Crossopterygians, composed of the ethmosphenoid (or its derivates) and its

removed from the matrix so as to expose both the dorsal and ventral sides; the other specimen consists of a right lower jaw lacking its most anterior and most posterior parts. The anterior half of the extant part of the jaw has also been removed from the matrix, whereas the posterior half is still left in the rock, exposed only from the dorsal and external sides. Both specimens are slightly compressed.

Holotype. — As holotype I choose the imperfect divisio cranialis anterior shown in figs. 4 A—B; 5 A—C.

Description. — a. General shape. The holotype is of the following dimensions: Length 47 mm in the median line. Total median length of the divisio cranialis anterior, allowing for the missing tip of the snout, probably attained 57 mm, and of the fronto-ethmoidal shield about 50 mm, whereas the total dorsal, median length of the head (fronto-ethmoidal shield + parietal shield + median extrascapular) may be estimated at about 92 mm. The centre of the pineal foramen is situated 15 mm from the hinder end of the frontals and 11 mm from the posterior end of the large median postrostral. Greatest breadth in the present, flattened state of preservation is 37 mm, but was probably not more than about 34 mm. What is preserved of the vomeres measures 12 mm in length. The parasphenoid is about 41 mm long.

What is left of the lower jaw measures 84 mm in length, but when complete it probably attained a length of about 95 mm. It probably belonged to a specimen of approximately the same size as the holotype.

The dimensions of *Eusthenopteron säve-söderberghi* are thus on the whole the same as of *Eusthenopteron foordi*.

b. Ornaments. The ornament consists of fairly delicate obtuse tubercles, often united in short ridges, in most cases formed by but two or three coalesced tubercles (fig. 3 A). Usually these ridges are arranged in rows parallel with the margins of the bones, as may be seen in figure 4 A, e. g., at the anterior end of the right frontal, or on the lower jaw, fig. 9 A, but the ridges there are rather long, and formed by several tubercles.

c. Ethmosphenoid. The ethmosphenoid (*Etsph*, figs. 4, 5 B, 6, 8) is strongly compressed in a dorso-ventral direction and but little can therefore be ascertained of its structure. In all essentials, however, this seems to agree with that of *Eusthenopteron foordi*.

In the ethmoidal region the posterior parts of the nasal capsules are preserved. The planum antorbitale (*pl.ant*, figs. 4 B, 8) is much com-

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dermal bones, i. e. the fronto-ethmoidal shield above, the vomeres, and the parasphenoid below; the parietal shield, the extrascapular and the otico-occipital, may correspondingly be called the divisio cranialis posterior. The term »Frontoethmoidal-Komplex» used for the former division by GROSS (1936, p. 69) may easily be confused with the fronto-ethmoidal shield, and is therefore not appropriate.

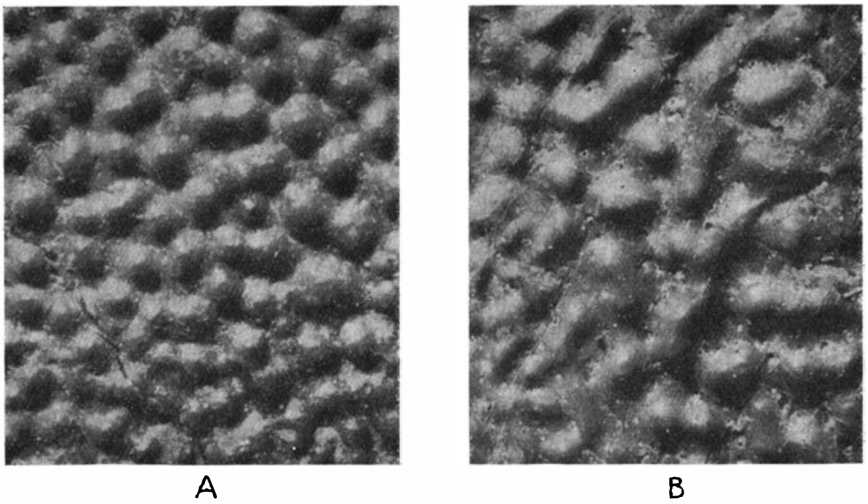


Fig. 3. Ornament of the anterior part of the frontal in two specimens of equal size. × 12. A, *Eusthenopteron säve-söderberghi* n. sp.; B, *Eusthenopteron foordi* WHITEAVES.

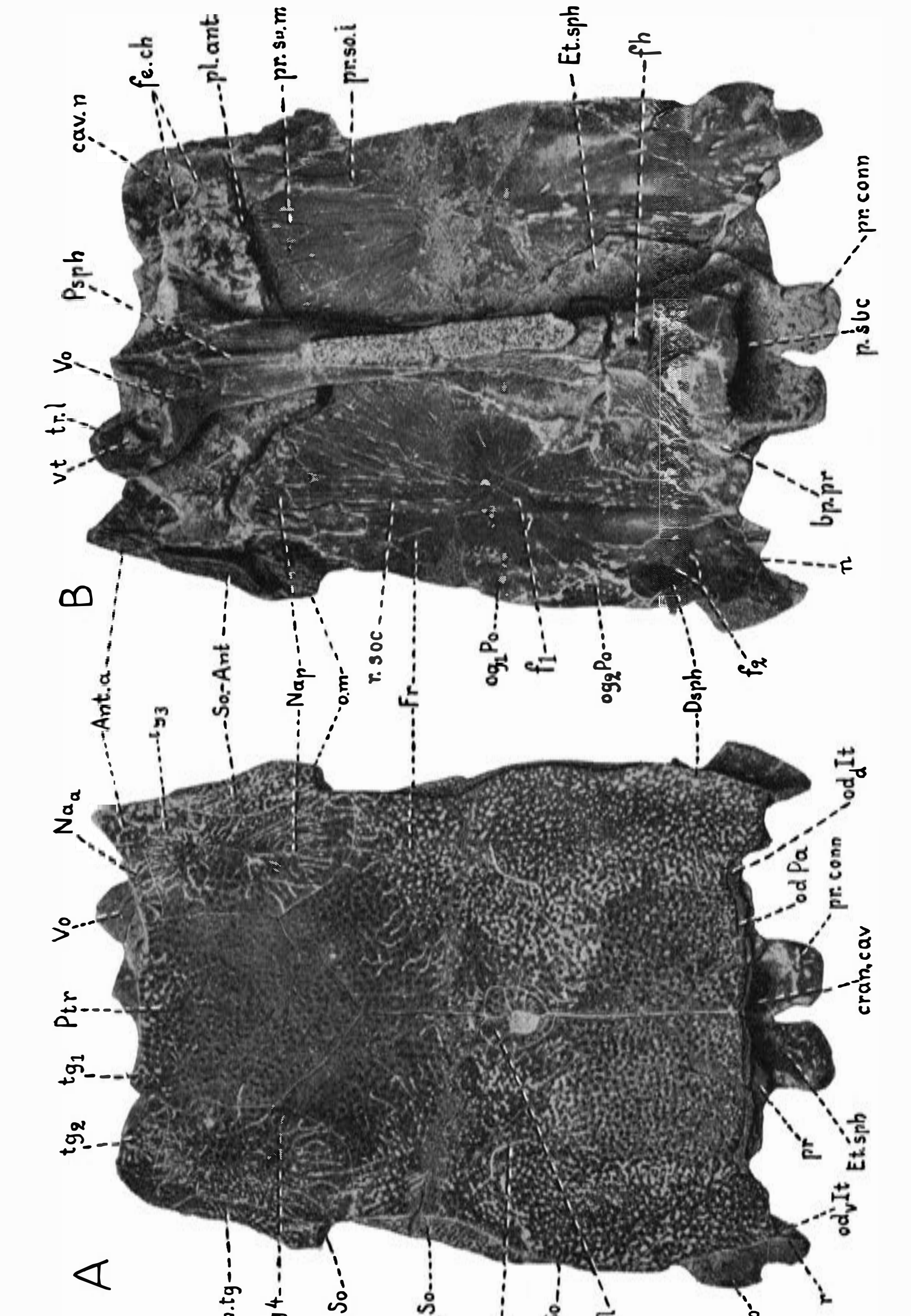
pressed and cannot be described. The nasal pits (*cav.n.* figs. 4 B, 8) are widely separated by a thick internasal wall (septum nasi). The smooth ventral face of this wall is covered by the vomeres and the anterior part of the parasphenoid. Laterally of each vomer we find the rather large fenestra choanalis (*fe.ch.* figs. 4 B, 8). The roof of the ethmoidal region is extended behind the planum antorbitale into two processes (*pr.so.l: pr.so.m,* figs. 4 B, 8) on each side. These processes overhang the orbita in front, and support parts of the dermal cranial roof in this region. The medial of these processes, the processus supraorbitalis medialis, is a broad and thin lamina situated medially of the low, indistinct ridge (*r.soc,* figs. 4 B, 8) on the ventral face of the frontal and the most posterior nasal, which is caused by the supraorbital lateral line canal. The lateral of the two processes, the processus supraorbitalis lateralis (*pr.so.l,* figs. 4 B, 8), is long and narrow, and extends further back than the medial process. It is situated immediately laterally of the above ridge. In *Eusthenopteron foordi* these two processes have only been found in one of the specimens ground by STENSIÖ (cf. STADTMÜLLER 1931, p. 269, Abb. 10, Supraorbital-leiste).

The most anterior portion of the orbito-temporal region is so much damaged that no details can be distinguished. Apparently, however it must have been high and narrow. In the posterior portion the lateral parts of the roof are well exposed in a ventral view. These parts of the roof widen towards the back extending posteriorly almost to the suture between the dermosphenotic and the frontal (figs. 4 B, 8). The lateral part of their posterior border is slightly concave, facing somewhat laterally, and produced into a blunt process, *pr* (figs. 4 A, 6). Medially of that process the roof covers the cranial cavity (*cran.cav*, 4 A, 5 B, 6). The lateral wall of the cranial cavity ends posteriorly on each side in a free concave margin. This margin begins dorsally below the process *pr*, runs in a ventro-posterior direction, and ends posteriorly in a blunt process, the processus connectens (*pr.conn*, figs. 4 A, 4 B, 5 A, 5 B, 6, 8). In *Eusthenopteron foordi* there is a well defined area, devoid of the shiny periostal bone-layer, on the lateral face of this process. That area was connected, probably by means of cartilage or connective tissue, to a corresponding area on the otico-occipital, a circumstance that justifies the name processus connectens.

The above posteriorly directed concave margin of the lateral cranial wall, i. e. the part of the posterior margin of the ethmosphenoid dorsal to the processus connectens, formed the anterior boundary of a large foramen, the equivalent of the one in *Eusthenopteron foordi* interpreted by HOLMGREN & STENSIÖ (1936, p. 344, Abb. 264 B, V) as the exit of the main branches of the nervus trigeminus. Between the processus connectens and its fellow on the opposite side, but ending a little anterior to the posterior end of that process, the floor of the cranial cavity is here extended further back than the roof (see figs. 4 A, 6). The roof, and in part also the lateral walls, of the cranial cavity are here formed by the otico-occipital. Ventral to the posteriorly extended portion of the floor just referred to, is in the posterior wall of the ethmosphenoid a wide pit (*p.sbc*, figs. 4 B, 5 B, 8) opening backwards. This pit is completely separate from the fossa hypophyseos. It forms the anterior end of the fossa subchordalis described by STENSIÖ in *Diplocercides* (STENSIÖ 1932, p. 23). On the ventral face of the ethmosphenoid, near the posterior end of the bone, where the parasphenoid has been destroyed, there is in the middle line the opening of a vertically ascending canal (*fh*, fig. 4 B), obviously representing the most ventral portion of the fossa hypophyseos. This canal probably pierced the parasphenoid, too, and opened on its ventral face (fh_1, fig. 8) as it does in *Eusthenopteron foordi*.

The basipterygoid process (*bp.pr*, figs. 4 B, 5 B, 8) is exposed on both sides of the present specimen, but it is too damaged to be described in any detail. It is situated a little anterior to the posterior end of and below the level of the processus connectens. In figure 8 it has been restored in accordance with the conditions found in *Eusthenopteron foordi*.

d. The fronto-ethmoidal shield. The dermal bones composing the fronto-ethmoidal shield are rigidly connected with each other, and the sutures between them are in many cases hard to trace. The posterior supraorbital is missing in the present specimen, however, but was apparently loosely connected with the fronto-ethmoidal shield. Nor is it found in detached fronto-ethmoidal shields of *Eusthenopteron foordi*.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Fragments of the premaxillaries — presumably rostro-premaxillaries as in *Eusthenopteron foordi* (*R.-Pmx,* figs. 6, 7 A) — are present. These fragments, which could not be removed from the rock, are too badly preserved to show any details. The other dermal bones from the tip of the snout are missing.

The anterior antorbital (*Ant.a,* figs. 4 A, 4 B, 5 A, 6, 7 A) is fragmentary, only its postero-medial part being preserved on either side. Posteriorly this is joined by a straight, oblique suture to the supraorbito-antorbital, and medially it meets the nasal series in a suture traceable only in its posterior part.

Some tubules of the supraorbital canal enter the medial part of the bone, and open into pores on its dorsal face.

The supraorbito-antorbital (*So-Ant,* figs. 4, 5 A, 5 C, 6, 7 A, 8) is a compound bone in *Eusthenopteron foordi,* so called because it is formed by the fusion of an anterior supraorbital and a posterior antorbital. Its anterior half rests on the posterior lateral part of the roof of the ethmoidal part of the ethmosphenoid, whilst its posterior half is situated behind that roof, and consequently does not cover any part of the endocranium.

The supraorbito-antorbital is almost completely preserved on both sides; only its lateral, bent-down margin is imperfect. In shape it is trapezoidal, of greater length than width. It has a postero-lateral and a lateral free margin, though the latter is imperfect. Anteriorly it is joined by a short straight suture to the anterior antorbital; medially it meets the posterior nasal in a straight, longtudinal suture; and postero-medially it is finally joined to the frontal, but only ventrally (fig. 5 C).

Fig. 4. *Eusthenopteron säve-söderberghi* n. sp. Imperfect divisio cranialis anterior. A.-dorsal; B.-ventral aspect. Photographed in xylol. × 2. Specimen in the Paleontological Institute, Uppsala. Figured by GROSS 1936, Abb. 9, Fig. 2.

Ant.a, anterior antorbital; *Dsph,* dermosphenotic; *Et.sph,* ethmosphenoid; *Fr,* frontal; Na_a, anterior nasal; Na_p, posterior nasal; *Pinpl,* pineal plate; *Psph,* parasphenoid; *Ptr,* postrostral: *So.-Ant,* supraorbito-antorbital; *Vo,* vomer; *ap,* anterior pit line of the cranial roof; *bp.pr,* basipterygoid process; *cav.n,* cavum nasi; *cran.cav,* cranial cavity; *fe.ch,* fenestra choanalis; *fh,* opening of the fossa hypophyseos on the ventral face of the ethmosphenoid; f_1, f_2, foramina transmitting nerves and vessels supplying the lateral line canals; *n,* notch in the posterior margin of the dermosphenotic; *od. Pa,* area of the frontal, overlapped by the parietal; od_dIt, dorsal area of the frontal, overlapped by the intertemporal; od_vIt, ventral area of the dermosphenotic, overlapped by the intertemporal; od_vPo, ventral area of the dermosphenotic, overlapped by the postorbital; od_1So, area of the supraorbito-antorbital, overlapped by the posterior supraorbital; od_2So, area of the frontal overlapped by the posterior supraorbital; od_3So, area of the dermosphenotic, overlapped by the posterior supraorbital; og_1Po, area of the frontal, overlapping the postorbital; og_2Po, area of the dermosphenotic, overlapping the postorbital; *o.m,* antero-dorsal part of the orbital margin; *pl.ant,* planum antorbitale; *pr,* blunt process at the posterior end of the roof of the ethmosphenoid; *pr.conn,* processus connectens; *pr.so.l,* processus supraorbitalis lateralis; *pr.so.m,* processus supraorbitalis medialis; *p.sbc,* pit in the posterior face of the ethmosphenoid, representing the most anterior end of the fossa subchordalis; *ptn.tg,* group of tubules, probably of the postnasal connection; *r,* ridge separating the overlapped areas od_vIt and od_vPo of the dermosphenotic; *r.soc,* ridge caused by the supraorbital lateral line canal tg_1—tg_6, groups of lateral line canal tubules; *tr.l,* transverse, tooth-bearing lamina of the vomer; *vt,* vomerine tusk.

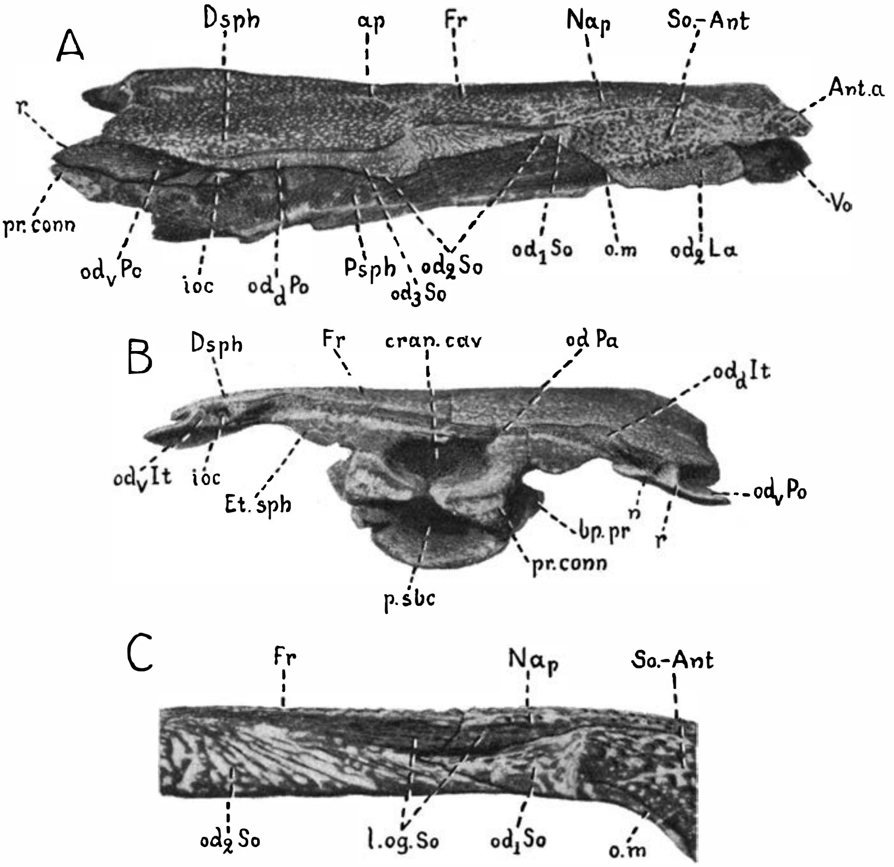

Fig. 5. *Eusthenopteron säve-söderberghi* n. sp. The same specimen as in figure 4. Photographed in xylol. A, — right, lateral aspect, × 2; B, — posterior aspect, × 2; C, — lateral margin of the posterior parts of the supraorbito-antorbital and the posterior nasal and of the anterior part of the frontal. Lateral aspect. × 8.

Ant.a, anterior antorbital; *Dsph*, dermosphenotic; *Et.sph*, ethmosphenoid; *Fr*, frontal; *Nap*, posterior nasal; *Psph*, parasphenoid; *So.-Ant*, supraorbito-antorbital; *Vo*, vomer; *ap*, anterior pit line of the cranial roof; *bp.pr*, basipterygoid process; *cran.cav*, cranial cavity; *ioc*, foramen for the infraorbital lateral line canal; *l.og.So*, lip of the frontal and posterior nasal, overlapping the posterior supraorbital; *n*, noth in the posterior margin of the dermosphenotic; *od Pa*, area of the frontal, overlapped by the parietal; *oddIt*, area of the frontal, overlapped by the intertemporal; *oddPo*, dorsal area of the dermosphenotic, overlapped by the postorbital; *odvIt*, ventral area of the dermosphenotic, overlapped by the intertemporal; *odvPo*, ventral area of the dermosphenotic, overlapped by the postorbital; *od$_2$La*, area at the lateral margin of the supraorbito-antorbital, overlapped by the lachrymal; *od$_1$So*, area of the supraorbito-antorbital, overlapped by the posterior supraorbital; *od$_2$So*, area of the frontal, overlapped by the posterior supraorbital; *od$_3$So*, area of the dermosphenotic, overlapped by the posterior supraorbital; *o.m*, antero-dorsal part of the orbital margin; *pr.conn*, processus connectens; *p.sbc*, pit in the posterior face of the ethmosphenoid, representing the most anterior end of the fossa subchordalis; *r*, ridge separating the overlapped areas *odvIt* and *odvPo* of the dermosphenotic.

It exhibits two unornamented, overlapped areas. The larger of these areas (*od$_2$La*, figs. 5 A, 7 A) is situated along the lateral, margin of the bone, which faces dorso-laterally. It is rather smooth, and was probably overlapped by the lachrymal. The other overlapped area (od_1So, figs. 4 A, 5 A, 5 C, 7 A), situated at the posterior end of the bone, is small, triangular in shape, and was certainly overlapped by the anterior end of the posterior supraorbital. Between these two overlapped areas there is a thin, concave, free margin (*o.m.,* figs. 4, 5 A, 5 C, 6, 7 A), bordering the orbit dorso-anteriorly.

The centre of radiation is situated almost in the centre of the bone.

