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POROLEPIS (CROSSOPTERYGII) FROM THE LOWER DEVONIAN
 OF THE HOLY CROSS MOUNTAINS

Abstract. — On the basis of the here described remains a new interpretation is given of the structure of the anterior part of the head in *Porolepis*. The writer postulates also the lack of direct relationship between holoptychioids (*Porolepiformes*) and tetrapods.

INTRODUCTION

The results are here reported of research work on the fossil remains of *Porolepis* from the Lower Devonian of the Holy Cross Mountains (Góry Świętokrzyskie).

The studied material was collected during the 1956 summer season at Daleszyce, 15 km east of Kielce. It consists of imprints of fish remains preserved in quartzitic sandstone. All the specimens represent negatives formed owing to the leaching of skeletal elements by solutions migrating through the rock after its consolidation. Though bony tissue has not been preserved, the here discussed imprints and casts reveal an astonishing number of minute structural details. It is often possible to distinguish even the boundary between parts previously occupied by cartilage and membraneous bones. Data have likewise been obtained in respect to the shape of various cavities and the position of most openings, nerve and vessel canals, though, naturally, their complete course cannot usually be traced. Lack of deformation in most specimens is another favourable circumstance. Their excellent and unbiased preparation, effected by nature herself, excludes the risk of the formation of artefacts during the preparation of the material. It is often difficult to avoid them, particularly so when differences between the tissue and the rock material in respect to colouration, hardness, etc., are hardly discernible.

The preparation of material consisted in the first place in the removal of the silt, filling cavities which represents casts of bone remains. The cleaning

was often a difficult task owing to the risk of damaging the minute canal casts. Since the studied specimens are in the form of cavities, with wall surfaces often invisible, the next stage of work consisted in the preparation of latex casts.

All these technical tasks, as well as the preparation of the paper, have been carried out at the Palaeozoological Department of the State Natural History Museum in Stockholm where the author could spend six months thanks to a grant from the Polish Academy of Sciences.

The most sincere thanks are here conveyed by the writer to Professor E. A. Stensiö and to his collaborators Professor E. Jarvik and Dr T. Ørvig, for their hospitality, the facilities offered for research work, the access to all the required technical equipment and comparative materials. Through their great courtesy, the writer was permitted the access to unpublished manuscripts of papers on placoderms, on the lepidomorial and the delamination theory, and provided with all the necessary explanations.

Before commencing his work in Stockholm the writer had the opportunity to visit a number of other European centres of palaeoichthyological studies and to inspect the faunal collections there. He now desires to make his acknowledgement of the courtesy and assistance rendered by Professor A. Heintz of Oslo, Professor J. P. Lehman of Paris, Dr Lector E. Nielsen and Dr H. Bjerring of Copenhagen, Professor D.M.S. Watson and Professor E. I. White of London.

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During the preparation of specimens and latex casts Miss A. Brash of the Palaeozoological Department of the State Natural History Museum in Stockholm offered kind help and valuable suggestions. Mr U. Samuelson of the same Department made some of the plate photographs. Others were made by Miss M. Czarnocka of the Palaeozoological Laboratory of the Polish Academy of Sciences in Warsaw. Mrs J. Humnicka has translated the paper into English.

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The terminology used in this work is chiefly that of E. Jarvik (1942). New terms have been introduced: 1° in the lack of a Latin equivalent of the existing English term, Jarvik's „olfactory ridge” has been replaced by „*eminentia olfactoria*”; 2° in view of some important difference of interpretation, due to which the heretofore accepted term would contradict the nature of

the given morphological element, or when a term was previously reserved for another non-homologous anatomic element (e.g. „crista rostro-caudalis” is replaced by „crista subnarina” with reference to the crest in the nasal cavity of *Porolepis*); 3° in the lack of a term for the described element.

DESCRIPTIVE PART

Porolepis ex grege posnaniensis (Kade, 1858)

Material. — Negatives of 5 fragments of the ethmoidal region, two with preserved orbital region; 1 basisphenoid; 6 fragments of the lower jaw; a number of detached teeth and scales, also fragments most probably representing the shoulder girdle and the gular bone.

Occurrence. — Lower Devonian (Emsian) from Daleszyce in the Holy Cross Mountains.

Description

Fronto-ethmoidal shield

A complete outline of the fronto-ethmoidal shield is discernible on specimens nos. 1 and 2 (pl. I A, B). It is widest on the level of preorbital corners (proc.) where it slightly (12 per cent) exceeds the length along the midline. Hence it is relatively short and broad.

The anterior margin, dorsally delimiting the mouth opening and enclosed in the subnarial corners corresponding to the posterior ends of intermaxillar elements, is sinuously curved owing to a dorsal elevation of the central portion, more conspicuously so on the sides than along the middle. This margin is thickened by a teeth-bearing lamina with the infraorbital sensory canal running along it.