The supraorbito-antorbital is pierced by several highly ramifying tubules (*ptn.tg*, figs. 4 A, 6), belonging to the lateral line system and opening into numerous superficial pores. All tubules appear to issue from the centre of radiation of the bone, and it seems very likely that they open into a lateral line canal traversing that centre. The only canal that might be concerned as having passed there is the postnasal connection (see SÄVE-SÖDERBERGH 1933, p. 7), which very likely was present here. I have not been able to observe that connection with certainty in *Eusthenopteron foordi*, although in that species, too, several conditions favour the assumption that it was present.

Only the posterior part of the nasal series is preserved. On each side there is thus a large posterior nasal (Na_p, figs. 4, 5 A, 5 C, 6, 7 A, 8), and an anterior nasal (Na_a, figs. 4 A, 6, 7 A), of which latter, however, only the posterior part is preserved. The nasal series covers a lateral part of the roof of the ethmoidal region, but also reaches backwards beyond the planum antorbitale. More precisely its posterior part lies so as to be visible in ventral view between the processes supraorbitalis lateralis and medialis (figs. 4 B, 8).

Medially there is a slightly undulating suture between it and the large median postrostral. Anteriorly it is broken; laterally it meets the anterior antorbital and the supraorbito-antorbital, as already described, and the lateral edge behind the latter slightly overlaps (the anterior part of *og.So,* fig. 7 A; the anterior part of *l.og.So,* fig. 5 B) the most anterior part of the medial margin of the posterior supraorbital. Posteriorly and postero-medially a convex suture joins it to the frontal, overlapping that bone to a considerable extent. The transverse suture between the two independent nasals of each side is situated far forward. Laterally this suture meets the medial margin of the anterior antorbital at about the middle of the preserved portion of that margin.

The position of the centre of radiation of the two independent nasals of each side could not be determined.

The nasal series is pierced by a portion of the supraorbital lateral line canal. Numerous pores can be seen on its dorsal face, connected with the lateral line canal by highly ramifying tubules, very superficial

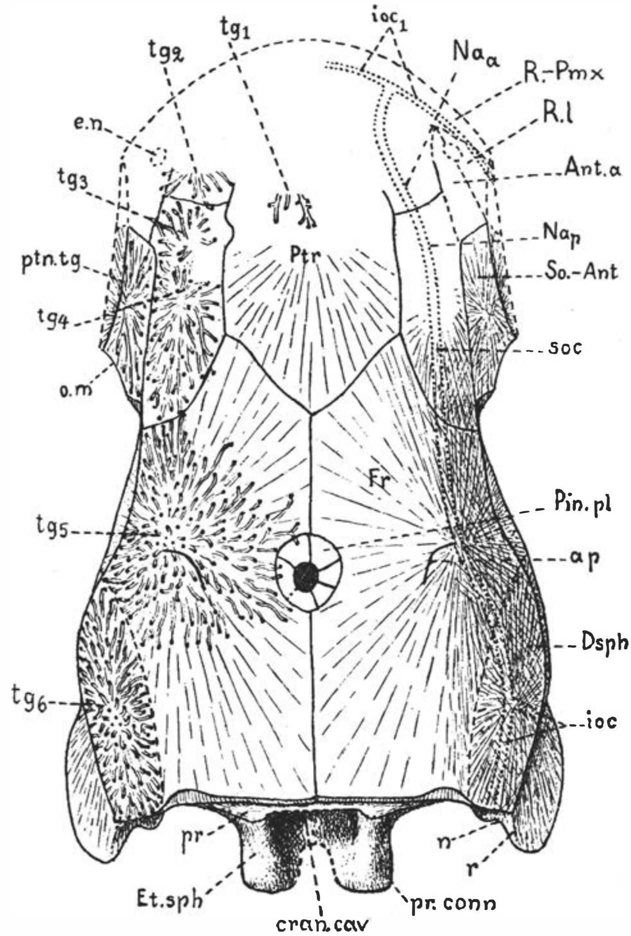

Fig. 6. *Eusthenopteron säve-söderberghi* n. sp. Attempted restoration of the dorsal aspect of the divisio cranialis anterior. × 2 natural size. Anterior part after *E. foordi*. Ornament omitted. Lateral line canals shown only on the right and lateral line tubules and pores only on the left side.

Ant.a, anterior antorbital; *Dsph,* dermosphenotic; *Et.sph,* ethmosphenoid; *Fr,* frontal; Na_a, anterior nasal; Na_p, posterior nasal; *Pin.pl.,* pineal plate; *Ptr,* postrostral; *R.l,* lateral rostral; R.-*Pmx,* rostro-premaxillary; *So.-Ant,* supraorbito-antorbital; *ap,* anterior pit line of the cranial roof; *cran.cav,* cranial cavity; *e.n,* external naris; *ioc,* infraorbital lateral line canal; ioc_1, ethmoidal commissure of the infraorbital lateral line canal; *n,* notch in the posterior margin of the dermosphenotic; *o.m,* antero-dorsal part of the orbital margin; *pr,* blunt process at the posterior end of the roof of the ethmosphenoid; *pr.conn,* processus connectens: *ptn.tg,* group of tubules; probably of the postnasal connection; *r,* ridge separating the overlapped areas *odvIt* and *odvPo* of the dermosphenotic; *soc,* supraorbital lateral line canal; tg_1—tg_6, groups of tubules of the lateral line canals.

distally. The tubules are arranged in three groups (tg_2—tg_4, figs. 4 A, 6), each of which probably represents a highly subdivided primary tube (cf. SÄVE-SÖDERBERGH 1933, p. 87). The most anterior of tubules, of which only the posterior part is preserved, is situated in the anterior fragmentary nasal, while the two remaining groups are rather close to one another in the anterior half of the large posterior nasal.

Of the postrostrals only a large median plate (*Ptr*, figs. 4 A, 6, 7 A) is preserved. Laterally this plate is joined by an undulating suture to the nasal series already described, and posteriorly by a long V-shaped suture to the frontals.

The centre of radiation is situated in the median line in the anterior half of the bone.

It is not traversed by any lateral line canal, but shows lateral line tubules in its most anterior part (tg_1, 4 A, 6). These tubules, which enter the bone from the front, probably belong to a group of tubules situated in the missing anterior part of the nasal series.

The frontal (*Fr*, figs. 4, 5, 6, 7 A, 8) is completely preserved on both sides of the specimen, and can be fully seen from above, from behind and partly also from below and from the side. In front it rests on the posterior margin of the posterior nasal, and is supported behind this overlapping portion by the hinder ends of the processes supraorbitalis lateralis and medialis. Medially and posteriorly it rests on the roof of the orbitotemporal region. The part of the frontal that does not rest on other bones shares directly in forming the orbital roof.

In the median line each frontal is joined to its fellow of the other side in a straight suture, interrupted by the pineal plates. The part of this suture in front of the pineal plates is about $^3/_5$ of the part of the same suture behind these plates. In front the frontal is joined by sutures to the postrostral and the posterior nasal, as already said. Its antero-lateral corner also meets the supraorbito-antorbital, but only ventrally, whereas dorsally it is separated from that bone by the posterior nasal (see fig. 5 C). Laterally it has met the posterior supraorbital, but that bone is now missing. Postero-laterally it is intimately joined to the dermosphenotic in a fairly long, probably almost straight suture, which can be traced only on the ventral face of the fronto-ethmoidal shield. Its posterior margin is transverse and practically straight. This margin does not reach quite as far back as the roof of the ethmosphenoid, and accordingly leaves a posterior, narrow strip of the roof of that bone uncovered (figs. 4 A, 6) but that strip was overlapped by the parietal shield.

The frontal shows the following overlapped and overlapping areas. Along its lateral margin a depressed area, facing dorso-laterally, is found. This area (od_2So, figs. 4 A, 5 A, 5 C, 7 A), which is devoid of ornament and rather rough, was overlapped by the posterior supraorbital. The area decreases in width forward, and forms a posterior continuation of the unornamented area (od_1So) at the posterior end of the supraorbito-antorbital. Another area, devoid of ornament and overlapped by the parietal shield, is found along the posterior margin of the frontal. This area consists of a medial, very narrow part (*odPa*, figs. 4 A, 5 B, 7 A), probably overlapped by the parietal, and a lateral somewhat broader part (od_dIt), overlapped by the intertemporal (og_dFr, fig. 7 E). It has already been mentioned that the frontal overlaps the posterior nasal and the supraorbito-antorbital. Postero-laterally on its ventral face, a well-defined area (og_1Po, figs. 4 B, 7 A, 8) overlaps the postorbital, and a small area (*og.So*, fig. 7 A) finally overlaps the posterior supraorbital. This latter area is the ventral face of a narrow edge (the posterior part of *l.og.So*, fig. 5 C) overhanging the anterior part of the area od_2So, (figs. 5 A, 5 C, 7 A) along the lateral margin of the frontal, and continued in front by a correspondingly developed edge along the adjacent part of the lateral margin of the posterior nasal (fig. 5 C).

The centre of radiation in the frontal is slightly antero-laterally of the centre of the bone.

The groove for the anterior pit line (*ap*, figs. 4 A, 5 A, 6, 7 A) is approximately in the middle of the dorsal face of the frontal. This groove begins in front near the centre of radiation, runs almost medially at first, and then turns sharply backwards, ending laterally of the hinder margin of the pineal foramen, midway between that foramen and the lateral margin of the frontal.

The anterior $^2/_3$ of the frontal are traversed by the supraorbital lateral line canal (*soc*, fig. 6). This canal goes through the centre of radiation and produces a low indistinct ridge (*r.soc*, figs, 4 B, 8) on the ventral face of the bone. Numerous lateral line pores are found in an area situated slightly in front of the middle of the bone. The tubules (tg_5, fig. 6) leading from these pores to the supraorbital canal all seem to join that canal approximately at the centre of radiation of the bone. The highly ramified system of tubules seems likely to come from a single subdivided primary tube. On the ventral face of the frontal a few foramina are to be noted (fig. 4 B), two of which (f_1, 4 B, 8) are situated close to the ridge *r.soc* (figs. 4 B, 8) a little behind the centre of radiation, Both these foramina lead into the lateral line canal from behind. One of them probably transmitted a branch of the ramus ophthalmicus lateralis, while the other probably gave passage to some vessels.

The dermosphenotic (*Dsph*, figs. 4, 5 A, 5 B, 6, 7 A—D, 8) forms the postero-lateral part of the fronto-ethmoidal shield. As it lies entirely to one side of the ethmosphenoid, the whole of it takes a direct part in the formation of the orbital roof. In shape it is roughly triangular. Its lateral part, originally connected with the dermal bones of the cheek, is gently bent down. Posteriorly, it is extended behind the posterior margin of the frontal, ending there in a rounded corner. Anteriorly there is a pointed end opposite the pineal foramen. Its antero-medial margin is intimately joined to the frontal by the fairly straight suture already described. There are also a short postero-medial and a rather long lateral margin, both of which are rather irregular and not coalesced with the adjacent bones.

Only the antero-medial part of the dermosphenotic is ornamented. Some overlapped areas are found along its lateral and posterior margins, and will now be considered.

The largest of these areas, od_vPo (figs. 4 A, 5 A, 5 B, 7 A, 7 C, 7 D) is situated along the lateral margin, and was overlapped by the postorbital. It faces dorso-laterally, and is much longer than broad. Its posterior part is rather wide and smooth, and wholly visible in dorsal view. Its anterior part, on the other hand, is narrow and uneven (see fig. 5 A), overhung by a dorsal lip *l.og.Po* (fig. 7 C) of the bone, and is not — or only partly — visible there in dorsal view. A groove is thus formed between it and this overhanging lip. In this groove in the lateral margin of the bone (figs. 5 A, 7 C) a ventral lip (fig. 7 C) of the dorso-medial edge of the postorbital was inserted; and at the bottom of the groove the infraorbital lateral line canal (*ioc,* fig. 7 C) entered the bone from the postorbital through a foramen (*ioc,* fig. 5 A).

A second overlapped area of the dermosphenotic, od_3So (figs. 4 A, 5 A, 7 A), is found along the anterior part of the lateral margin. It is on a higher level than the area, od_vPo, just described. In front it is continuous with the overlapped area od_2So (figs. 4 A, 5 A, 7 A) along the lateral margin of the frontal, and — like the latter — was probably overlapped by the posterior supraorbital.

On the right dermosphenotic of the specimen available there is a third overlapped area od_dPo (figs. 5 A, 7 A—B). This area is a posterior continuation of the area od_3So, and occupies the lateral part of the dorsal face of the lip *l.og.Po* (fig. 7 C) overhanging the area od_vPo. Most probably it was overlapped by an upper lip (*d.l,* figs. 7 B, 7 C) of the postorbital.

Finally, there is a fourth overlapped area, od_vIt (figs. 4 A, 5 B, 7 A) along the postero-medial margin of the dermosphenotic. This area is smooth and rather small, and was overlapped by the area og_vDsph (fig. 7 E) of the intertemporal. It consists of a lateral part sloping ventro-medially from a ridge *r* (figs. 4 A, 5 A, 5 B, 6, 7 A), which separates it from the area od_vPo, and a medial, horizontal part. The latter part has a lateral notch (*n*, figs. 4, 5 B, 6, 7 A) in its hinder margin, and is in front overhung by a posterior dorsal lip of the bone, the extent of which is indicated by a thick line of dashes on figure 7 A (og_dIt). Another groove, though rather shallow, is thus formed in the posterior margin of the bone. A part of the anterior end of the intertemporal (denoted od_1Dsph on fig. 7 E) fitted into this groove, in the bottom of which there is a foramen (*ioc,* fig. 5 B) through which the infraorbital lateral line canal left the dermosphenotic to enter the intertemporal.

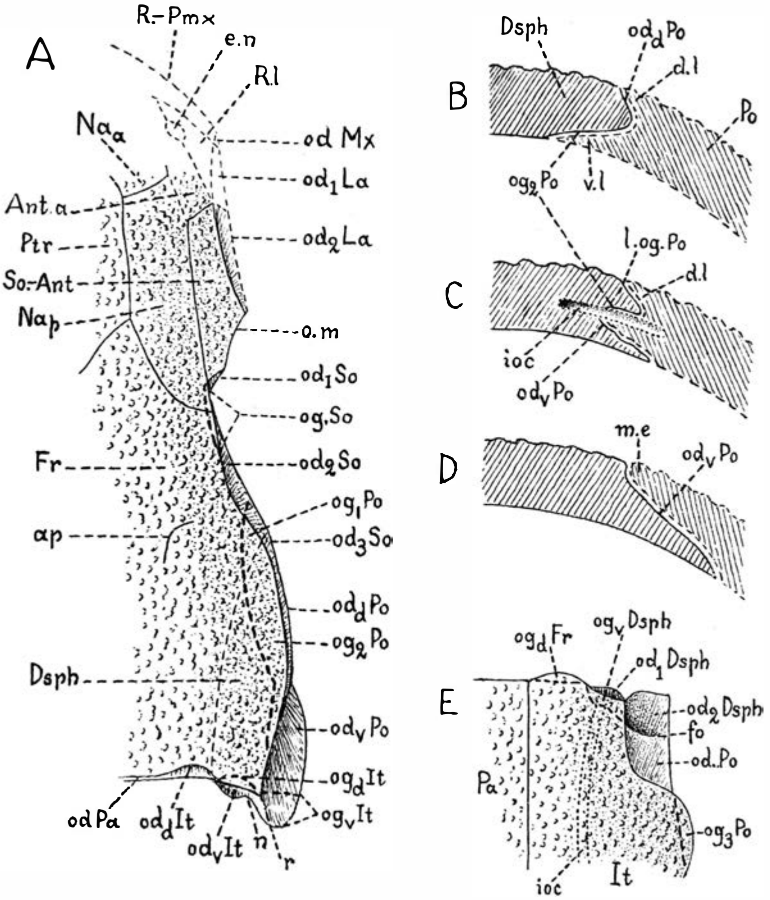

Fig. 7 A, *Eusthenopteron säve-söderberghi* n. sp. Right side of the fronto-ethmoidal shield shown in fig. 6. Showing ornament and overlapped areas; overlapping areas indicated by thick lines of dashes. × 2. Fig. 7 B—D. *Eusthenopteron säve-söderberghi* n. sp. Transverse sections through B, — the anterior, C, — the middle, D, — the posterior part of the lateral part of the dermosphenotic. Adjacent margin of the postorbital restored. × 4.

Fig. 7 E. Attempted restoration of the antero-lateral part of the parietal shield. Anterior margin and ornament after *Eusthenopteron säve-söderberghi*. Other particulars after *E. foordi*. × 2.

Ant.a, anterior artorbital; *Dsph*, dermosphenotic; *Fr*, frontal; *It*, intertemporal; *Na_a*, anterior nasal; *Na_p*, posterior nasal; *Pa*, parietal; *Po*, postorbital; *Ptr*, postrostral; *R.l*, lateral rostral; *R.-Pmx*, rostro-premaxillary; *So.-Ant*, supraorbito-antorbital; *ap*, anterior pit line of the cranial roof; *d.l*, dorsal lip of the postorbital overlapping the dermosphenotic; *e.n*, external naris; *fo*, fold on the intertemporal, overlapping the most posterior end of the dermosphenotic; *ioc*, infraorbital lateral line canal; *l.og.Po*, lip of the dermosphenotic, overlapping the postorbital; *m.e*, edge of the postorbital overlapping the dermosphenotic; *n*, notch in the posterior margin of the dermosphenotic; *od.Mx*, area of the rostro-premaxillary, overlapped by the maxillary; *od.Pa*, area of the frontal, overlapped by the parietal; *od.Po*, area of the intertemporal, overlapped by the postorbital; *od_dIt*, area of the frontal, overlapped by the intertemporal; *od_dPo*, dorsal area of the dermosphenotic, overlapped by the postorbital; *od_vIt*, ventral area of the dermosphenotic, overlapped by the intertemporal; *od_vPo*, ventral area of the dermosphenotic, overlapped by the postorbital; *od_1Dsph*, medial, ventral area of the intertemporal, overlapped by the dermosphenotic; *od_1La*, area of the lateral rostral, overlapped by the lachrymal;

The overlapping areas of the dermosphenotic are as follows: The most important (og_2Po, figs. 4 B, 7 A—C, 8), which overlapped the postorbital, occupies the entire ventral face of the dorsal lateral lip (*l.og.Po*, (fig. 7 C) of the bone that overhangs the area od_vPo, in front of which it also continues — visible in ventral view — as an impression (og_2Po, figs. 4 B, 8) traceable also on the adjacent part of the frontal (og_1Po, figs. 4 B, 8). Another area (og_dIt, fig. 7 A) is fairly small and probably overlapped the intertemporal (od_1Dsph, fig. 7 E). It is situated on the ventral face of the posterior dorsal lip of the bone overhanging the area od_vIt. Finally, judging by the conditions in *Eusthenopteron foordi*, the posterolateral part of the bone (og_vIt, fig. 7 A) certainly overlapped to a considerable extent (od_2Dsph, fig. 7 E) the large depressed area at the anterolateral corner of the intertemporal.

The centre of radiation in the dermosphenotic is near the centre of the bone.

The dermosphenotic lodges the most posterior portion of the supraorbital lateral line canal (*soc*, fig. 6). This canal enters the bone at its antero-medial margin and goes to the centre of radiation, where it joins the infraorbital lateral line canal (*ioc*, fig. 6). This latter canal (*ioc*, figs. 5 A, 7 C) enters the bone in the bottom of the groove at its lateral margin, as described above. From there it runs through the centre of radiation, joins the supraorbital canal, and then turns sharply backwards, to open in the bottom of the groove at the posterior end of the bone (*ioc*, fig. 5 B). Numerous lateral line pores are spread over the ornamented face of the dermosphenotic. The pores are found in a defined area probably representing its whole ornamented face, and on the restorations, figs. 6, 7 A, the suture between the dermosphenotic and the frontal has accordingly been drawn approximately at the antero-medial limit of this area. All the tubules (tg_6, fig. 6) connecting the pores with the lateral line canals appear to converge towards the centre of radiation. On the ventral face of the dermosphenotic some small foramina (f_2, figs. 4 B, 8) are found,

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od_1So, area of the supraorbito-antorbital, overlapped by the posterior supraorbital; od_2Dsph, lateral ventral area of the intertemporal, overlapped by the dermosphenotic; od_2La, area of the supraorbito-antorbital, overlapped by the lachrymal; od_2So, area of the frontal, overlapped by the posterior supraorbital; od_3So, area of the dermosphenotic, overlapped by the posterior supraorbital; *og.So*, extent of the area of the posterior nasal and the frontal, overlapping the posterior supraorbital; og_dFr, extent of the area of the intertemporal overlapping the frontal; og_dIt, extent of the area of the dermosphenotic overlapping the intertemporal; og_vDsph, extent of the area of the intertemporal overlapping the area od_vIt, of the dermosphenotic; og_vIt, extent of the area of the dermosphenotic overlapping the area od_2Dsph of the intertemporal; og_1Po, extent of the area of the frontal overlapping the postorbital; og_2Po, extent of the area of the dermosphenotic overlapping the postorbital; og_3Po, extent of the area of the intertemporal overlappning the postorbital; *o.m*, antero-dorsal part of the orbital margin; *r*, ridge separating the overlapped areas od_vIt, and od_vPo of the dermosphenotic; *v.l*, ventral lip of the postorbital.

some of which most probably transmitted branches of nerves and vessels supplying the lateral line canals.

The oval pineal foramen is surrounded by a number of small bones, the pineal plates. Judging from the sutures, only five independent plates of this sort are present (*Pin.pl*, fig. 4 A), but the fairly long plate on the left side of the foramen may conceivably be composed of two plates, though I have not been able to find any separating suture. There are thus most probably six pineal plates (*Pin.pl*, fig. 6), the same number as in *Eusthenopteron foordi*. The plates increase in size forwards (cf. fig. 18). Two rather large anterior plates meet here in a median suture, while *Eusthenopteron foordi* has a large anterior median plate. All the plates are ornamented in the same manner as the other dermal bones, and some lateral line tubules extending into them from the frontal open with pores on their dorsal face. The pineal plates are beyond any doubt dermal bones and have nothing to do with sclerotic plates (which in *Eusthenopteron foordi* are thin, elongated bony plates, very finely striated on part of their outer surfaces). The tuberculated ridges found on the pineal plates of *Diplopterax* (JAEKEL 1903, pp. 37—38, cf. also EDINGER 1929, p. 201), and on the rhombic area surrounding the pineal foramen of *Osteolepis macrolepidotus* (SÄVE-SÖDERBERGH 1933, pp. 54, 70, 114; pl. 10, figs. 1, 3; pl. 13, fig. 2) are most probably due to a partial (SÄVE-SÖDERBERGH 1933, pp. 54, 70) or complete (WESTOLL 1936, pp. 166—170) resorbtion of a cosmine sheet, originally continuous in these forms.

e. Dermal bones of the lower side of the ethmosphenoid. The paired vomer (Vo, figs. 4, 5 A, 8) is almost completely preserved on both sides, lacking only its most anterior part (the anterior half of the left vomer could not be removed from the stone, in which the fronto-ethmoidal shield originally was embedded, and is therefore not visible on the photograph, fig. 4 B). As its dorsal face is attached to the ventral face of the ethmoidal region of the ethmosphenoid, the vomer is only exposed in ventral view.

Each vomer is a roughly triangular bone with an anterior transverse margin, a latero-posterior free margin, and a medial rather long margin sutured to the parasphenoid. Its most anterior portion, badly or not at all preserved in the present specimen, probably met its fellow on the other side in a median suture, as in *Eusthenopteron foordi* and *E. wenjukowi* (see below, p. 106, and figs. 15, 16). The most anterior part preserved has a transverse vertical lamina (*tr.l*, figs. 4 B, 8) bearing a row of small teeth (*vot*, fig. 8) along its ventral edge. Laterally this lamina curves backwards. Just behind this lamina a large tusk is attached to the bone, and close to that tusk there is a rather large pit (*p.rt*, fig. 8), probably for a replacement tooth. This pit very likely also received the most anterior coronoid tusk as it does in *E. foordi*. In the left vomer the tusk is near

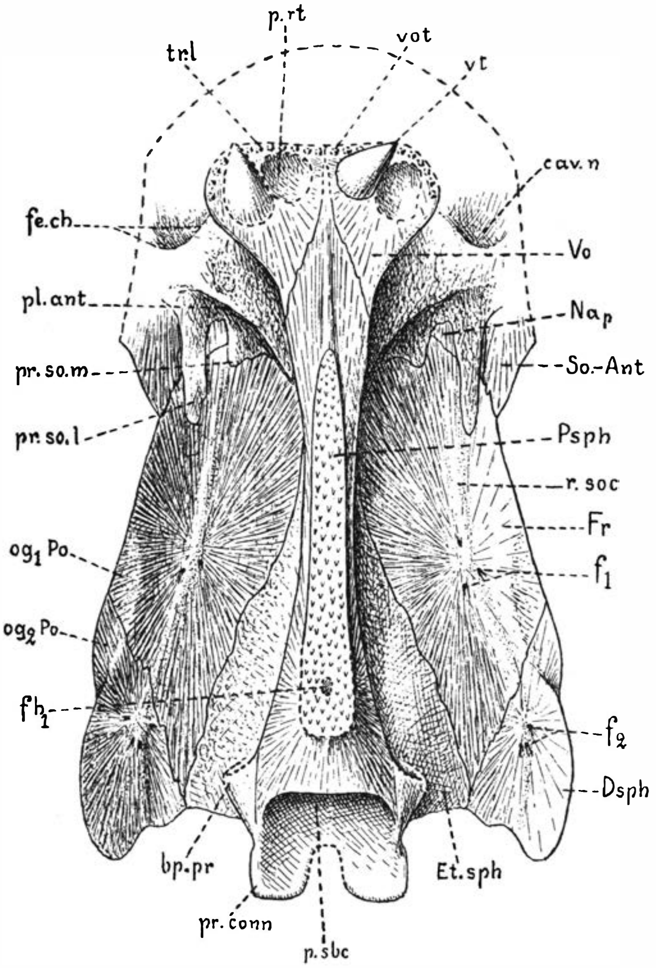

Fig. 8. *Eusthenopteron säve-söderberghi* n. sp. Ventral aspect of the divisio cranialis anterior. × 2. Mainly from the holotype, partly restored. The basipterygoid processes and the anterior part of the outline from *E. foordi*.

Dsph, dermosphenotic; *Et.sph,* ethmosphenoid; *Fr,* frontal; *Nap,* posterior nasal; *Psph,* parasphenoid; *So.-Ant,* supraorbito-antorbital; *Vo,* vomer; *bp.pr,* basipterygoid process; *cav.n,* cavum nasi; *fe.ch,* fenestra choanalis; f_1, f_2, foramina transmitting nerves and vessels supplying the lateral line canals; fh_1, opening of the fossa hypophyseos on the ventral face of the parasphenoid; og_1Po, area of the frontal, overlapping the postorbital; og_2Po, area of the dermosphenotic, overlapping the postorbital; *pl.ant,* planum antorbitale; *pr.conn,* processus connectens; *pr.so.l,* processus supraorbitalis lateralis; *pr.so.m,* processus supraorbitalis medialis; *p.rt,* pit of the vomer for a replacement tusk, but also receiving the tusk of the coronoid I; *p.sbc,* pit in the posterior face of the ethmosphenoid representing the most anterior part of the fossa subchordalis; *r.soc,* ridge caused by the supraorbital lateral line canal; *tr.l,* transverse, tooth-bearing lamina of the vomer; *vot,* tooth of this lamina; *vt,* vomerine tusk.

the medial margin, and the pit lateral to it, whereas the positions of tusk and pit are reversed in the right vomer. The left vomerine tusk, the only one preserved, is straight, slender, and smooth, being only slightly striated at the base. It is almost round in section, with rather indistinct cutting edges.

The centre of radiation in the vomer is situated above the lateral tusk (or pit).

The parasphenoid (*Psph*, figs. 4 B, 5 A, 8) is almost complete, lacking only the extreme anterior and posterior parts of its ventral, tooth-bearing ridge. Its front end is wedged between the vomeres, and ends just dorsally of the transverse lamina at the anterior end of the preserved part of the vomeres. The part between these bones is nothing but a thin, posteriorly broadening lamina, which covers the median part of the ventral face of the ethmoidal region. Further back, underneath the ventral wall of the orbito-temporal region of the endocranium, its dorsal face is gutter-shaped and increases in width. Its dorso-lateral edges support the basipterygoid processes. Posteriorly it ends abruptly with a transverse margin just ventrally of the posterior margin of the large pit (*p.sbc*, figs. 4 B, 5 B, 8) on the posterior face of the ethmosphenoid. Ventrally it is provided with a median elevated area, which begins in front between the vomeres and ends posteriorly a little in front of posterior margin of the bone. Except anteriorly and most posteriorly, where this elevated area is sharp and narrow, its ventral face is flattened and furnished with fine denticles. The ventral opening of the fossa hypophyseos (fh_1, fig. 8; cf. above p. 73) was probably situated in the median line of this tooth-bearing area, near its posterior end.

The centre of radiation of the parasphenoid is situated near the posterior end of the bone.

f. The lower jaw. The preserved part of the lower jaw has been almost completely cleaned from all sides, but is compressed to such an extent that very few of its details can be studied.

The Meckelian bone (*Mb*, fig. 9 B) is visible only at the bottom of the posterior part of the adductor fossa (*ad.f*, figs. 9 A, 9 B), but nothing can be said of its shape or size.

The dentary (*De*, figs. 9 A—D) is a long bone, increasing in height forward. Its dorsal, oral edge, which is visible also on the lingual side, is smooth and rounded posteriorly, laterally of the posterior part of the adductor fossa; anteriorly it is thickened and carries teeth (*det*, figs. 9 B, 9 C; omitted in the restoration fig. 9 D), of which, however, in their present state of preservation nothing but their bases remain. Downwards the dentary is joined to the series of infradentaries by a suture, which is indistinct anteriorly, but clearly traceable posteriorly. The outer face of the dentary is ornamented, except for its most posterior part, where there is a smooth area devoid of ornament. This area (*od.Quj*, figs. 9 A, 9 D) was overlapped by the quadratojugal when the mouth was closed.

The centre of radiation of the dentary is situated near the anterior end of the bone.

Of the four bones of the infradentary series (figs. 9 A, 9 C, 9 D) the postsplenial (*Ptsp*) and the angular (*Ang*) are well preserved, while the two others, the splenial (*Sp*) and the supraangular (*Sang*), are both imperfect. The suture between the splenial and the postsplenial is distinct only on the medial side, while the sutures between the other infradentaries can be clearly seen from the outside. The lower margins of the supraangular, angular, and the posterior half of the postsplenial form an area rather broad towards the back (*od.Br.r,* fig. 9 A) and devoid of ornament. This area faced ventrally when the jaw was in its natural position, and was overlapped by the branchiostegal rays. In its most posterior part it is partly roofed over by a lateral lip of the postero-ventral corner (*og.l,* fig. 9 A) of the supraangular. The anterior half of the dorsal margin of the hindmost branchiostegal ray was probably inserted in the furrow thus formed.

The centre of radiation in the supraangular is in the posterior third of the bone, whereas in the angular, postsplenial, and splenial the centres seem to be approximately in the centre.

The coronoids (probably three in number, Co I, Co II, Co III, figs. 9 C) are much compressed. The hindmost of them cover the anterior parts of the adductor fossa (*ad.f,* figs. 9 A, 9 B); in front they probably rest on the Meckelian bone, as they do in *Eusthenopteron foordi* and *Eusthenopteron wenjukowi* (see below, p. 111). Laterally the coronoids are attached to the upper part of the medial face of the dentary, medially to the prearticular. The dorsal part of the lateral margins of the coronoids are free, unconnected with the dentary, and provided with a row of rather small teeth (*cot,* figs. 9 A, 9 C, 9 D) only partly preserved. Medially of this free tooth-bearing margin the large coronoid tusks are attached. Of these tusks (ct_1—ct_4, figs. 9 A—D), four in number, only the two centre ones are wholly preserved. The anterior of these (ct_2) is rather large and pointed, its apex curving slightly inwards, whereas the posterior tusk (ct_3) is shorter, straight, and obtuse. Both these tusks are striated only at the base, and both are provided with two cutting edges.

The prearticular (*Prart,* figs. 9 A—C) is the main bone of the inner face of the lower jaw. Its anterior portion is attached dorsally to the coronoids; posteriorly it forms the medial wall of the adductor fossa (*ad.f,* figs. 9 A, 9 B); and there its free upper edge is rounded. Ventrally it meets and is sutured to the infradentaries. In front this suture runs along a narrow ridge (*re,* fig. 9 C), which forms the ventral border of a groove along the ventral margin of the prearticular. At the bottom of this groove there are two small foramina (f_a, f_p, fig. 9 C) probably transmitting nerves or vessels.

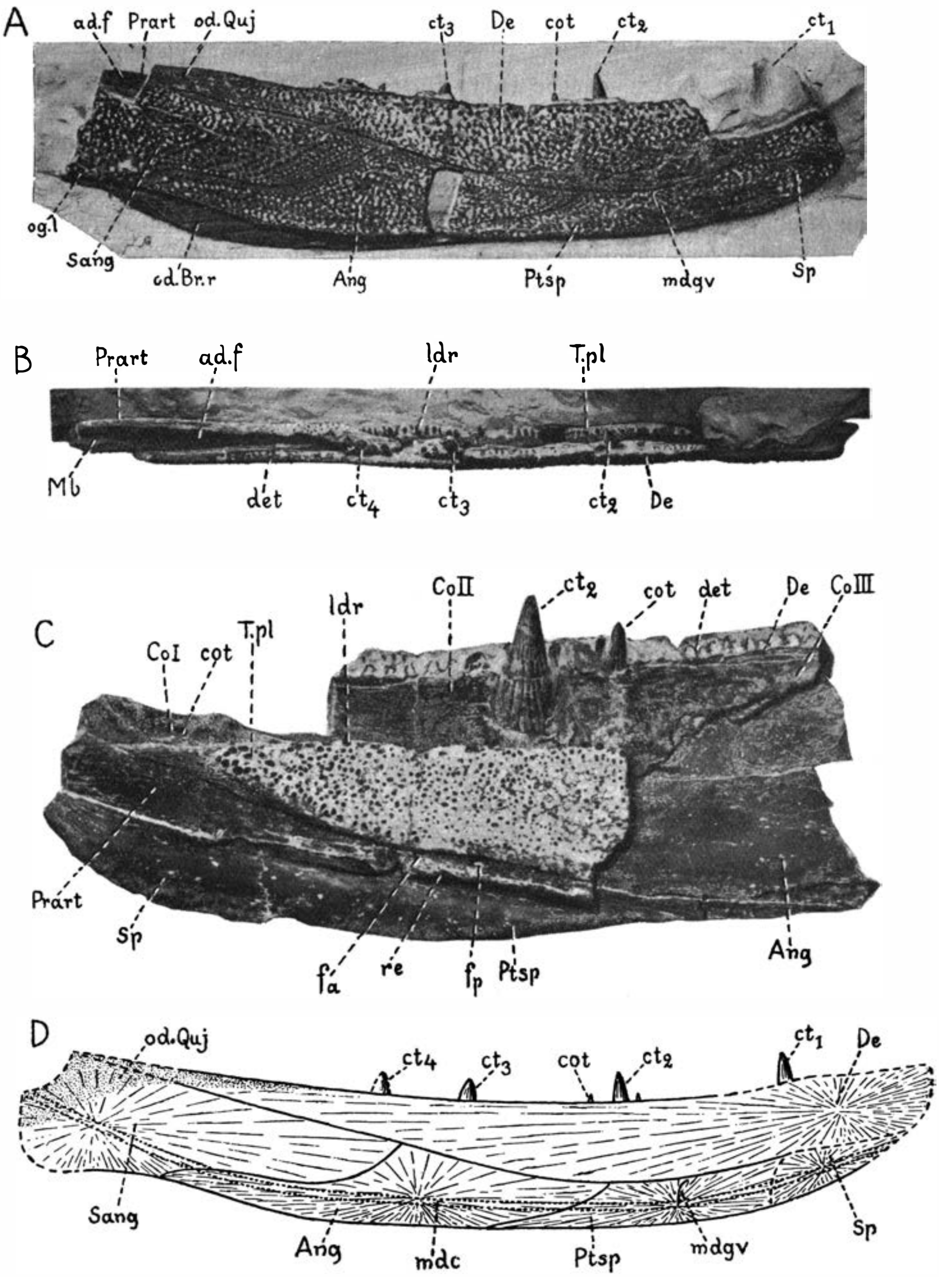

Fig. 9. *Eusthenopteron säve-söderberghi* n. sp. A—C, imperfect right ramus of the lower jaw. A, lateral aspect, × $^{6}/_{5}$; B, dorsal aspect, × $^{6}/_{5}$; C, medial aspect of the anterior half, × $^{12}/_{5}$. Photographed in xylol. Specimen in the Paleontological Institute, Uppsala; figured by GROSS 1936, Abb. 9, Fig. 3. D, attempted restoration of the lateral aspect of the right ramus of the lower jaw. × $^{6}/_{5}$. Ornament, teeth of the dentary, and most teeth of the coronoids omitted. From the above specimen, but most anterior and most posterior parts from *E. foordi*.

Except in its anterior part, the medial face of the prearticular is covered by an independent bony plate (*T.pl,* figs. 9 B, 9 C), not hitherto recorded as found in any Crossopterygian, but found also in *Eusthenopteron wenjukowi* (see below on p. 112). The anterior part of the medial face of this bony plate (excepting the most anterior portion, which is smooth) is covered with closely set denticles, apparently replaced posteriorly by low anastomosing ridges.[1] Along its dorsal margin the plate bears a row of somewhat larger denticles (*ldr,* figs. 9 B, 9 C; a similar row of teeth along the dorsal margin of the prearticular has been described by GROSS, 1933, p. 53; Abb. 29, in »*Polyplocodus*» *rhombolepis*). The plate ends in a point anteriorly, only slightly behind the most anterior coronoid tusk. It thus reaches further forward in the present species than in »*Polyplocodus*» *rhombolepis*[2], where, judging by GROSS's restoration (1933, Abb. 29) there is probably a similar plate.

Several lateral line pores are found on the ventral part of the outer face of the infradentaries. These pores certainly belong to the mandibular lateral line canal (*mdc,* fig. 9 D), which traverses all the infradentaries. This canal is not shown, however, but the tubules leading from it to the pores are partly dicernible. The horizontal part of the mandibular pit line (see SÄVE-SÖDERBERGH 1933, p. 92) can not be seen, but might have been situated in the groove laterally of the suture between the dentary and the infradentaries. The transverse, vertical part (*mdgv,* figs. 9 A, 9 D) of that pit line, on the other hand, is present. It is situated in the postsplenial, where it crosses the centre of radiation.

Remarks. — *Eusthenopteron säve-söderberghi* is distinguished from *E. foordi* by the following characteristics: A closer arrangement of the tubercles on the external face of the dermal bones (cf. figs. 3 A and 3 B); a greater extension backwards of the nasal series; the presence of a short

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[1] Such ridges also occur in Coelacanthids (cf. STENSIÖ 1922 b, p. 191).

[2] As has been said above (p. 69) the genus name *Polyplocodus* should not be used. As the fragments of the lower jaw described by GROSS as »*Polyplocodus*» *rhombolepis* differ considerably from the lower jaw of *Eusthenopteron,* as well as from the jaw described by GROSS as »*Dendrodus biporcatus*», they most probably belong to a genus of their own, a new name for which must be introduced.

Ang, angular; *Co I,* coronoid I; *Co II,* coronoid II; *Co III,* coronoid III; *Dc,* dentary; *Mb,* Meckelian bone; *Prart,* prearticular; *Ptsp,* postsplenial; *Sang,* supraangular; *Sp,* splenial; *T.pl,* tooth-bearing plate of the medial face of the jaw; *ad.f,* adductor fossa; *cot,* coronoid teeth; *ct*$_1$, the tusk of the coronoid I; *ct*$_2$, the tusk of the coronoid II; *ct*$_3$, *ct*$_4$, the tusks of the coronoid III; *det,* the bases of the dentary teeth; *fa, fp,* foramina probably transmitting nerves or vessels; *ldr,* row of larger denticles along the dorsal margin of the tooth-bearing plate; *mdc,* mandibular lateral line canal; *mdgv.* vertical part of the groove for the mandibular pit line; *od.Br.r,* areas of the postplenial, angular, and supraangular, overlapped by the branchiostegal rays; *od.Quj,* areas of the dentary and supraangular, overlapped by the quadratojugal; *ogl,* lip of the supraangular, overlapping the hindmost branchiostegal ray; *re,* ridge along the suture between the postplenial and prearticular.

suture between the most posterior part of the nasal series and the most anterior part of the posterior supraorbital; a shorter (about $^4/_5$ of the length in *E. foordi*) supraorbito-antorbital, (and a correspondingly lengthened posterior supraorbital); and larger and somewhat differently arranged pineal plates.

Geological horizon and locality. — Lowermost Upper Devonian; the *Bothriolepis cellulosa* marl at Kokenhusen, Livonia.

2. Eusthenopteron wenjukowi (ROHON, 1889).

(figs. 10—17.)

1880. *Dendrodus biporcatus,* TRAUTSCHOLD *(errore)* pp. 139—145, Tafel 3—5.
1883. *Dendrodus,* TRAUTSCHOLD *(errore)* p. 164.
1889. *Dendrodus biporcatus,* ROHON *(errore)* p. 49, Tafel 1, figs. 1, 5, 9.
1889. *Cricodus (Polyplocodus) wenjukowi,* ROHON p. 49, Tafel 1, figs. 3, 4, 6, 11.
1890. *Cricodus,* TRAUTSCHOLD p. 621, Tafel 23, 24, 25, figs. 1—5, 6?, 7.
1891. *Cricodus wenjukowi,* WOODWARD p. 363.
1930. *Polyplocodus wenjukowi,* OBRUTSHEV p. 93.

The jaw-fragment, teeth, and scales described by GROSS (1933, p. 54, Tafel 6, figs. 6—8, 16) as *Polyplocodus wenjukowi* are indeterminable, and have therefore not been included in the above list of synonymes.

Diagnosis. — *Eusthenopteron wenjukowi* is imperfectly known, and can therefore not be well defined. The diagnosis at present possible is as follows: Fish of large size. Total length of head in the median line about 250 mm, and total length of fronto-ethmoidal shield about 135 mm. Ethmosphenoid well ossified; lateral wall of the nasal capsule almost complete, with only a fairly small fenestra narina. Crista suspendens strongly developed. The posterior opening of the intervomerine canal developed into a median slit, behind which the vomeres meet in a short median suture. Ornament consists of closely set tubercles, very often united to form vermiculating ridges.

Material. — I have at my disposal the three specimens figured by ROHON on Tafel 1, figs. 1, 5, 9; 3; and 11. One of these (figs. 12, 14, 15 below) consists of the very well preserved anterior part of the divisio cranialis anterior. Another of them (figs. 10, 11), also consists of the corresponding part of the cranium, but is not preserved as far back as the first specimen, and is moreover flattened. The third specimen (fig. 17), finally, is an anterior, fragmentary portion of the right ramus of the lower jaw. All the specimens are fairly completely cleaned from matrix, which to a large extent was done already by ROHON.

Holotype. — One of the two specimens referred to *Cricodus wenjukowi* by ROHON (1889) must be selected as the holotype of *Eusthenopteron wenjukowi.* Of these I choose the specimen figured by him on Tafel 1, fig. 3 (figs. 10, 11 in the present paper).

Description. — a. General shape. The total length of the preserved part of the most complete specimen (figs. 12, 14, 15) is 105 mm, its maximum width is 65 mm, and its maximum height 50 mm; the total length of the fronto-ethmoidal shield may be estimated at not less than 135 mm; the thickness of the internasal wall is about 25 mm; the distance between the foramina apicalia is about 20 mm. Each vomer is 22 mm broad and 60 mm long. The distance from the ventral edge of the premaxillary to the transverse, vertical, tooth-bearing lamina of the vomeres, i. e. the length of the fossa apicalis, measures 20 mm in the median line.

The holotype is of approximately the same size as the above specimen, and agrees with it in all essentials.

The part preserved of the lower jaw is 45 mm long. The independent tooth-bearing plate on the internal side of the pre-articular ends 23 mm from the tip of the jaw. The total length of the complete jaw may be estimated at about 110 mm, and this jaw fragment therefore certainly belonged to a considerably smaller individual than the holotype (the lower jaw of the latter was probably about 250 mm long).

b. Ornament. The ornament consists of obtuse tubercles, frequently united so as to form a net-work of vermiculating ridges.

c. Endocranium. The part of the endocranium at my disposal consists of approximately the anterior half of the ethmosphenoid (*Et.sph,* figs. 10, 11, 14); more precisely of the ethmoidal and the anterior part of the orbito-temporal region. The ethmoidal region is covered by dermal bones, and is only exposed posteriorly and partly also from the lateral and ventral sides, whereas the remaining part of the orbito-temporal region is only covered by dermal bones ventrally.

The ethmoidal region is formed by the much widened anterior portion of the ethmosphenoid, in the lateral parts of which the nasal capsules are situated. Posteriorly, laterally of the part continuous with the interorbital wall, it ends in a broad; high planum antorbitale.

The upper face of the ethmoidal region is covered by a continuous shield of dermal bones, and therefore cannot be studied. It is clear, however, that it must be sloping downwards both in front and at the sides. Laterally, this slope is almost vertical (figs. 12, 13).

Ventrally the anterior and median parts of the ethmoidal region have a large almost plane face covered by the main part of the vomeres, the most anterior part of the parasphenoid, and the palatal laminae (*pal.l,* figs. 10 B, 15, 16), of the premaxillaries. Between these laminae in front and the vomeres behind is a short but broad area (*v.ar,* figs. 10 B, 15, 16) uncovered by any dermal bones. At each lateral end of this area there is a fairly wide foramen (*f.ap,* figs. 10 B, 15, 16), the foramen apicale (or naso-basale). Postero-laterally of the ventral plane face just described there is a large opening, the fenestra choanalis, (*fe.ch,* figs. 10 B, 11, 15).

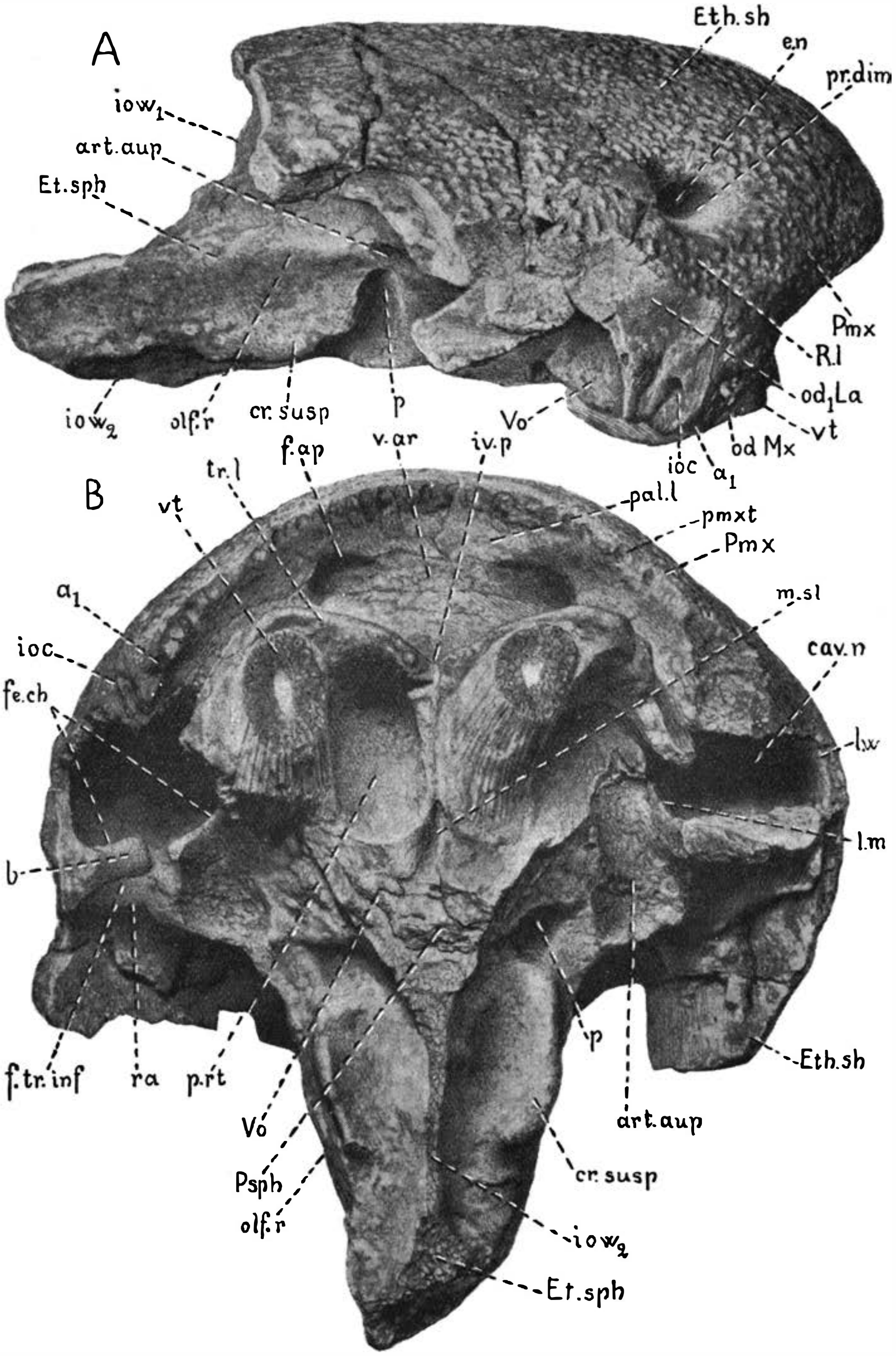

Fig. 10. *Eusthenopteron wenjukowi* (ROHON, 1889). Holotype. Imperfect, anterior part of the divisio cranialis anterior. A, lateral, B, ventral aspect. × $^3/_2$. Photographed in xylol. Specimen in the Geological Institute, Leningrad. Figured by ROHON (1889, Tafel I, fig. 3).

The nasal capsule has a fairly small rounded nasal cavity (or cavum nasi; *cav.n,* figs. 10 B, 11, 15, 16; its extent is indicated by means of red interrupted lines in figs. 13, 16), which is widely separated from that on the other side by a thick solid internasal wall. As this wall is much broader posteriorly than the adjacent thin dorsal and ventral parts of the interorbital wall (iow_1, iow_2, figs. 10, 12, 13, 14), its posterior part extends lateral to the interorbital wall and forms the medial part of the planum antorbitale (inw_1, inw_2, figs. 12, 13). Further forward the internasal wall thickens and decreases in height, and finally merges most anteriorly into the low anterior wall of the nasal capsule. On the concave, posterior face of this anterior wall of the capsule four foramina are found (not shown in any of the figures). The largest of these, situated on the ventro-lateral part of the face, close to the internasal wall and below the processus intermedius (*pr.im,* fig. 11) described below, could in *Eusthenopteron foordi* be shown to be the back opening of a short rostro-caudal canal, the canalis apicalis, the anterior opening of which is the foramen apicale (*f.ap,* figs. 10 B, 15, 16) already described (p. 91). This canal most probably transmitted the distal ends of the r. medialis narium of the n. profundus and vessels. The remaining three foramina are all situated above the processus intermedius. They are smaller than the one described and — as far as can be judged — transmitted branches of nerves and vessels. In this connection an additional, rather wide foramen may be considered. This foramen is lateral to the back opening of the canalis apicalis just described, and separated from it by a low dorso-ventral ridge. It very likely represents the posterior opening of a rostro-caudal canal that in *E. foordi* is enclosed between an inner dorso-ventral lamina of the rostro-premaxillary and the ventral face of the ethmosphenoid excavated in this part, and which probably transmitted the distal branches of the truncus infraorbitalis and its accompanying vessels.

Eth.sh, ethmoidal shield; *Et.sph,* ethmosphenoid; *Pmx,* premaxillary (possibly rostro-premaxillary); *Psph,* parasphenoid; *R.l,* lateral rostral; *Vo,* vomer; *art.aup.* area — devoid of the lining periostal membrane — against which the pars autopalatina abutted; a_1, corner at the posterior end of the premaxillary, forming the most ventral part of the ethmoidal shield; *b,* bar of the planum antorbitale, ventral to the foramen for the truncus infraorbitalis and vessels; *cav n,* cavum nasi; *cr susp,* crista suspendens; *e.n,* external naris; *f.ap,* foramen apicale; *fe.ch,* fenestra choanalis; *f.tr.inf,* foramen, probably transmitting the truncus infraorbitalis and vessels; *ioc,* foramen transmitting the infraorbital lateral line canal; iow_1, dorsal, and iow_2, ventral, thin part of the interorbital wall; *iv.p,* intervomerine pit, conceivably housing the intermaxillary gland; *l.m,* postero-medial part of the fenestra choanalis boundary; *l.w,* lateral wall of the nasal capsule; *m.sl,* median slit between the vomeres, conceivably the opening of the intermaxillary gland; *od.Mx,* area of the premaxillary, overlapped by the maxillary; od_1La, area of the lateral rostral overlapped by the lachrymal; *olf.r,* olfactory ridge; *p,* pit in front of crista suspendens; *pal.l,* palatal lamina of the premaxillary; *pmxt,* remains of premaxillary tooth; *pr.dim,* processus derm-intermedius of the lateral rostral; *p.rt,* pit of the vomer for a replacement tooth, receiving also the most anterior coronoid tusk; *ra,* ridge on the posterior face of the planum antorbitale; *tr.l,* transverse, tooth-bearing lamina of the vomer; *v.ar,* area on the ventral face of the ethmosphenoid not covered by dermal bones; *vt,* vomerine tusk.

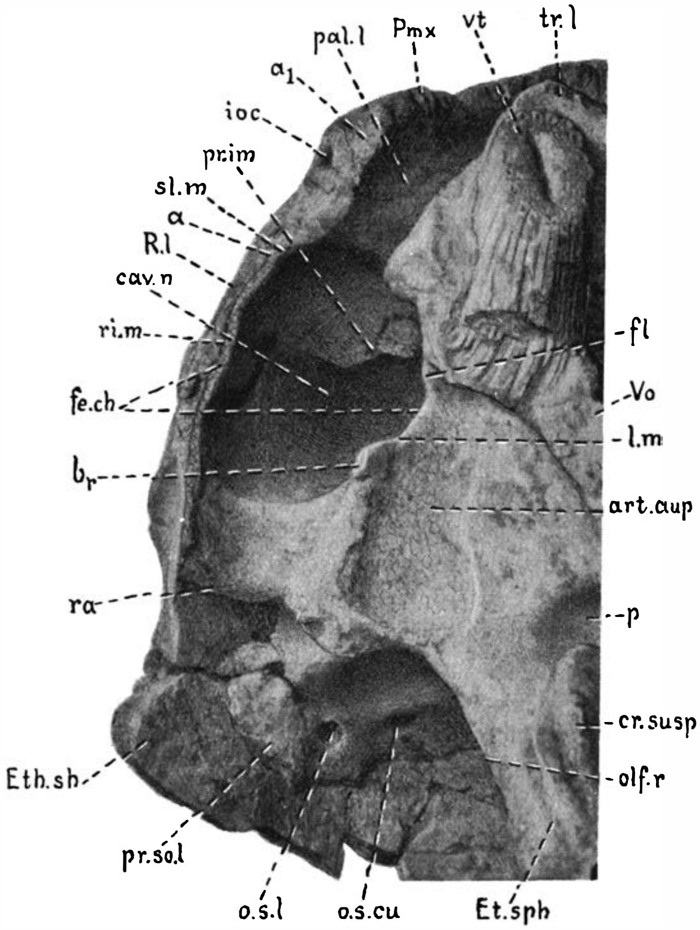

Fig. 11. *Eusthenopteron wenjukowi* (ROHON, 1889). Oblique ventro-posterior aspect of the right side of the holotype, showing the nasal capsule and surroundings. Part of the lateral wall of the nasal capsule and of the bar *(b)* of the planum antorbitale removed. × 2. Photographed in xylol.

Eth.sh, ethmoidal shield; *Et.sph*, ethmosphenoid; *Pmx*, premaxillary; *R.l*, lateral rostral; *Vo*, vomer; *a*, corner of the ventral margin of the lateral wall of the nasal capsule; *art.aup*, area — devoid of the periostal lining membrane — against which the pars autopalatina abutted; a_1, corner of the posterior end of the premaxillary; b_r, remains of the bar of the planum antorbitale; *cav.n*, cavum nasi; *cr.susp*, crista suspendens; *fe.ch*, fenestra choanalis; *fl*, floor of the nasal capsule; *ioc*, foramen transmitting the infraorbital lateral line canal; *l.m*, postero-medial part of the fenestra choanalis boundary; *olf.r*, olfactory ridge; *o.s.cu*, foramen, probably transmitting general cutaneous branches of the r. ophthalmicus superficialis; *o.s.l*, foramen, probably transmitting the r. ophthalmicus superficialis lateralis; *p*, pit in front of crista suspendens; *pal.l*, palatal lamina of the premaxillary; *pr.im*, processus intermedius of the lateral wall of the nasal capsule; *pr.so.l*, the proximal part of the processus supraorbitalis lateralis; *ra*, ridge on the posterior face of the planum antorbitale; *ri.m*, imperfect part of the ventral margin of the lateral wall of the nasal capsule, facing postero-ventrally; *sl.m*, part of the ventral margin of the lateral wall of the nasal capsule, facing antero-ventrally; *tr.l*, transverse, tooth-bearing lamina of the vomer; *vt*, vomerine tusk.

The roof and lateral wall of the nasal capsule, which are complete except for the fenestra narina (see next page), merge in front into the anterior wall of the capsule, and are continuous posteriorly with the dorsal and lateral parts of the planum antorbitale; the roof is in addition continuous dorso-medially with the upper part of the internasal wall. The fairly thin lateral wall (*l.w*, figs. 10 B, 14 A, 15) has a free ventral margin forming the lateral boundary of the large fenestra choanalis *(fe.ch)*. The anterior part of that margin, facing downwards and slightly forwards (*sl.m*, fig. 11; see also figs. 12, 13, where it is in front of the angle denoted *a*), is situated almost on a level with the plane ventral face of the ethmoidal region. Judging from conditions in *E. foordi*, this part of the margin rests in a rostro-caudal groove formed by the lateral rostral and the rostro-premaxillary. The posterior, far longer part of this margin (*ri.m*, figs. 11, 13, 16), imperfect in both specimens at my disposal, forms an obtuse (though nearly right) angle (*a*, figs. 11, 12, 13, 16) with the anterior part of the margin, and rises backwards so as to join the ventro-lateral corner of the planum antorbitale. This part accordingly faces downwards and backwards.

The floor of the nasal capsule is rather incomplete, and only developed medially (*fl*, figs. 11, 14 A). It consists of a narrow horizontal ledge extending laterally from the ventral part of the internasal wall and forming the anterior part of the medial boundary of the fenestra choanalis. The posterior wall of the nasal capsule is made up of the lateral parts of the planum antorbitale described below. Its extent is indicated by a red interrupted line in fig. 13.

The fenestra narina piercing the antero-lateral part of the lateral wall is rather small, oval in shape, and well defined. In *Eusthenopteron foordi*, on the other hand, it is larger and extends further back, a condition, which most probably is due to a less degree of ossification of the lateral wall. Its ventral margin is bent inwards and produced into a blunt process, the processus intermedius (*pr.im*, fig. 11). This process, which is attached to the anterior wall by the proximal part of its anterior margin, has a postero-medial direction. It projects far into the cavum nasi, and divides the anterior part of that cavum incompletely into a dorsal and a ventral space. It corresponds, at least partly, to the crista intermedia in the nasal capsules of the *Anura* (cf. ECKER, WIEDERSHEIM, GAUPP 1896, p. 47).

The planum antorbitale (figs. 12, 13) is separated from its counterpart on the other side by the most anterior portion of the orbito-temporal region, and merges postero-medially, without any boundary line, into that region. The most anterior part of the interorbital wall is thin dorsally and ventrally (*iow*$_1$, *iow*$_2$, figs. 10, 12, 13, 14), but its middle part, which houses the canals for the olfactory nerves, is much thicker. In fact, therefore, the olfactory canals have developed a broad, pronounced ridge on the anterior part of the interorbital wall. This olfactory ridge (*olf.r*, figs. 10—16)

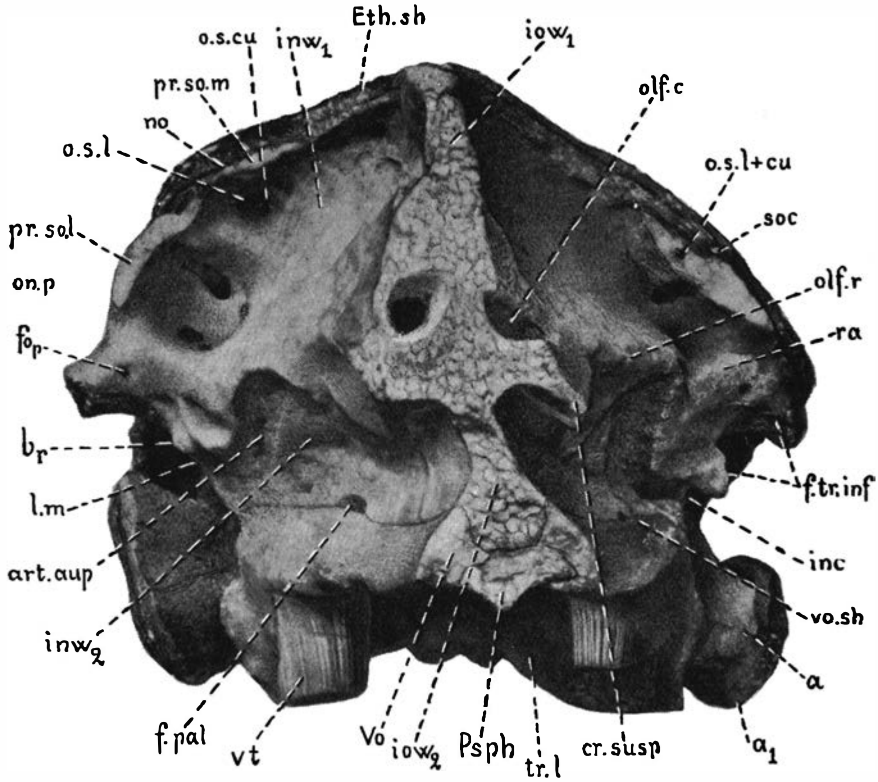

Fig. 12. *Eusthenopteron wenjukowi* (ROHON, 1889). Imperfect, anterior part of the divisio cranialis anterior. Posterior aspect, showing mainly the planum antorbitale. The same specimen as in fig. 14; the posterior parts of the ethmosphenoid and parasphenoid removed. × $^{3}/_{2}$. Photographed in xylol. Specimen in the Geological Institute, Leningrad; figured by ROHON (1889, Tafel I, figs. 1, 5, 9).

Eth.sh, ethmoidal shield; *Psph*, parasphenoid; *Vo*, vomer; *a*, corner of the ventral margin of the lateral wall of the nasal capsule; *art.aup*, area — devoid of the periostal lining membrane — against which the pars autopalatina abutted; *a*$_1$, corner of the posterior end of the premaxillary; *br*, remains of the bar of the planum antorbitale; *cr.susp*, crista suspendens; *fop*, posterior aperture of a canal for a nerve or vessel; *f.pal*, foramen, probably transmitting a branch of the n. palatinus; *f.tr.inf*, foramen, probably transmitting the truncus infraorbitalis and vessels; *inc*, incisure in the ventral margin of the planum antorbitale; *inw*$_1$, dorsal, and *inw*$_2$, ventral part of the posterior face of the internasal wall; *iow*$_1$, dorsal, and *iow*$_2$ ventral thin part of the interorbital wall; *l.m*, postero-medial part of the boundary of the fenestra choanalis; *no*, notch between the processes supraorbitalis lateralis and medialis; *olf.c*, olfactory canal; *olf.r*, olfactory ridge; *on.p*, orbito-nasal pit; *o.s.cu*, foramen, probably transmitting general cutaneous branches of the r. ophthalmicus superficialis; *o.s.l*, foramen, probably transmitting the r. ophthalmicus superficialis lateralis; *o.s.l.* + *cu*, foramen, probably transmitting general cutaneous + lateralis branches of the r. ophthalmicus superficialis; *pr.so.l*, proximal end of the processus supraorbitalis lateralis; *pr.so.m*, proximal end of the processus supraorbitalis medialis; *ra*, ridge on the posterior face of the planum antorbitale; *soc*, supraorbital lateral line canal; *tr.l*, transverse, tooth-bearing lamina of the vomer; *vo.sh*, shelf of the vomer; *vt*, vomerine tusk.

can be traced as far as to the medial part of the back face of the planum antorbitale, where it is almost directly continued by a rounded ridge *ra* (figs. 10 B, 11, 12, 13, 15), which passes slightly upwards and ends at the lateral margin of the planum antorbitale. The olfactory ridge and the ridge *ra* divide the posterior face of the planum antorbitale into a dorsal and a ventral division.

The dorsal division is overhung by a roof projecting backwards from the dorsal margin of the planum antorbitale. This roof, which forms part of the orbital roof, is in front continuous with the roof of the ethmoidal region; postero-medially it merges into the thin lateral edge along the very dorso-lateral margin of the interorbital wall. As shown in figs. 12 and 13 it is distinctly thickened at two places *(pr.so.m, pr.so.l),* in such a way as to make it evident that there was here a processus supraorbitalis lateralis and a processus supraorbitalis medialis (fig. 16) of a type similar to that in *E. säve-söderberghi* (fig. 8), though these processes have been broken on the specimens examined. That the processes were originally present is further supported by the fact that the posterior margin of the roof is unbroken between the thickenings (*no,* figs. 12, 13, 16).

The posterior face of the dorsal division of the planum antorbitale consists of a dorso-medial, smooth, concave area inw_1 (figs. 12, 13), — which is continued backwards in the lateral face of the dorsal part of the interorbital wall — and a ventro-lateral, fairly large pit, the orbito-nasal pit, *on.p* (figs. 12, 13).

The area, inw_1, forms the posterior face of the internasal wall. In the specimen figured (fig. 12) this area has two small foramina (*o.s.l, o.s.cu,* figs. 12, 13) on its left side, both of which are situated in a slight depression separated from the orbito-nasal pit by a small ridge. The lateral of these foramina probably transmitted the anterior portion of the lateralis branches of the r. ophthalmicus superficialis, while the medial foramen probably gave passage to the general cutaneous portion of the same nerve. On the corresponding area (inw_1) of the right side, on the other hand, there are no foramina at all. The anterior portions of the r. ophthalmicus superficialis must have entered the ethmoidal region there through a common foramen situated on the posterior, broken margin of the roof (*o.s.l.* + *cu,* figs. 12, 13) in the processus supraorbitalis lateralis, a disposition which is also found in *Eusthenopteron foordi.* Intermediate conditions of position and development of the foramina just described are shown in the specimen depicted in fig. 11.

The orbito-nasal pit *(on.p)* is in the thick dorsal part of the posterior wall of the nasal capsule. The oblique eye-muscles may have been attached in this pit. Several foramina are found at its bottom (figs. 12, 13), four on the left side and five on the right in the specimen figured, whereas in *Eusthenopteron foordi* only one foramen is found in the corresponding part of the posterior face of the planum antorbitale. One of these foramina is situated dorsally in the pit (two on the right), two ventrally, and one laterally. At least some of these foramina must have led into canals running forward into the cavum nasi. However, only two openings have as yet been observed on the anterior face of the posterior wall of that cavum. These are situated dorso-laterally of the anterior opening of the olfactory canal. They conceivably gave passage to the n. profundus and the orbito-nasal artery and vein.

Of the ventral division of the planum antorbitale, the part below the olfactory ridge, *olf.r* (figs. 12, 13), will first be considered. This part consists of a medial portion forming the postero-ventro-lateral part of the internasal wall (*inw*$_2$, figs. 12, 13), and a lateral portion forming the ventro-medial part of the posterior wall of the nasal capsule. This latter portion of the planum antorbitale is not vertical like its other parts but is inclined in such a way that, seen from the rear, it faces postero-ventrally. It therefore meets the floor (*fl*, figs. 11, 14 A) of the nasal capsule at an obtuse angle (see fig. 11). As seen in fig. 13, it has a free lateral margin ventrally, *l.m* (see also figs. 10 B, 11, 12, 16), which bounds the fenestra choanalis postero-medially. On its posterior face we find an oblong depressed area (*art.aup,* figs. 10—13, 14 A, 15, 16) devoid of the shiny, superficial, periostal bone-layer, an area, which — like the whole of this portion of the planum antorbitale — faces postero-ventrally. This depressed area is of similar shape and extent to a certain area found in *Eusthenopteron foordi* on the most anterior end of the pars autopalatina of the palatoquadrate, and it is therefore obviously the articulation face for the autopalatine. It was conceivably capped by cartilage. Its position and curved shape clearly show that the movements of the palato-quadrate against it must have been very small, or almost none. This opinion of the articulation between the ethmoidal region and the palatoquadrate is, as will be shown below (p. 114), also confirmed by the complex and firm attachment of the palatoquadrate to the whole divisio cranialis anterior. This attachment is even of such a nature that a fusion between the palatoquadrate and the endocranium may be strongly suspected.

The part of the planum antorbitale situated below the ridge *ra* (figs. 10 B, 11, 12, 13, 15), is vertical and transverse, and forms the ventrolateral part of the posterior wall of the nasal capsule (see fig. 13). It is rather thin, and pierced by a wide foramen, (*f.tr.inf,* figs. 10 B, 12, 13) which most probably transmitted the truncus infraorbitalis (the ramus maxillaris trigemini and the ramus buccalis of the nervus facialis) and its accompanying vessels. A small foramen (*fo*$_p$, figs. 12, 13) on the postero-ventral face of the ridge *ra* is the posterior opening of a canal leading to the cavum nasi. This narrow canal probably transmitted a branch of the said nerves or vessels. Ventrally, the wide foramen *f.tr.inf* is bridged by a thin, horizontal bar, though this is imperfect in the specimens examined. This bar (*b*, figs. 10 B, 13, 16; *b*$_r$, figs. 11, 12, 14 A, 15), situated considerably above the level of the plane ventral face

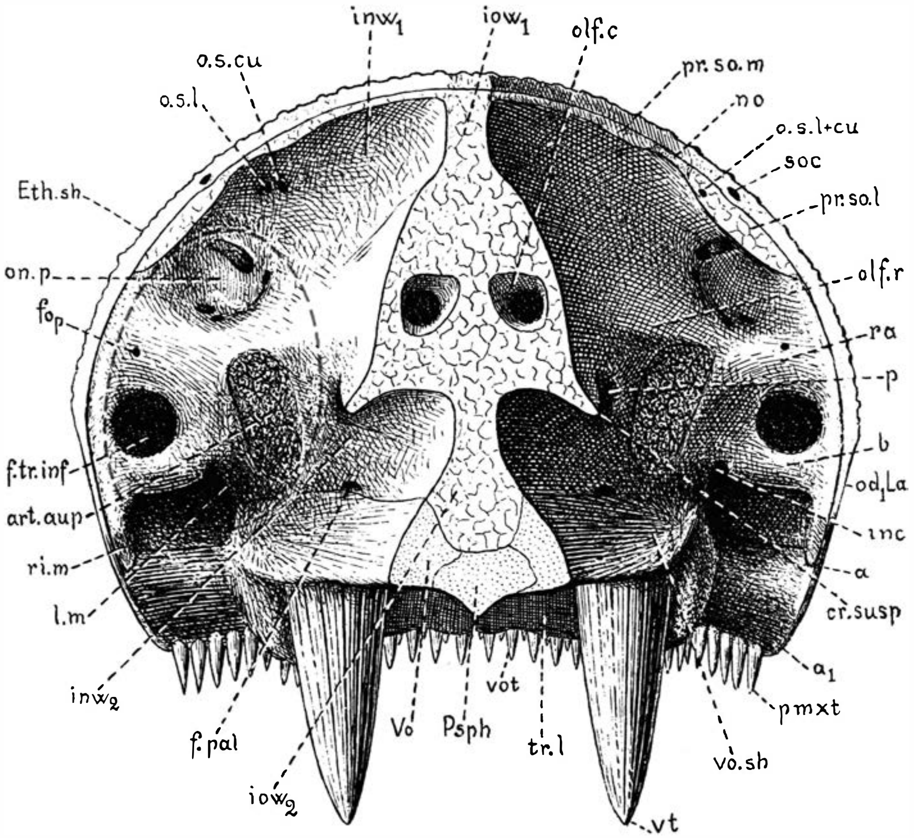

Fig. 13. *Eusthenopteron wenjukowi* (ROHON, 1889). Attempted restoration of the posterior aspect of the ethmoidal region and its dermal bones. Mainly from the specimen shown in figure 12. × $3/2$. The extent of the cavum nasi is indicated by a red, interrupted line.

Eth.sh, ethmoidal shield; *Psph*, parasphenoid; *Vo*, vomer; *a*, corner of the ventral margin of the lateral wall of the nasal capsule; *art.aup*, area — devoid of the periostal lining membrane — against which the pars autopalatina abutted; a_1, corner of the posterior end of the premaxillary; *b*, bar of the planum antorbitale; *cr.susp*, crista suspendens; *fop*, posterior aperture of a canal for a nerve or vessel; *f.pal*, foramen, probably transmitting a branch of the n. palatinus; *f.tr.inf*, foramen, probably transmitting the truncus infraorbitalis and vessels; *inc*, incisure in the ventral margin of the planum antorbitale; inw_1 dorsal, and inw_2 ventral part of the posterior face of the internasal wall; iow_1, dorsal, and iow_2 ventral thin part of the interorbital wall; *l.m*, postero-medial part of the boundary of the fenestra choanalis; *no*, notch between the processes supraorbitalis and medialis; od_1La, area of the lateral rostral, overlapped by the lachrymal; *olf.c*, olfactory canal: *olf.r*, olfactory ridge; *on.p*, orbito-nasal pit; *o.s.cu*, foramen, probably transmitting general cutaneous branches of the r. ophthalmicus superficialis; *o.s.l*, foramen, probably transmitting the r. ophthalmicus superficialis; *o.s.l* + *cu*, foramen, probably transmitting general cutaneous + lateralis branches of the r. ophthalmicus superficialis; *p*, pit in front of crista suspendens; *pmxt*, premaxillary tooth; *pr.so.l*, proximal end of the processus supraorbitalis lateralis; *pr.so.m*, proximal end of the processus supraorbitalis medialis; *ra*, ridge on the posterior face of the planum antorbitale; *ri.m*, part of the ventral margin of the lateral wall of the nasal capsule, facing postero-ventrally; *soc*, supraorbital lateral line canal; *tr.l*, transverse, tooth-bearing lamina of the vomer; *vot*, tooth on the tooth-bearing lamina of the vomer; *vo.sh*, shelf of the vomer; *vt*, vomerine tusk.

of the ethmoidal region, forms the postero-ventral margin of the posterior wall of the nasal capsule, and borders the fenestra choanalis posteriorly. Laterally it is joined to the lateral wall of the nasal capsule, which wall is extended slightly below the level of its ventral face (figs. 13, 16). Medially its dorsal half is joined to the postero-medial margin *l.m* (figs. 10 B, 11, 12, 13, 16), whereas its ventral half is free medially, forming the lateral boundary of an incisure (*inc*, figs. 12, 13, 15, 16). In this incisure, bordered dorso-medially by the above-mentioned margin *l.m*, the most anterior part of the dermopalatine was most probably inserted, judging by the conditions found in *Eusthenopteron foordi*.

The olfactory canal (*olf.c*, figs. 12—14) runs entirely intercranially. Its opening into the postero-medial corner of the nasal capsule is wide and funnel-shaped. This opening is close to the internasal wall, ventro-medially of the openings of the above canals transmitting branches of the profundus nerve and its accompanying vessels.

Of the orbito-temporal region only approximately the anterior third now remains. Dorsally and ventrally it is rather thin (*iow*$_1$, *iow*$_2$, figs. 10, 12, 13, 14) whereas its middle part, lodging the cranial cavity (*cran.cav*, fig. 14) and the diverging olfactory canals (*olf.c*, figs. 12—14), is fairly thick. Its dorso-lateral margin (*iow*$_1$) is produced, at least anteriorly, into a lateral edge protruding a little above the orbit. Antero-laterally this edge is directly continuous with the roof of the ethmoidal region, which extends backwards above the orbit, beyond the planum antorbitale (cf. above p. 97). That part of the region which is ventral to the cranial cavity and the olfactory canals (*iow*$_2$, figs. 10, 12, 13, 14), is very thin and partly missing (see fig. 14 A), but as it is shown complete in the figure given by ROHON 1889, Tafel 1, fig. 9, it was probably complete at that time. Judging from ROHON's figure it was probably not fenestrated. Its ventral part is thickened; its ventral face, convex in transverse section, rests in a furrow formed by the vomeres and parasphenoid (figs. 12, 13). Forward it broadens and merges into the ventral part of internasal wall (*inw*$_2$, figs. 12, 13), and its ventral face becomes plane and passes into the plane ventral face of the ethmoidal region. In the lateral margin of that face, slightly behind the planum antorbitale, is a notch bridged over ventrally by the vomer. The foramen (*f.pal*, figs. 12, 13, 14 A) thus formed between the vomer and the ethmosphenoid leads into a canal running antero-medially. Most probably this canal transmitted a branch of the r. palatinus of the n. facialis.

The part of the interorbital wall lodging the cranial cavity and the olfactory canals is on each side provided with a strongly developed crista, the crista suspendens (*cr.susp*, figs. 10—16). This crista ends abruptly in front behind a small pit (*p*, figs. 10, 11, 13, 14 A, 15). This pit is situated behind the posterior upper end of the area *art.aup* (figs. 10, 11, 12, 13, 14 A, 15, 16), and below the olfactory ridge, which is rather sharp in this region. The ventral face of the crista suspendens is concave transversely, and therefore forms a shallow rostro-caudal groove with a rather uneven bottom. The upper face of the crista is directed dorso-laterally, and passes dorso-medially into the main lateral face of the interorbital wall. The crista suspendens — which in *Eusthenopteron foordi* is represented only by a few protuberances concave ventrally — conceivably prevented the anterior part of the palatoquadrate from sliding upwards, and the dorsal margin of the anterior part of the palatoquadrate was probably suspended from it in ligaments.

The preserved part of the cranial cavity (*cran.cav,* fig. 14) is rather narrow, and oval in section. It is 7.5 mm high or only about $^1/_7$ of the total height of the interorbital wall, and about 6 mm wide. In front it is divided into the two diverging olfactory canals (*olf.c*, figs. 12—14). At the place, rather far behind the planum antorbitale (see fig. 14 A), where they leave the cranial cavity, the olfactory canals are incompletely separated by a low, median, ventral ridge (*m.r,* fig. 14 A). Anteriorly this ridge rapidly increases in width and height, and soon joins the roof of the canals, which thus become completely separated from each other by a median wall merging in front into the internasal wall.

d. Dermal bones of the cranial roof. That part of the dermal cranial roof which covers the ethmoidal region is practically all that is preserved in the specimens at my disposal. The bones composing this part form a continuous shield, which for the sake of brevity may be called the ethmoidal shield (*eth.sh.* figs. 10—16). As in *E. foordi* and *E. säve-söderberghi* it is certainly made up of several dermal bones (see fig. 6), though only some of the sutures between these bones can be traced. In specimens of *E. foordi* exposed in external view, the sutures between the dermal bones of the snout are also rarely visible.

The ethmoidal shield has an upper, gently domed, ornamented face sloping downward in front as well as to the sides. In front it descends below the level of the ventral face of the endocranium, where it ends in a rather sharp, tooth-bearing margin (*Pmx,* figs. 10, 11, 14 A, 15, 16) formed by the premaxillaries and constituting the anterior part of the upper oral margin. It is not horizontal, but faces ventrally and slightly anteriorly. Its configuration is otherwise well shown by the figures cited. Posteriorly it ends abruptly (a_1, figs. 10, 11, 12, 13, 14 A, 15, 16) below the corner *a* (figs. 11, 12, 13, 16) of the ventral margin of the lateral wall of the nasal capsule, thus rather far in front of the transverse plane of the planum antorbitale. Postero-ventrally the ethmoidal shield has a free margin which forms an almost right angle, a_1, with the tooth-bearing margin already described. This free margin lies external to, and corresponds in posterior extent and configuration fairly well with the posterior part (*ri.m*, figs. 13,

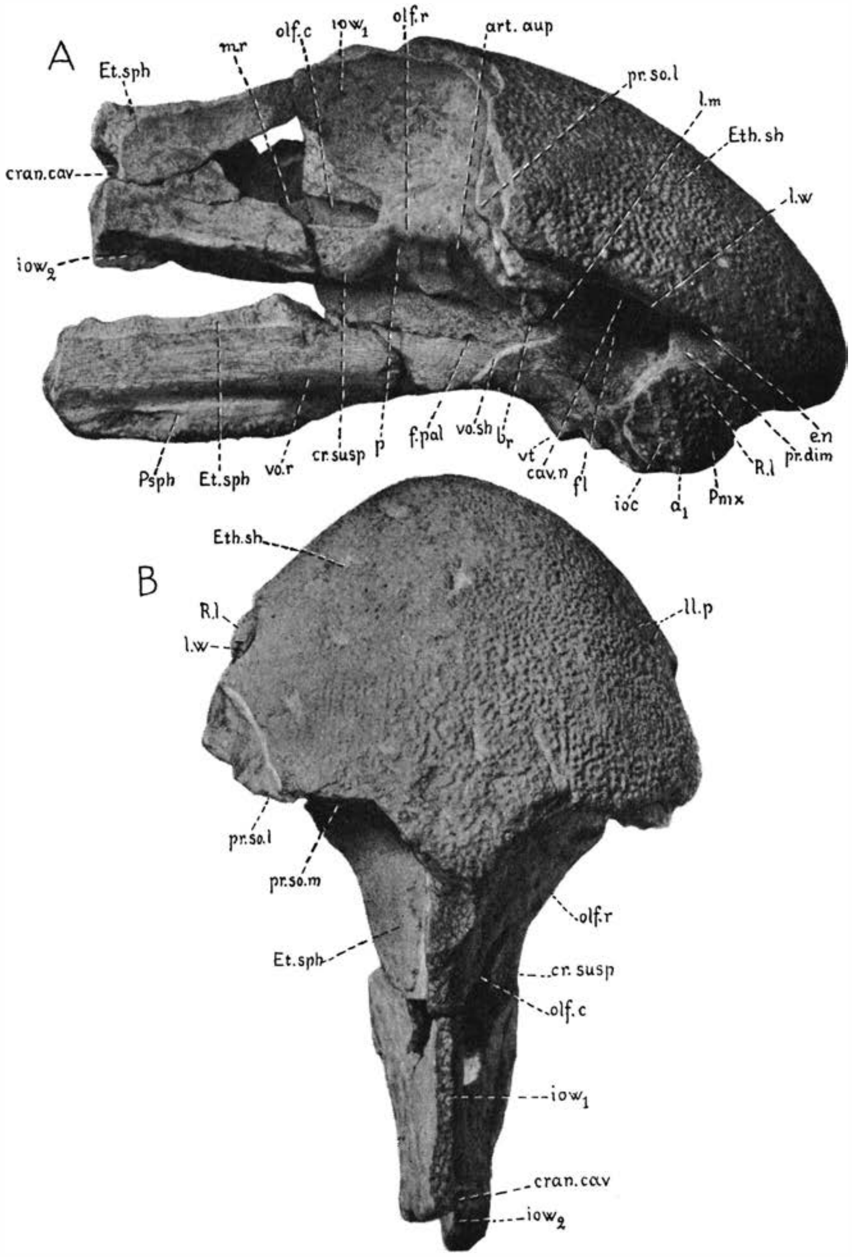

Fig. 14. *Eusthenopteron wenjukowi* (ROHON, 1889). Imperfect anterior part of the divisio cranialis anterior. The same specimen as in fig. 12. A, lateral; B, dorsal aspect. Natural size. *Eth.sh,* ethmoidal shield; *Et.sph,* ethmosphenoid; *Pmx,* premaxillary (possibly rostro-premaxillary), *Psph,* parasphenoid; *R.l,* lateral rostral; *Vo,* vomer; *art.aup,* area — devoid of the lining periostal membrane — against which the pars autopalatina abutted; a_1, corner at the posterior end of the premaxillary, forming the most ventral part of the ethmoidal shield; b_r, remains of the bar of the planum antorbitale: *cran.cav,* cranial cavity; *cr.susp,* crista suspendens; *e.n,* external naris; *fl,* floor of the nasal cap-

16) of the ventral margin of the lateral wall of the nasale capsule. Along this margin there is a rather large overlapped area of the fronto-ethmoidal shield (*od₁La, od.Mx,* figs. 10 A, 13; cf. figs. 6, 7 A), devoid of ornament.[1] As may be seen in figure 10 A, this overlapped area, which is rather imperfectly preserved, has a strongly curved boundary towards the ornament-bearing part of the ethmoidal shield. Its dorso-medial larger part is smooth, whereas its ventral, laterally facing part is rather uneven. On this uneven part there is a rostro-caudal suture, and immediately dorsally of this the opening of a canal (*ioc,* figs. 10, 11, 14 A). Judging by the conditions in *Eusthenopteron foordi* this suture probably joined the premaxillary and the lateral rostral, and the foramen dorsally of the suture probably transmitted the ethmoidal commissure (cf. SÄVE-SÖDERBERGH 1933, p. 7) of the infraorbital lateral line canal. No other sutures can be seen on the external face of the available ethmoidal shields, but the specimen figured by ROHON in 1889 on Tafel I, figs. 4 and 6, has a short median slit at the most anterior end of the snout. This slit certainly separates the premaxillaries of each side (a median suture between these two bones is shown on their palatal face as described below, p. 105). The foramina situated dorsally of that slit, marked X on ROHON's figure 6, are most probably widened lateral line pores.

The external nostril (*e.n,* figs. 10 A, 14 A) — there is one on each side — is situated outside the fenestra narina, on the part of the ethmoidal shield that faces antero-laterally and antero-dorsally of the corner a_1. It is oval in shape, of about the same size as the fenestra narina, and distinctly bounded by dermal bones. Its ventral margin is bent inward, and projects into the nasal cavity as a process. This process, the processus derm-intermedius (*pr.dim,* figs. 10 A, 14 A) rests on and is intimately connected with the endocranial processus intermedius (see on p. 95 above). In the present species these two processes are of equal length, whereas in *Eusthenopteron foordi*[2] the processus derm-intermedius

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[1] In *Eusthenopteron foordi* the corresponding unornamented area is situated on the rostro-premaxillary, the lateral rostral, and the supraorbito-antorbital (see fig. 7 A), and is overlapped there by the anterior parts of the lachrymal and the maxillary; in *Eusthenopteron säve-söderberghi* the part of this area (*od₂La,* fig. 7 A) belonging to the supraorbito-antorbital is the only one preserved.

[2] Shown in a series of grinding sections made by professor STENSIÖ.

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sule; *f.pal,* foramen, probably transmitting a branch of the n. palatinus; *ioc,* foramen transmitting the infraorbital lateral line canal; *iow₁,* dorsal, and *iow₂,* ventral, thin part of the interorbital wall; *ll.p,* pores of the lateral line canals; *l.m,* postero-medial part of the fenestra choanalis boundary; *l.w,* lateral wall of the nasal capsule; *m.r,* median ridge separating the olfactory canals: *olf.c,* olfactory canal; *olf.r,* olfactory ridge; *p,* pit in front of crista suspendens; *pr.dim,* processus derm-intermedius of the lateral rostral; *pr.so.l,* proximal end of the processus supraorbitalis lateralis; *pr.so.m,* proximal end of the processus supraorbitalis medialis; *vo.r,* ridge on the lateral face of the parasphenoid, formed by the posterior tapering end of the vomer; *vo.sh,* shelf of the vomer; *vt,* vomerine tusk.

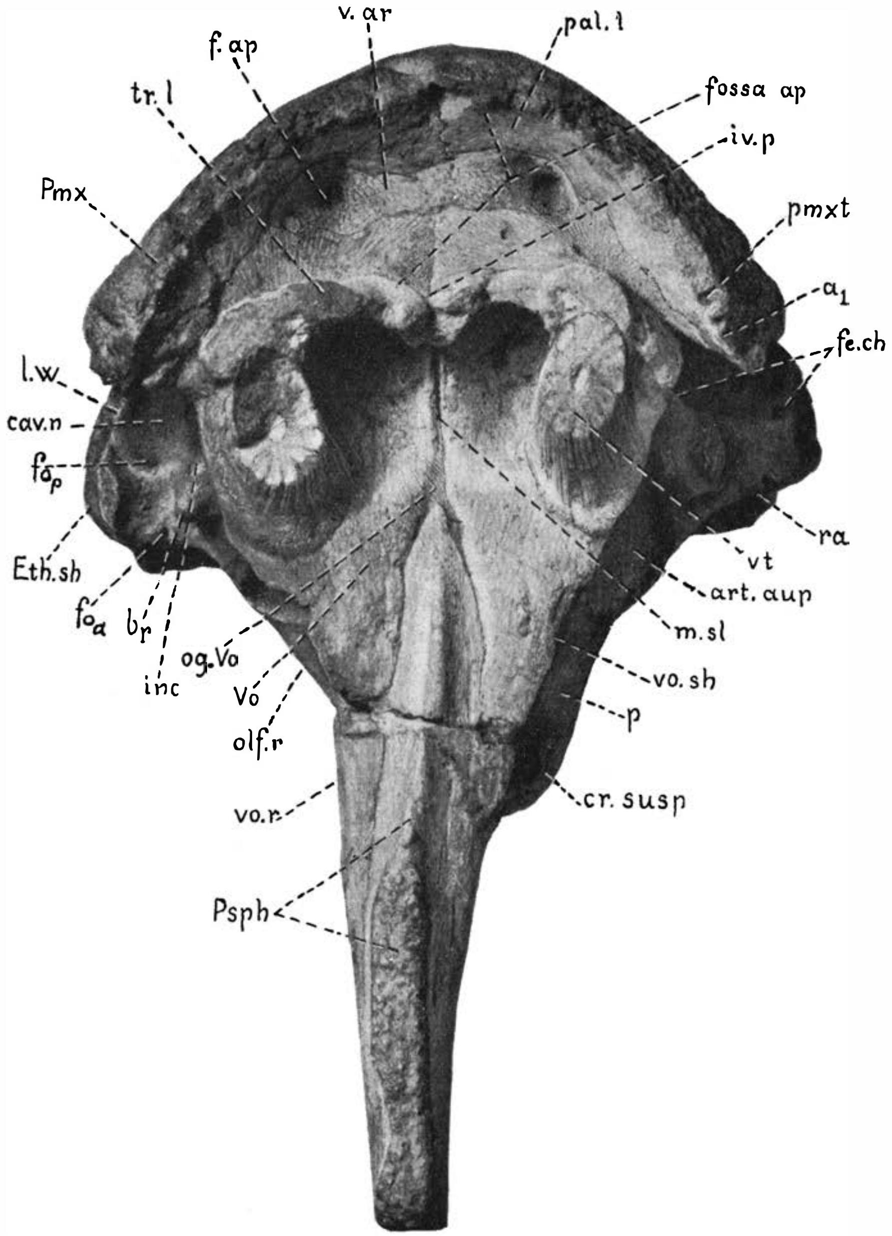

Fig. 15. *Eusthenopteron wenjukowi* (ROHON, 1889). Ventral aspect of the imperfect divisio cranialis anterior shown in fig. 14. × 3/2. Photographed in xylol.

Eth.sh, ethmoidal shield; *Pmx*, premaxillary; *Psph*, parasphenoid; *Vo*, vomer; *art.aup*, area — devoid of the periostal lining membrane — against which the pars autopalatina abutted; a_1, corner of the posterior end of the premaxillary; b_r, remains of the bar of the planum antorbitale; *cav.n*, cavum nasi; *cr.susp*, crista suspendens; *f.ap*, foramen apicale; *fe.ch*, fenestra choanalis; fo_a, posterior, and fo_p, anterior aperture of canal for a branch of a nerve of vessel; *fossa ap*, fossa apicalis; *inc*, incisure in the ventral margin of the planum antorbitale for the most anterior end of the dermopalatine; *iv.p*, intervomerine pit; *l.w*, lateral wall of the nasal capsule; *m.sl*, median slit between is the longest. As is proved by the conditions in *E. foordi,* the processus derm-intermedius belongs to the lateral rostral.

e. Dermal bones of the lower side of the ethmosphenoid. The ethmoidal shield covers not only the dorsal face of the ethmoidal region, but also as mentioned above, its anterior tooth-bearing margin, which is formed by the premaxillaries reaches down below the ventral face of the endocranium. This downward-directed anterior part of the ethmoidal shield forms the anterior and lateral boundaries of a crescent-shaped space on the lower side of the cranium, a space, which may be called the fossa apicalis (*fossa ap,* figs. 15, 16; see also fig. 10 B). The transverse tooth-bearing lamina of each vomer (*tr.l,* figs. 10 B, 13, 15, 16) is the posterior boundary of this fossa, and is described below. The roof of the fossa is formed posteriorly by that part of the vomer which is situated in front of the transverse lamina; its middle part by the ethmosphenoid (*v.ar,* figs. 10 B, 15, 16), which is there destitute of dermal bones, and anteriorly and laterally by a palatal lamina of each premaxillary (*pal.l,* figs. 10 B, 15, 16).

The palatal lamina, *pal.l,* of the premaxillary just referred to covers the most antero-lateral marginal portion of the ventral face of the ethmosphenoid. It is joined to the lamina of the other side by a short median suture, which shows that the species is provided with two premaxillaries (possibly rostro-premaxillaries as in *Eusthenopteron foordi;* cf. above p. 103). Its ventral face meets and is continuous with the inner (oral) face of tooth-bearing margin of the same bone; its posterior margin borders the area *v.ar* (figs. 10 B, 15, 16) on the ventral face of the ethmoidal region anteriorly, behind which it is thickened and joined by suture to the antero-lateral corner of the vomer of its side. Postero-laterally of its suture with the vomer it narrows rapidly, ending a little dorsally of the corner a_1 (figs. 10, 11, 12, 13, 14 A, 15, 16) of the premaxillary. In this most posterior part it forms the antero-lateral boundary of the internal nostril.

The vomer (*Vo,* figs. 10—14 A, 15, 16) is composed of a roughly triangular horizontal plate broad in front, but narrowing towards the back, and a transverse, vertical, tooth-bearing lamina (*tr.l,* figs. 10 B, 11, 12, 13, 15, 16) above referred to.

The horizontal plate of the vomer forms the main part of the bone. To a large extent this plate is situated beneath the ethmoidal region, but also reaches backward beneath an anterior part of the orbito-temporal

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the vomeres; *og.Vo,* area of the right vomer overlapping the left vomer; *olf.r,* olfactory ridge; *p,* pit in front of the crista suspendens; palatal lamina of the premaxillary; *pal.l,* palatal lamina of the premaxillary; *pmxt,* premaxillary tooth; *ra,* ridge on the posterior face of the planum antorbitale; *tr.l,* transverse, tooth-bearing lamina of the vomer; *v.ar,* area on the ventral face of the ethmosphenoid, not covered by dermal bones; *vo.r,* ridge on the lateral face of the parasphenoid, formed by the posterior tapering end of the vomer; *vo.sh,* shelf of the vomer; *vt,* vomerine tusk.

region (see figs. 12, 13). In front it has a transverse margin forming the posterior border of the area *v.ar* (figs. 10 B, 15, 16) on the ventral face of the ethmosphenoid, and most laterally it is bent slightly upward into the foramen apicale (*f.ap*, figs. 10 B, 15, 16). Antero-laterally its anterior margin is thickened and connected by suture to the thickened portion of the palatal lamina of the premaxillary, as described above. Behind this suture the horizontal plate of the vomer has a long, free postero-lateral margin, the most anterior part of which forms part of the medial boundary of the internal nostril (elsewhere the internal nostril was bounded medially by the lateral margin of the most anterior part of the dermo-palatine). Further to the back, immediately behind the planum antorbitale, i. e. beneath the orbito-temporal region, the horizontal plate is situated lateral to the parasphenoid and the most ventral part of the orbito-temporal region, where it forms a pronounced ridge. Owing to this position there are here not only a free ventral face, but also a free dorso-lateral face separated from the former by a lateral, sharp edge. Just below the area *art.aup*, (figs. 12, 13) the dorso-lateral face is rather broad and slightly depressed, and forms a shelf (*vo.sh*, figs. 12, 13, 14 A, 15) which probably supported the palatoquadrate. In its hindmost part the horizontal plate becomes rounded in transverse section, and appears as a low rounded ridge *vo.r*, (figs. 14 A, 15, 16) on the lateral face of the parasphenoid. The exact point where this ridge (and thus the vomer) ends posteriorly could not be ascertained.

In front of the parasphenoid the horizontal plate of the vomer is joined to its fellow on the other side in a median suture interrupted by a median slit (*m.sl*, figs. 10 B, 15, 16). In the specimen shown in fig. 15 there is an area, *og.Vo*, behind that slit on the right hand horizontal plate, which probably overlapped the left vomer. The suture between the vomeres is interlocked in front of the slit.

Immediately behind the transverse lamina *tr.l* a large tusk (*v.t*, figs. 10—14 A, 15, 16) is attached to the ventral face of the horizontal plate of the vomer. Beside this tusk there is a rounded pit (*p.rt*, figs. 10 B, 15, 16) for the replacement tooth. The same pit also received the most anterior coronoid tusk. It is rather shallow, and does not pierce the horizontal plate.

The transverse tooth-bearing lamina *tr.l* (figs. 10 B, 11, 12, 13, 15, 16) of the vomer, already referred to several times, is vertical and crosses the horizontal plate a little behind its anterior margin. The lateral part of the lamina is bent back, and ends in a vertical margin situated medially of the anterior part of the internal nostril. The lamina is thickened medially and joined there to the corresponding lamina of the opposite side in a suture. On the anterior side of the two laminae, in the dorsal part of the suture between them, there is a well developed pit, the intervomerine pit (*iv.p*, figs. 10 B, 15, 16), which is bounded dorsally by the medial, slightly

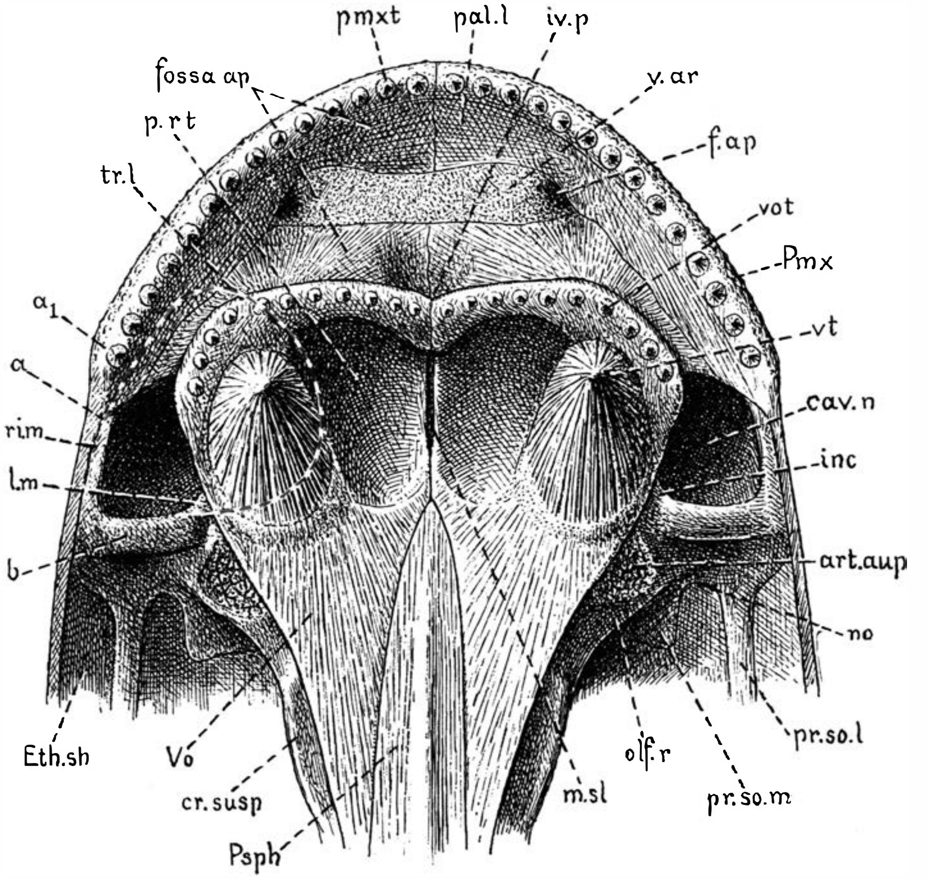

Fig. 16. *Eusthenopteron wenjukowi* (ROHON, 1889). Attempted restoration of the ventral aspect of the anterior part of the divisio cranialis anterior. Mainly from the specimen shown in fig. 15. × 3/2. The extent of the cavum nasi is indicated by a red, interrupted line.

Eth.sh, ethmoidal shield; *Pmx,* premaxillary; *Psph,* parasphenoid; *Vo,* vomer; *a,* corner of the ventral margin of the lateral wall of the nasal capsule; *art.aup.* area — devoid of the periostal lining membrane — against which the pars autopalatina abutted; a_1, corner of the posterior end of the premaxillary; *b,* bar of the planum antorbitale; *cav.n,* cavum nasi; *cr.susp,* crista suspendens; *f.ap,* foramen apicale; *fossa ap,* fossa apicalis; *inc,* incisure in the ventral margin of the planum antorbitale for the most anterior end of the dermopalatine; *iv.p,* intervomerine pit (conceivably housing the intermaxillary gland); *l.m,* postero-medial part of the boundary of the fenestra choanalis; *m.sl,* median slit between the vomeres; conceivably the opening of the intermaxillary gland; *no,* notch between the processes supraorbitalis lateralis and medialis; *olf.r,* olfactory ridge; *pal.l.* palatal lamina of the premaxillary; *pmxt,* premaxillary tooth; *p.rt,* pit of the vomer for a replacement tooth, and for the most anterior coronoid tusk; *pr.so.l,* processus supraorbitalis lateralis; *pr.so.m,* processus supraorbitalis medialis; *ri.m,* part of the ventral margin of the lateral wall of the nasal capsule facing postero-ventrally; *tr.l,* transverse, tooth-bearing lamina of the vomer; *v.ar,* area on the ventral face of the ethmosphenoid, not covered by dermal bones; *vot,* tooth on the tooth-bearing lamina of the vomer; *vt,* vomerine tusk.

depressed anterior parts of the horizontal plates. From this pit a median canal, the intervomerine canal, runs back between the laminae, and opens into the median slit between the horizontal plates (*m.sl*, figs. 10 B, 15, 16). In *Eusthenopteron foordi* this canal passes ventrally of the most anterior part of the parasphenoid, which in that species ends just above the transverse laminae. The posterior face of the transverse lamina is closely attached to the large tusk of the horizontal plate, and also forms the anterior wall of the pit *p.rt*, for the replacement tusk. Its ventral margin is rather worn in the specimens at my disposal and therefore shows only the bases of a few teeth (figs. 10 B, 15, *vot* fig. 16; cf. ROHON 1889, Tafel I, fig. 4).

The part preserved of the parasphenoid (*Psph*, figs. 10 B, 12, 13, 14 A, 15, 16), is narrower in ventral view than the corresponding part of the parasphenoid of *Eusthenopteron säve-söderberghi* (cf. above p. 86; figs. 4 B, 8). It is covered laterally in its anterior parts by the horizontal plates of the vomeres, and (see figs. 14 and 15) it is impossible to say whether it extended far enough forward to reach the transverse plane of the lamina, *tr.l*, as it does in *E. foordi* and *E. säve-söderberghi*. Otherwise the parasphenoid of the present species agrees well with that of these two species.

f. The lower jaw. The part of a lower jaw at my disposal consists of approximately the anterior third of the right lower jaw. It is almost uncrushed, but its lateral parts are to a large extent missing. The following bones can be observed in it: the strongly developed Meckelian bone, the dentary, the postsplenial, the splenial, the prearticular, the coronoids I and II, and a tooth-bearing plate covering the prearticular.

The Meckelian bone, M. b, (figs. 17 A, 17 C, 17 D; cf. STENSIÖ 1932, p. 258; in *Eusthenopteron foordi* shown to extend throughout the whole length of the lower jaw) has most anteriorly a medially directed small circular area, uncovered by dermal bones, forming the bottom of a pit, the symphysial pit (*sy.p*, figs. 17 B, 17 D). This area, which is rather rough and has no periostal lining membrane, was most probably capped with cartilage, which filled up the symphysial pit and joined the jaws in the symphysis. The medial face of the Meckelian bone is covered by dermal bones throughout its extent, which prevents its configuration from being studied. The lateral face is in front covered by dermal bones, whereas posteriorly it lacks such bones in its present state of preservation. On this face there are certain grooves, which originally were all covered laterally by dermal bones forming canals. These canals certainly contained nerves and vessels. The longest and largest of them consists of an anterior forward-running, almost horizontal portion c_2 (figs. 17 A, 17 D), and a short posterior, vertically descending portion c_1 (figs. 17 A, 17 B, 17 D). The latter opens on the ventral face of the jaw. Just in front of this opening the Meckelian bone, which was not here covered by dermal bones, forms a small knob (*k*, figs. 17 B, 17 D). The posterior end of the canal-portion c_2 gives off two branches, a wide dorsal branch c_3, (figs. 17 A, 17 D), and a much narrower antero-dorsal branch c_4 (figs. 17 A, 17 D). The latter branch is situated in the angle between c_2 and c_3. The branch c_3 in its turn gives off a narrow branch c_5 (figs. 17 A, 17 D), running in a postero-ventral direction. Behind the canals just described, immediately in front of the back end of the jaw fragment, there is a lateral depression (*ad.f,* figs. 17 A, 17 D), which in front communicates with the canals. This depression appears to represent the most anterior end of the adductor fossa. Ventrally of this depression, between the Meckelian bone and the prearticular, there is a narrow rostro-caudal groove (c_6, figs. 17 B, 17 D), which opens on the ventral face of the jaw.

On the dorsal face of the Meckelian bone two depressions form the bottom and ventral parts of the walls (the remaining parts of which are formed by the coronoids) of two rather large, oval pits on the dorsal face of the jaw. The anterior of these pits (p_1, figs. 17 B, 17 C) most probably received the large vomerine tusk, while the posterior (p_2, figs. 17 A, 17 C) received the dermopalatine tusk. The other parts of the dorsal face of the Meckelian bone are covered by the coronoids and in front also — though incompletely — by the prearticular and dentary, between which a narrow strip of the Meckelian bone is exposed in dorsal view (see fig. 17 C).

Only the most anterior part of the dentary (*De,* figs. 17 A—D) is present, and has a lateral, ornamented face. In front there is a small triangular striated area (*tr.a,* fig. 17 B) facing antero-medially. The postero-medial margin of this area is concave, and forms the anterior border of the symphysial pit. It most probably met the corresponding margin of the left jaw. The triangular areas of the two jaws bordered between them a median, V-shaped notch between the anterior ends of the jaws, in front of the symphysis. The dentary bears two rows of teeth along its dorsal margin. In the inner of these rows (*i.det,* figs. 17 B, 17 C) the teeth are rather large, attached to the medial face of the dorsal margin, while the teeth in the external row (*e.det,* fig. 17 C) are very small. All the teeth are broken at their base in the present specimen. Below the internal row of teeth a smooth strip of the medial face of the dentary can be seen (*De,* fig. 17 B), the ventral part of which is attached to the coronoid I, and below that to the Meckelian bone. Ventrally, the dentary is sutured to the small fragment of the splenial still preserved. As far as I can see it does not meet the prearticular.

The centre of radiation in the dentary appears to have been situated near the posterior, broken end of the bone, i. e. well to the front.

The ventral face of the small preserved fragment of the splenial (*Sp,* figs. 17 B, 17 D) is striated. Medially its margin is straight, and most probably met the corresponding margin of the other jaw. Its anterior part forms the ventral part of the medial margin of the symphysial pit. Dorso-medially the splenial is joined to the prearticular, and dorso-laterally to

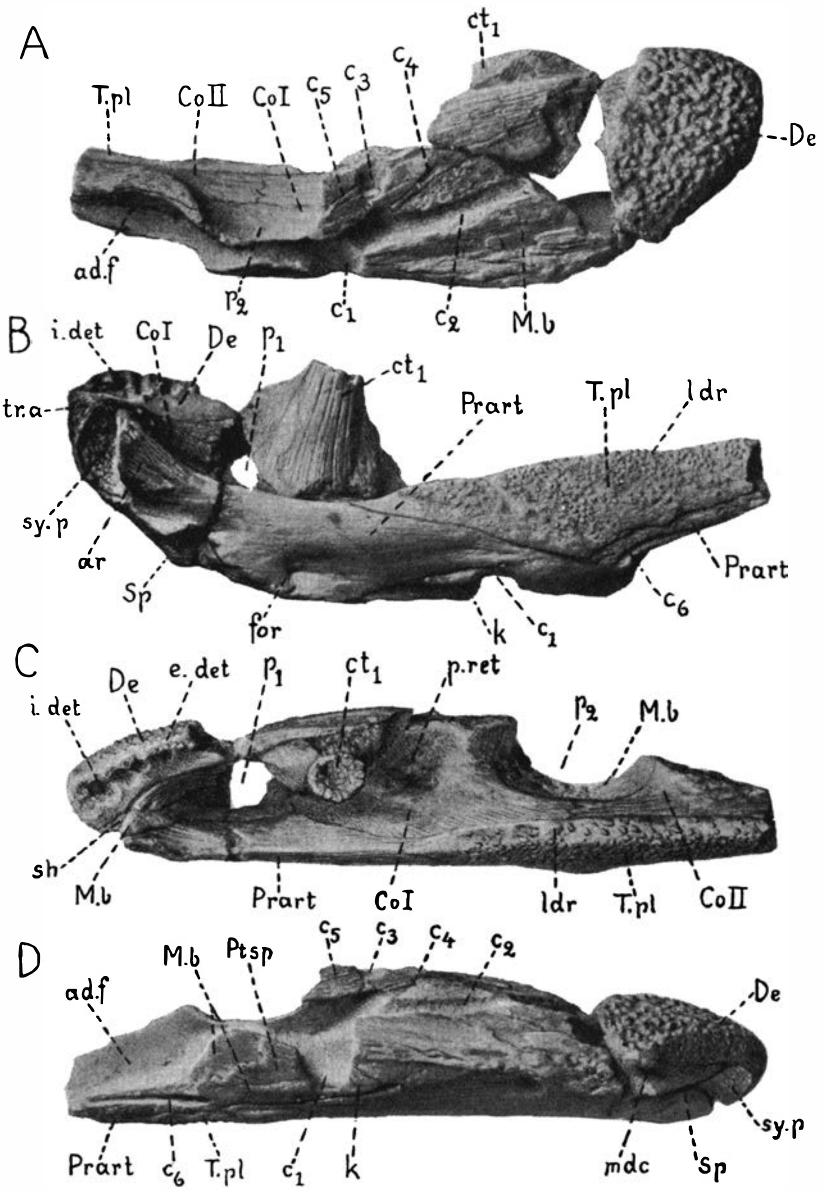

Fig. 17. *Eusthenopteron wenjukowi* (ROHON, 1889). Imperfect, anterior part of the right ramus of the lower jaw of a small specimen. A, lateral; B, medial; C, dorsal; D, ventral aspect. × 2. Specimen in the Geological Institute, Leningrad; figured by ROHON (1889, Tafel I, fig. 11).

CoI, coronoid I; *CoII*, coronoid II; *De*, dentary; *M.b*, Meckelian bone; *Prart*, prearticular; *Ptsp*, postsplenial; *Sp*, splenial; *T.pl*, independent tooth-bearing plate; *ad.f*, depression, probably the most anterior end of the adductor fossa; *ar*, triangular, rough area of the prearticular; ct_1, tusk of the coronoid I; c_1—c_6, grooves on the face of the Meckelian bone for nerves or vessels; *e.det*, external row of small teeth of the dentary; *for*, foramen piercing the prearticular; *i.det*, inner row of teeth of the dentary; *k*, knob on the ventral face of the Meckelian bone; *ldr*, row of larger denticles along the dorsal the dentary. At its posterior broken end there is a notch (*mdc,* fig. 17 D), continued on the ventral, striated face by a short antero-medially running groove ending at the median margin of the bone, and most probably housing the anterior part of the mandibular lateral line canal. This canal thus seems to have joined the canal on the other side below and slightly behind the symphysis.

Of the postsplenial (*Ptsp,* fig. 17 D) only a small fragment remained.

The coronoid I (*CoI,* figs. 17 A, 17 B, 17 C) is preserved in its whole length, but its lateral part is missing. In the main it is a thin bone, and covers the Meckelian bone dorsally. Its middle part is equipped with a large tusk (ct_1, figs. 17 A—C), but as its lateral tooth-bearing margin is lacking, no other teeth remain. On its dorsal face, immediately behind the large tusk, there is a shallow rough-bottomed pit (*p.ret,* fig. 17 C) which most probably lodged a tusk, now replaced by the tusk ct_1. In front of its tusk, the coronoid I is continued as a thin lamina, which forms part of the lateral wall of the pit p_1 for the vomerine tusk. Dorsally, the lateral face of that lamina is attached to the medial face of the dentary, and its most anterior part, which is broken in the present specimen, however, rested on a narrow shelf of the dentary (*sh,* fig. 17 C) in front of the pit p_1. The ventral part of the lateral face of the same lamina is attached to the Meckelian bone. Medially of its tusk, the coronoid I becomes broader and gains contact with the prearticular. Behind the pit *p.ret* (fig. 17 C) it shares in the formation of both the anterior wall of the pit p_2 and the anterior half of the medial wall of that pit (fig. 17 C). Posteriorly, the coronoid I is sutured to the coronoid II.

The centre of radiation in the coronoid I is situated in the middle point of the bone, below the base of the tusk.

Of the coronoid II (*CoII,* figs. 17 A, 17 B), only the antero-medial portion is preserved. This portion forms part of the posterior half of the medial wall of pit p_2 (figs. 17 A, 17 B). Medially it is sutured to the prearticular.

The part preserved of the prearticular (*Prart,* figs. 17 B, 17 C, 17 D) has most anteriorly a smooth medial face. Posteriorly that face is covered by the tooth-bearing plate described below, and consequently not exposed. On the exposed part of the smooth medial face, near its ventral margin, there is a shallow groove deepening forward and leading to a small foramen (*for,* fig. 17 B) for a nerve or vessel. At the anterior end of this part of the face we notice a second groove, leading to the symphysial pit. Dors-

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margin of the tooth-bearing plate; *mdc,* groove on the splenial, probably housing part of the mandibular lateral line canal; *p.ret,* pit for replacement tusk; p_1, pit probably receiving the vomerine tusk; p_2, pit probably receiving the dermopalatine tusk; *sh,* shelf of the dentary for the most anterior part of the coronoid I; *sy.p,* symphysial pit; *tr.a,* triangular, striated area of the dentary.

ally of the latter groove the medial face is flatter than further back, and forms a rather rough triangular area (*ar*, fig. 17 B), the anterior margin of which is the posterior border of the symphysial pit. This area was most probably in contact with the corresponding area of the left lower jaw. In front of the tooth-bearing plate, the prearticular forms the lateral wall of the pit p_1 (fig. 17 C), with a rounded dorsal margin and a smooth lateral face. Its most anterior ends rests on the Meckelian bone, but does not meet either the dentary or the coronoid I. Behind the pit p_1 its upper margin is in contact with the coronoids laterally. Ventrally it is sutured to the splenial, as already described.

The tooth-bearing plate (*T.pl,* fig. 17 A—C) attached to the medial face of the prearticular ends in front in a point opposite the posterior part of the tusk of the coronoid I. Its medial face is provided with a shagreen of small teeth except for its most anterior and antero-ventral area, which is smooth, like the adjacent medial face of the prearticular. Along its dorsal border the plate has somewhat larger teeth (*ldr,* figs. 17 B, 17 C), exactly as the *Eusthenopteron säve-söderberghi* (see p. 89).

Remarks. — *Eusthenopteron wenjukowi* differs from *Eusthenopteron foordi* in the following respects: far larger size (the fronto-ethmoidal shield is at least 1.5 times longer than in the largest of my numerous specimens of *E. foordi;* and about 2.5—3 times longer than in a specimen of *E. foordi* of average size); stronger development of the crista suspendens; stronger development of the lateral wall of the nasal capsule; the presence of separate foramina for the nervus profundus and the orbito-nasal artery and vein on the posterior face of the planum antorbitale; the presence of a narrow, median slit between the vomeres.

It is distinguished from *Eusthenopteron säve-söderberghi* by the following characteristics: far larger size (the fronto-ethmoidal shield may be estimated to have been about 2.5 times longer than in *E. säve-söderberghi*); somewhat different arrangement of the tubercles on the external faces of the dermal bones; the presence of a median slit between the vomeres.

Geological horizon and locality. Lower Upper Devonian; Upper Variegated Series, Juchora on the river Sjass, Russia.

III. Some concluding remarks.

1. — **The kinetism of the head.** A well-known peculiar characteristic of the Crossopterygians is that the cranium — endocranium as well as dermal bones — is divided into two divisions, here called the divisio cranialis anterior and posterior respectively by a fissure approximately at the trigeminal exit. Most authors (WATSON 1921, pp. 328, 334; 1926, p. 195; GOODRICH 1930, p. 288; ALDINGER 1930, pp. 40—46; 1931;

STENSIÖ 1932, pp. 23—24; HOLMGREN and STENSIÖ 1936, p. 347) maintain that the presence of this fissure means that there was a movable joint between these cranial divisions. They assume that the divisio cranialis anterior could be bent somewhat downward. STENSIÖ (1932, p. 23) suggested the possibility of this movement being effected by the contraction of a subcephalic portion of the trunk musculature occupying the fossa subchordalis and inserted in front in the wide pit (*p.sbc,* fig. 5 B) on the posterior face of the ethmosphenoid.

According to ALDINGER (1931, p. 302) this movement would also cause a movement of the dermal bones of the cheek. The postorbital would slide over certain areas of the intertemporal and dermosphenotic (marked *od.Po* and od_vPo respectively on figs. 7 A and 7 E in this paper), and these areas should consequently be interpreted as sliding surfaces.

Several conditions in *Eusthenopteron foordi,* and in the *Eusthenopteron* species described above, however, indicate not only that the divisio cranialis anterior and posterior were rigidly connected one to the other, but also that the palatoquadrate-cheek complex (the palatoquadrate, the dermal bones of the palatoquadrate, and the dermal bones of the cheek[1]) was rigidly attached to the cranium.

The following conditions prove that there cannot have been any real joint between the divisio cranialis anterior and posterior. The development of the posterior margin of the dermosphenotic and the frontal (fig. 7 A), and of the adjacent margin of the intertemporal (fig. 7 E), shows that the connection between the dermosphenotic and the frontal on the one hand and the intertemporal on the other must have been firm. The intertemporal was overlapped antero-laterally by the dermosphenotic (od_2Dsph) and the postorbital (*od.Po,* fig. 7 E), while further back part of its lateral margin og_3Po (fig. 7 E) overlapped the postorbital. It will be shown below that the postorbital certainly was rigidly connected with the divisio cranialis anterior, but the very fact that at the same time it both overlapped and was overlapped by the intertemporal must obviously have prevented practically every movement between the divisio cranialis anterior and posterior. The rigid connection between the divisio cranialis anterior and posterior is further supported by the most posterior end of the dermosphenotic, which end overlaps the intertemporal and was overlapped by the postorbital, in certain specimens of *Eusthenopteron foordi,* was resting in a fold (*fo,* fig. 7 E) of the intertemporal.

Besides the subdivision by a fissure of the endocranium into an anterior and a posterior part, the presence in Crossopterygians of a straight posterior transverse margin of the fronto-ethmoidal shield, and of a corresponding anterior margin of the parietal shield, has been one of the

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[1] The bones forming the palatoquadrate cheek complex are all rigidly connected by sutures, and consequently form a single unit from the point of view of kinetism.

chief arguments for the opinion that their cranium was provided with a movable joint.[1] Not only in some specimens of *Eusthenopteron foordi*, however, but also in an as yet undetermined Osteolepid specimen[2], the fronto-ethmoidal and parietal shields are so irregularly connected that a movable articulation between them is very improbable (fig. 18).

The opinion that the diviso cranialis anterior and posterior were immovably joined is further supported by the way in which the processus connectens (*pr.conn*, figs. 4, 5 A, 5 B, 6, 8) of the ethmosphenoid is connected with the otico-occipital, and by the presence of a powerful processus oticus on the palatoquadrate provided with a large area facing dorso-medially and without any shiny periostal bone-layer (*E. foordi*) in such a way as to indicate that it may have been attached to the otico-occipital, and thus to the endocranium.

As I have said in the above description of *E. wenjukowi*, the pars autopalatina of the palatoquadrate seems to have been rigidly connected with the posterior face of the planum antorbitale and adjacent parts of the interorbital wall. It was thus inserted between the crista suspendens (p. 100; *cr. susp*, figs. 12, 13) above and the shelf of the vomer (*vo.sh*) below. Its anterior tip — which in *Eusthenopteron foordi* has an articular face — must have abutted on the large postero-ventrally facing area (p. 98; *art.aup*, figs. 12, 13, 16) on the posterior face of the planum antorbitale. The most anterior end of the dermopalatine, projecting slightly in front of the palatoquadrate, rests in an incisure (p. 100; *inc*, figs. 12, 13) in the postero-medial margin of the fenestra choanalis. Moreover, the anterior parts of the lachrymal and maxillary, which bones are constitutents of the palatoquadrate-cheek complex rest on the large, partly rough, overlapped area (*odMx*, od_1La, p. 103; fig. 10 A) on the postero-lateral portion of the ethmoidal shield, in which the infraorbital lateral line canal (*ioc*, fig. 10 A; see also fig. 6) leaves the lateral rostral to enter the lachrymal.

From the above we may conclude that the anterior part of the palatoquadrate-cheek complex was rigidly connected with the divisio cranialis anterior. From the description of *Eusthenopteron säve-söderberghi* (pp. 80—81 and figs. 7 A—D) we have seen that the postorbital, which is another constituent of the palatoquadrate-cheek complex[3], also largely overlapped the dermosphenotic (od_vPo, figs. 7 A, 7 C, 7 D; cf. ALDINGER 1931; GROSS

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[1] In this connection it may be noted that NIELSEN has recently shown (1936, pp. 29—30) that a part corresponding to the posterior part of the fronto-ethmoidal shield of the *Rhipidistia* probably is included in the parietal shield of the Coelacanthids. The fissure separating the parietal and fronto-ethmoidal shields would thus be differently placed in the *Rhipidistia* and in the Coelacanthids.

[2] This specimen (*Thursius?*), No. 53397 of the Geological Survey, London, which has come from the shores of Thurso, has kindly been placed at my disposal by Dr. G. SÄVE-SÖDERBERGH.

[3] See foot-note on p. 113.

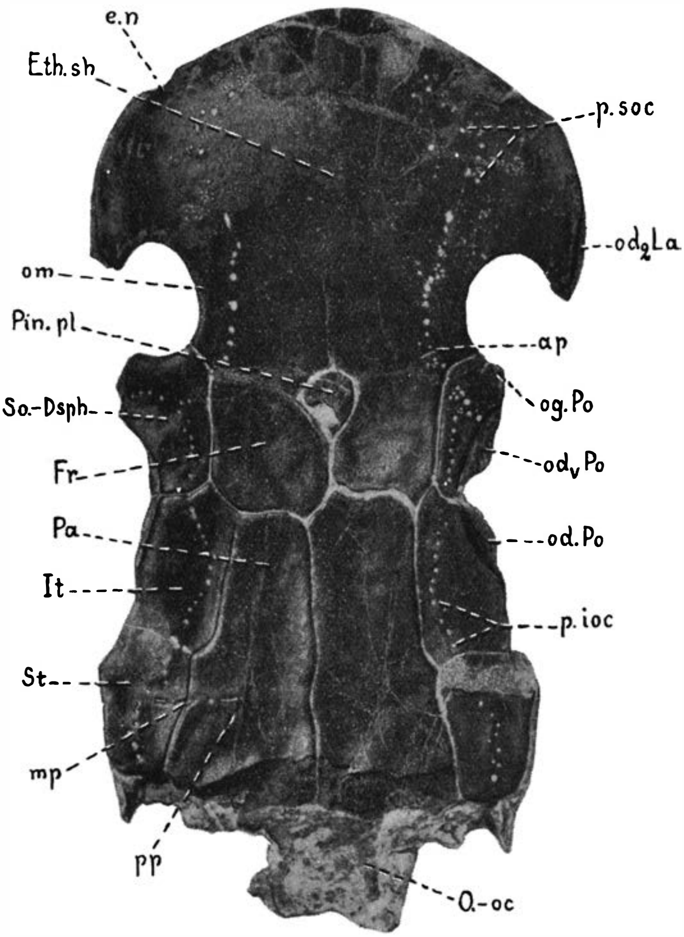

Fig. 18. Indetermined Osteolepid *(Thursius?)*. Dorsal aspect of the cranial roof. The zigzag suture between the parietal and fronto-ethmoidal shields indicates that the divisio cranialis posterior and anterior were immovably connected. The most anterior part of the ethmoidal shield — including the external nares — is pressed in underneath the ventral side of the divisio cranialis anterior and therefore not visible. × 2. Specimen No. 53397 in the Geological Survey, London. G. SÄVE-SÖDERBERGH, Photo.

Eth.sh, ethmoidal shield; *Fr.* frontal (fused anteriorly with the ethmoidal shield and antero-laterally probably also with one or several supraorbitals); *It,* intertemporal; *O.-oc,* otico-occipital; *Pa,* parietal; *Pin.pl,* pineal plates; *So.-Dsph,* surpraorbito-dermosphenotic; *St,* supratemporal; *ap,* groove for the anterior pit line; *e.n,* external naris; *mp,* groove for the middle pit line; *od.Po,* area of the intertemporal, overlapped by the postorbital; *odvPo,* area of the supraorbito-dermosphenotic, overlapped by the postorbital; od_2La, area of the ethmoidal shield, overlapped by the lachrymal; *og.Po,* part of the supraorbito-dermosphenotic, overlapping the postorbital; *o.m,* orbital margin; *p.ioc,* pores of the infraorbital lateral line canal; *pp,* groove for the posterior pit line; *p.soc,* pores of the supraorbital lateral line canal.

1936), and was partly inserted in a groove in the lateral margin of that bone (fig. 7 C; cf. GROSS 1936, p. 70, fig. 8 b), and was finally to a large extent overlapped by the dermosphenotic (og_2Po, figs. 4 B, 7 A—C, 8) and the frontal (og_1Po, figs. 4 B, 7 A, 8). This very complicated attachment to the dermosphenotic must certainly have prevented the postorbital, and thus the whole palatoquadrate-cheek complex, moving in a dorso-lateral or ventro-medial direction. That the postorbital could not slide on the in part uneven overlapped area od_vPo (figs. 7 A, 7 C, 7 D) of the dermosphenotic, as maintained by ALDINGER (1931, p. 302), can be understood from the way, shown in figs. 7 B—D, in which the postorbital is connected with the dermosphenotic. Furthermore, such a sliding was impossible because the postorbital was overlapped by the posterior supraorbital *(E. foordi)*, which — judging by the overlaps (see figs. 5 A, 5 C) and by the fact that in *E. foordi* numerous lateral line canal tubules pass over to it from the frontal — was firmly connected with the other bones of the fronto-ethmoidal shield. The overlapped area of the postorbital is rough, and does not look like a sliding surface. The palatoquadrate-cheek complex is finally connected to the divisio cranialis anterior by a processus ascendens and a processus basalis. Both these processes, which can be clearly seen in *E. foordi,* lack the shiny, periostal bone-layer on a portion of their medial faces. The palatoquadrate-cheek complex accordingly seems to have been practically rigidly connected to both the anterior and posterior parts of the divisio cranialis anterior.

From the above the following conclusions may be drawn:

a. The divisio cranialis anterior was most probably immovably joined to the divisio cranialis posterior.

b. The palatoquadrate-cheek complex was most probably immovably joined to the two cranial divisions, and thus to the cranium.

If these conclusions are correct, the faces of the palatoquadrate (on the tip of the pars autopalatina, and on the processes ascendens, oticus, and basalis), and of the endocranium (*art.aup,* figs. 12, 13, on the processus basipterygideus, on the processus connectens, and on the inner face of the antero-ventral corner of the otico-occipital) where there is no shiny, periostal bone-layer[1], cannot have been articular surfaces, but would indicate the places where the palatoquadrate was in a beginning fusion with the endocranium, and where the ethmosphenoid and the otico-occipital were rigidly attached to each other by cartilage. One is therefore led to think that all these faces mark synchondroses. Most likely, however, the presumed synchondroses between the palatoquadrate and the endocranium were only in an early stage of development. The opinion that the divisio cranialis anterior and posterior were joined by a synchondrosis has previously been advanced by STENSIÖ (1922 a, p. 1242; 1922 b, p. 175).

The circumstance that the palatoquadrate of the Rhipidistids thus is

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[1] Such faces — on the ethmosphenoid fitting the processus ascendens, and on the otico-occipital fitting the processus oticus — have hitherto not been identified with certainty in *E. foordi.*

connected to the endocranium in such a way that, as in *Eusthenopteron*, it may easily become fused to it is of great interest from the point of view of comparative anatomy. A fairly firm connection of this kind between the palatoquadrate and the endocranium must obviously also have existed in the primitive choanate forms, which according to modern opinion were the ancestors of the Crossopterygians and the Stegocephalians (STENSIÖ 1921, pp. 146—147; WATSON 1926, pp. 195—199; SÄVE-SÖDERBERGH 1932 b, pp. 87—105, 1936, pp. 136—168).

In the vertebral column of *Eusthenopteron foordi* there is beneath the spinal canal a wide canal for the notochord. The latter canal is continued in the endocranium by the subchordal fossa, which is of approximately the same diameter as the canal. It is therefore evident that at least the posterior part of that fossa was occupied by the notochord. In some specimens of *E. foordi* this fossa is almost completely bridged by bone ventrally. It is, therefore, hardly probable that any muscles entered it from behind or from below, but whether it was wholly occupied by the notochord, or also held other structures, is as yet difficult to decide. In the Coelacanthids it is wider in the middle than further back, and it is therefore evident that, at least in these, it cannot have held the notochord alone (information supplied by STENSIÖ).

2. — **The fossa apicalis.** The space — here called the fossa apicalis (p. 105; *fossa ap,* figs. 15, 16) — on the most anterior part of the ventral face of the divisio cranialis anterior, shows some interesting features, which will now be briefly considered.

The paired canalis apicalis (p. 93) opens in its roof in a wide paired foramen, the foramen apicale (p. 91; *f.ap*, figs. 10 B, 15, 16). Between the foramina apicalia a fairly short but broad portion (p. 91; *v.ar,* figs. 10 B, 15, 16) of the ventral face of the ethmosphenoid is exposed in the gap between the palatal laminae of the premaxillaries (p. 105; *pal.l,* figs. 10 B, 15, 16) and the vomeres. Assuming that the rostral part of the ethmosphenoid had failed to ossify, we would of course in the place of the area *v.ar* find a large, unpaired opening. This opening would closely resemble the anterior palatal vacuity in certain Stegocephalians, e. g. *Ichtyostega* (SÄVE-SÖDERBERGH 1932 b, text-figs. 5, 8, 9), *Orthosauriscus* (WATSON 1926, fig. 9), *Capitosaurus* (WATSON 1919, fig. 29 C), *Benthosaurus* (BYSTROW 1935, fig. 33 B), *Lyrocephalus rapax* (SÄVE-SÖDERBERGH 1935, text-fig. 65). If then, under the above assumed conditions in *Eusthenopteron*, we imagine that the median parts of the palatal laminae of the premaxillaries are produced backwards so as to cross the median part of the gap below the area *v.ar* and join the vomeres, a paired foramen would arise, which would strikingly resemble the paired anterior palatal foramen of several Stegocephalians, e. g. *Trematosaurus* (WATSON 1919, fig. 25), *Metoposaurus* (WATSON 1919, fig. 20), *Trematosuchus* (KUSMIN 1933, fig. 2), *Lyrocephalus* *euri* (SÄVE-SÖDERBERGH 1936, text-figs. 4 A, 4 B, 5). The agreement in the position and relations between on the one hand the foramina apicalia and the area *v.ar* in *Eusthenopteron* and on the other the anterior palatal foramina and the palatal vacuity in Stegocephalians render it probable that these are homologus structures, an opinion which receives further support from the relations shown to exist between the Rhipidistid Crossopterygians and the Stegocephalians (STENSIÖ 1921, pp. 146—147; WATSON 1926, pp. 195—199; SÄVE-SÖDERBERGH 1932 b, pp. 87—105, 1936, pp. 136—168).

In *Eusthenopteron foordi* and *E. wenjukowi* the foramina apicalia and the area *v.ar*, have nothing to do with the large anterior tusks of the lower jaws, which fit into large pits (*p.rt*, figs. 10 B, 16) on the ventral face of the vomeres. In the Stegocephalians, on the other hand, the anterior palatal foramina (vacuity) are generally considered to have been developed for large anterior teeth in the lower jaws. Whether this is so seems to me to require confirmation. At any rate, that opinion of the function of the anterior palatal foramina (or vacuity) of the Stegocephalians in my opinion is very uncertain.

Other interesting features of the fossa apicalis are, as we have seen (p. 106 above), the presence of a median unpaired intervomerine pit (*iv.p*, figs. 10 B, 13, 14), and a canal leading backwards from it between the vomeres. The only possible explanation that can at present be given of that pit is that it lodged a gland. This gland, which had a well protected position in the pit, probably opened into the mouth cavity through the median slit (*m.sl*) between the vomeres, behind the transverse laminae (p. 106). The gland must have been developed from the pre-choanal part of the mucous membrane of the roof of the mouth, i. e. from the corresponding part of that membrane from which the intermaxillary gland of the *Amphibia* originates, and may therefore be considered homologous to that gland (cf. FAHRENHOLZ 1937, pp. 121, 135—137). Its opening was situated as in certain Urodeles, e. g. *Cryptobranchus, Triton* (WIEDERSHEIM 1877, figs. 22, 141). In certain other Urodeles, however, e. g. in *Salamandra, Anaides* (WIEDERSHEIM 1877, figs. 72, 106), the opening of the intermaxillary gland is almost wholly in front of the vomeres, and on the whole the position of the opening (or openings) of this gland seems to vary both in the *Urodela* (SEIFERT 1932, p. 185) and the *Anura* (MÜLLER 1932, p. 144). Actually, the opening may be found almost anywhere on the prechoanal part of the mucous membrane of the palate, and its varying position there is presumably of small phyletic importance (cf. SÄVE-SÖDERBERGH 1935, pp. 26—28).

The above account clearly shows that the anatomical relations of the palatal vacuity of the Stegocephalians are such that its presence is no evidence of the existence of an intermaxillary gland in that group. The presence of an interrostral fenestra (SÄVE-SÖDERBERGH 1935, pp. 25—28;

see also WERNER 1930, p. 111, »Facialgrube»), however, in certain Stegocephalians is an indication that these forms possessed an intermaxillary gland.

3. — **The nasal capsule and the septomaxillary.** The structure of the ethmoidal region of the ethmosphenoid, and the relations of that region to its dermal bones, will be discussed in detail in the forthcoming monograph on *Eusthenopteron foordi* repeatedly referred to above. In this connection I will only point out a few features of the nasal capsule, and describe the relations of one of the dermal bones, the lateral rostral, to that capsule.

The description given here (pp. 93—95) shows that in the nasal capsule there are a large fenestra choanalis (*fe.ch,* figs. 4 B, 8, 10 B, 11, 15) and a fairly small fenestra narina. The position and relations of these two fenestrae are such that with a high degree of probability they must be considered the homologues of the correspondingly termed openings of the *Tetrapoda.* The canalis apicalis (p. 93) — which leads from the cavum nasi to the fossa apicalis (pp. 105, 117; *fossa ap,* figs. 15, 16), where it opens in the foramen apicale (p. 91; *f.ap,* figs. 10 B, 15, 16) — which conceivably transmitted branches of the r.medialis narium of the n.profundus and vessels, is therefore presumably homologous to the foramen apicale of the nasal capsule of the Tetrapods.

The most anterior part of the cavum nasi has been shown to be incompletely subdivided by a processus intermedius (p. 95; *pr.im,* fig. 11) into a dorsal and a ventral space, of which the latter opens anteriorly through the canalis apicalis just referred to. It is interesting to note that the Rhipidistid Crossopterygians show this tendency to a subdivision of the cavum nasi, as a similar subdivision, though much more developed, is found in another group of the *Choanata,* viz. the *Anura* (for particulars see ECKER-WIEDERSHEIM-GAUPP 1896, pp. 47—48, fig. 23; STADTMÜLLER 1936, pp. 549—558), which group — according to SÄVE-SÖDERBERGH (1936, p. 168) — belongs to an evolutionary line *(Ichtyostegalia-Labyrinthodontia-Phyllospondyli-Anura)* that may be descended from ancestors related to the *Rhipidistia.*

The lateral rostral (p. 103; *R.l,* figs. 6, 7 A, 10 B, 14 A), which contains part of the ethmoidal commissure of the infraorbital lateral line canal, is situated postero-ventrally of the fenestra narina, and covers the postero-ventral part of the lateral wall of the nasal capsule. It forms the ventral border of the external naris, from which border a bony process, the processus derm-intermedius (*pr dim,* figs. 10 A, 14 A), projects into the cavum nasi through the fenestra narina. This process is attached to the dorsal face of the processus intermedius mentioned above. From its relations to the nasal capsule it is evident that the lateral rostral is homo-

Age	Scotland and the Orkneys	The Baltic States
Upper Upper Devonian (lower part)	Rosebrae beds; Dura Den *Bothriolepis major; cristata;* *Phyllolepis concentrica;* *Glyptopomus minor;* *Phaneropleuron andersoni;*	
Lower Upper Devonian	Alves or Scaat Craig *Psammosteus pustulatus;* » *taylori;* *Bothriolepis major;* *Holopthychius giganteus;* » *nobilissimus;* *Dendrodus biporcatus.*	Upper Old Red *Psammosteus maeandrinus;* *Bothriolepis panderi;* » *maxima;* *Coccosteus (trautscholdi?);* *Holoptychius giganteus;* » *nobilissimus;*
		D. o. 1—D. o. 3 (marine) *Ptyctodus obliquus.*
	Whitemire *Asterolepis maxima;* *Bothriolepis major.*	*Bothriolepis cellulosa* marl (D. o. 1; lowermost part) *Psammosteus? serrulatus;* *Bothriolepis cellulosa;* *Coccosteus;* *Eusthenopteron säve-söderberghi;* *Osteolepis grewingki.*
Upper Middle Devonian	Nairn beds *Psammosteus tesselatus;* *Asterolepis maxima;* *Coccosteus magnus;* *»Polyplocodus» leptognathus.*	*Asterolepis* beds (D. m. 4—D. m. 5) *Psammolepis paradoxa; Asterolepis ornata; Coccosteus livonicus; Onchus concinnus; Glyptolepis baltica; »Polyplocodus» rhombolepis; »Dendrodus biporcatus».*
	John o'Groats Sandstone Group; Eday sandstone *Microbrachius dicki;* *Tristichopterus alatus;* *Pentlandia macropterus.*	
	Thurso Flagstone; Rousay beds *Cephalaspis magnifica; Asterolepis orcadensis; Coccosteus decipiens; Coccosteus minor; Homostius milleri; Osteolepis microlepidotus; Thursius pholidotus; Glyptolepis paucidens; Dipterus valenciennesi.*	*Heterostius* beds (D. m. 3) *Psammolepis imperfecta; Pycnosteus palaeformis; Heterostius; Homostius; Glyptolepis baltica; Osteolepis* sp.
	Sandwick fish-bed; Achanarras; Tynet Burn etc. *Pterichthyodes milleri; Coccosteus productus; Coccosteus decipiens; Homostius milleri; Osteolepis macrolepidot.; Glyptolepis paucidens; Diplopterax agassizi; Dipterus valenciennesi; Cheirolepis trailli.*	*Pterichthyodes* beds (D. m. 1—D. m. 2) *Psammolepis striata; Psammolepis heterolepis; Pterichthyodes concatenatus; Coccosteus* cf. *minor; Osteolepis* sp.; *Glyptolepis* sp.

<table>
<tr><th colspan="2">U. S. S. R.</th><th>Canada</th></tr>
<tr><td>**Bureghi beds**
Spirifer tenticulum.</td><td>**Upper variegated series Msta river sect. (u. part)**
Bothriolepis cf. *ornata;*
Phyllolepis sp.</td><td rowspan="8">Euscauminac formation
Euphanerops longaeves;
Cephalaspis laticeps;
Diplacanthus horridus;
Acanthodes concinnus;
» *affinis;*
Bothriolepis canadensis;
» *traquari;*
Coccosteus canadensis;
Eusthenopteron foordi;
Holoptychius quibecensis;
Scaumenacia curta;
Cheirolepis canadensis.</td></tr>
<tr><td>**Ilmen beds**
Spirifer disjunctus.</td><td rowspan="4">**Sjass river section**
Dyptychosteus tesselatus;
Bothriolepis panderi;
Coccosteus trautscholdi;
Holonema radiatum;
Eusthenopteron wenjukowi;
Holoptychius nob.; giganteus;
Dipterus verneuili.</td></tr>
<tr><td>**Svinord beds**</td></tr>
<tr><td>**Shelon beds**
Spir. verneuili
a. *Rhynchonella bifera.*</td></tr>
<tr><td>**Chudovo beds**
Spir. muralis a. *S. verneuili.*</td></tr>
<tr><td>**Pskov beds**
Spirifer muralis; Rhyn. (Ladogia) meyendorfi; Psammosteus; Dyptychosteus; Bothriolepis panderi; Coccosteus mironowi; Ptyctodus obliquus; Holoptychius.</td><td rowspan="3">Montzevo-Yachnowo beds
Bothriolepis panderi.</td></tr>
<tr><td>**Snetnaia beds**
Psammosteus maeandrinus; Bothriolepis panderi; Asterolepis sp.; *Coccosteus; Ptyctodus obliquus; Osteolepis; Glyptolepis; Dipterus.*</td></tr>
<tr><td>**Subsnetnaia beds**
Asterolepis radiata;
Bothriolepis cellulosa;
Holoptychius.</td></tr>
<tr><td>Oredesch beds
Psammosteus; Asterolepis ornata; A. cristata; Coccosteus livonicus; Osteolepis; Dipterus.</td><td></td><td rowspan="3"></td></tr>
<tr><td>Luga beds
Pycnosteus palaeformis; Ganosteus stellatus; Homostius; Heterostius; Asterolepis sp.; *Coccosteus livonicus.*</td><td></td></tr>
<tr><td>Narowa beds
Pterichthyodes concatenatus; Byssacanthus dilatatus; B. crenulatus; Osteolepis fischeri; Glyptolepis quadrata; Dipterus.</td><td></td></tr>
</table>

logous to the septomaxillary[1] of the Tetrapods (cf. STADTMÜLLER 1936, p. 622—624). SÄVE-SÖDERBERGH's (1932 b, p. 102; 1935, p. 118) opinion that the septomaxillary of the Tetrapods is the homologue of the anterior antorbital of the Crossopterygians therefore cannot be correct. In *Eusthenopteron foordi* the latter bone (*Ant.a,* figs. 6, 7 A) lies between the lateral rostral and the nasal series, i. e. dorso-medially of the external naris, and forms the dorso-medial border of that naris.

4. — **Stratigraphical distribution.** The table on pp. 120—121, has been compiled in order to show the stratigraphical distribution of the Crossopterygians discussed in the present paper. This table includes the Old Red areas in which these Cossopterygians have been found, and is compiled from recent papers dealing with these areas. The most important of these papers are: for Scotland and the Orkneys EVANS 1929, WATSON 1935, WILSON and others 1935; for the Baltic States GROSS 1933; for U. S. S. R. OBRUTSHEV 1930, 1933, HECKER, PHILIPPOVA, BARKHATOVA 1932; for Canada ALCOCK 1935; and for the whole subject SÄVE-SÖDERBERGH 1932 a, 1933, 1934 b. Particulars have also been used from GROSS 1930, 1936, DELLE 1935, ORVIKU 1935, TSCHEREISKY 1934, ROMER and GROVE 1935, CLARKE 1913.

As the parallelizations of the different beds and localities shown in the table are based mainly on the fossil vertebrates, lists of these are included in the table to indicate how far the parallelizations are justified. The lists of fossils are taken from the above papers, in some cases directly, in others slightly modified. In several cases badly determined or otherwise uncertain forms have been excluded.

As seen from the table, *Eusthenopteron säve-söderberghi* is found in the lowermost part of the Upper Devonian, whilst *E. wenjukowi* comes from somewhat younger strata. The age of the strata — the Euscaminac formation — in which *E. foordi* is found, is still uncertain. The presence of *Bothriolepis* refers them to the Upper Devonian. The flora also suggests Upper Devonian age (ALCOCK 1935, p. 88). However, the presence of such forms as *Euphanerops*, *Cephalaspis*, and *Cheirolepis* indicates that the age of the *Euscauminac* formation ought to be early Upper Devonian, in which case *E. foordi* and *E. säve-söderberghi* would be approximately contemporaneous.

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[1] The bone marked *Spt.mx* on GREGORY's and others restoration of the skull roof of *Eusthenopteron foordi* (1935, fig. 3 A), which they apparently interpret as a septomaxillary, is the anterior antorbital, and the external naris is in reality situated laterally of that bone. In this connection it should also be noted that the ethmoidal commissure is not situated in the postrostrals as shown in that restoration. Actually, the medial part of that commissure pierces the rostral part of the compound rostro-premaxillary, which follows antero-medially of the lateral rostral.

IV. **Summary.**

The most important results gained from this investigation may be briefly summarized as follows:

1. The generic names *Dendrodus* OWEN, *Cricodus* AGASSIZ, and *Polyplocodus* PANDER cannot be used, because they are given to indeterminable fragments.

2. The external shape of the teeth is of little or no importance to the classification of Rhipidistid Crossopterygians.

3. The distinguishing characteristics of *Tristichopterus* and *Eusthenopteron* are discussed, and a new distinction between these two genera detected.

4. The Crossopterygian remains from the Baltic Upper Devonian described by GROSS (1936) as *Eusthenopteron foordi* belong to a new species, for which the name *E. säve-söderberghi* has been introduced.

5. The Crossopterygians from the Russian Upper Devonian described by ROHON (1889) as *Dendrodus biporcatus* and *Cricodus (Polyplocodus) wenjukowi* in all probability belong to the genus *Eusthenopteron* and have been redescribed as *E. wenjukowi*.

6. The medial face of the prearticular has an independent tooth-bearing plate.

7. The pineal foramen is surrounded by 6 pineal plates, which are true dermal bones.

8. The fossa hypophyseos pierces the parasphenoid, opening on its ventral face.

9. The endocranial orbital roof extends laterally of the supraorbital lateral line canal only in its anterior part, where it is represented mainly by two processes situated close to the ridge on the ventral face of the dermal cranial roof housing the supraorbital lateral line canal. One of these processes, the processus supraorbitalis lateralis, is lateral to, and the other, the processus supraorbitalis medialis, medial to the ridge referred to.

10. The fundamental structure of the nasal capsule has been ascertained. There is a fenestra narina, a fenestra choanalis, and a foramen apicale (canalis apicalis), all probably homologous to the correspondingly termed openings of the Tetrapod nasal capsule.

11. The tendency of the nasal capsule to a subdivision of the most anterior part of the cavum nasi into a dorsal and a ventral space by a processus intermedius is in striking agreement with the conditions obtaining in the *Anura*.

12. An independent lateral rostral is present. This bone and the septomaxillary of the Tetrapods are homologous.

13. The premaxillaries possess palatal laminae.

14. A space, the fossa apicalis, in front of the tooth-bearing laminae of the vomeres is described. In the roof of this fossa the ethmosphenoid is exposed in a gap between the dermal bones, and laterally in this gap are the foramina apicalia on either side. The foramina apicalia and the gap agree well with the anterior palatal foramina and the anterior palatal vacuity respectively in the Stegocephalians.

15. There is a median pit on the anterior face of the posterior wall (the tooth-bearing laminae of the vomeres) of the fossa apicalis. Conceivably this pit housed a gland, a homologue of the intermaxillary gland in the *Amphibia*.

16. The anterior and posterior cranial divisions were rigidly joined to each other.

17. The palatoquadrate-cheek complex was rigidly joined to the cranium.

18. The palatoquadrate was intimately connected — conceivably by beginning synchondroses — to the endocranium in four places.

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