The lateral margin is provided with three more conspicuous notches. The anterior one corresponds to the suture between the fronto-ethmoidal shield and the lachrymo-maxillary. The anterior, vertical margin of the lachrymo-maxillary notch is slightly damaged in all the available specimens. Probably owing thereto the writer has not been able to detect the fenestra exonarina posterior (Jarvik, 1942) although its presence is suggested by the shape of the adjacent part of the ethmosphenoid. A surface on which the lachrymal was superimposed, is situated above the posterior, horizontal part of the margin of the lachrymo-maxillary notch. The next orbital notch starts from the top of the subnarial corner, extending to the postorbital corner. There it passes into the posterior notch, narrowing the fronto-ethmoidal shield to about 56 per cent of its width on the level of the preorbital corner.

The whole surface of the imprint is closely granulated by minute pore casts indicating that the fronto-ethmoidal shield had been covered by cosmine.

Anteriorly of the lachrymo-maxillary notch is the slit-like fenestra exonarina anterior. Below it, from the subnarial corner stretches a row of pores of the infraorbital sensory canal. In its antero-medial course this canal gradually rises to the level of the anterior tip of the fenestra exonarina anterior, there passing into the supraorbital sensory canal and uniting with the rostral commissural canal. The latter descends, gently arched, in the extreme case reaching to the oral margin (spec. no 5). The course of the supraorbital sensory canal is not so readily traceable since, owing to the considerable length of the tubules and their ramification, the pores are haphazardly dispersed nearly throughout the shield surface. The position of the terminal end of the canal — before it joins the infraorbital canal — as well as that of the openings for the otical and postorbital parts of the infraorbital sensory canal (specimen no. 1), suggest that the supraorbital canal originally stretched medially from its junction with the infraorbital canal in the rostral area. Thereafter it arches laterally at some distance behind the fenestra exonarina anterior, finally to turn to the rear where it joins the postorbital and otical part of the infraorbital canal near to the posterior edge of the fronto-ethmoidal shield.

Sphenethmoid

a. *Basisphenoid*. Specimen no. 6 (pl. II A) is a fragmentary basisphenoid of a large individual. The anterior part constituting the dorsum sellae, as well as a considerable upper portion, have not been preserved. The body of the basisphenoid is cylindrical, 20 mm in length and 30 mm in diameter, as measured from the caudal end which forms a concavity (cav.ch.) to fit the anterior end of the notochord. The side surface is convex anteriorly where the horizontal diameter of the basisphenoid body diminishes to 20 mm. Posteriorly it forms the basiptyergoid process (pr.bp.), 17 mm wide as measured along the vertical axis, and 10 mm long as measured along the posterior edge of the basisphenoid body. The antero-lateral edge elongates into a side lamina, afterwards arching downwards and towards the front. Thus the width of the anterior surface of the process attains 15 mm. In its latero-upper part is a coarse area for a junction with the palatoquadrate.

The antero-lower part of the process passes into the posterior part of the suborbital ledge which widens out up to 20 mm, being horizontally placed so as to support the parasphenoid. A groove occurs there between the posterior part of the supporting ledge and the body of the basisphenoid, posteriorly broad, narrowing anteriorly and medially. The groove is filled in

by a laminar tongue-like process (*pr.ling.*) projecting without distinct delimitation from the hind surface of the basiptyergoid process. It runs along the curve of the groove towards the hypophysial opening (*f.h.*) on the ventral side of the basisphenoid body, at a distance of 21 mm from the posterior edge. Together with the adjacent part of the basisphenoid body it delimits the groove (*sulc.aci.*), which runs antero-medially. On the level of the hypophysial opening the groove is branched laterally and posteriorly (*sulc.apse.*) and then directed anteriorly and medially.

Above the basiptyergoid process, on the lateral plane of the body, runs the broad and shallow jugular vein groove.

b. *Interorbital wall.* Both the left and the right sides of the interorbital wall are preserved on specimen no. 1 (*pl. I A, II B*), showing a height from 20 to 25 mm. The lower edge of the wall is slightly oblique to the ventral side of the ethmoidal region. The edge widens out laterally to form a laminar suborbital ledge, ventrally covered by the parasphenoid (*pl. II B, Psph.*). The suborbital ledge ventrally delimits the autopalatine fossa (*f.aup.*) stretching over a distance of 14 mm, that is to the midlength of the interorbital wall and attaining a width (height) of 8 mm. On the level of the fossae autopalatinae the interorbital wall is extremely thin (less than 1 mm), while posteriorly it is thickened up to 4 mm on the level below the optic nerve foramen (*c. II*). Dorsally the fossa autopalatina is delimited by the olfactory ridge (*e.olf.*) and by the suspensory crest (*cr. susp.*). The crest is interrupted on the level opposite the optic nerve opening (*o.II*), where a shallow, roughly bottomed cavity (*pl. II B, ar.mm.obl.*) is noted. Above this area, on the interorbital wall, a small opening occurs (*o.vca.*). On the left side of the specimen this region is somewhat damaged so that the presence of the opening could not be ascertained. The appearance of the left side, however, suggests a natural opening. Beyond the *ar.mm.obl.* cavity a horizontal groove extends on either side of the interorbital wall, 2 mm in diameter, running from the optic nerve opening. Beyond this the interorbital wall thickens out to 8 mm, retaining this thickness nearly to the orbital roof. There it slightly narrows owing to the presence of grooves (*pl. I A, culc.o.lat.*) on both sides. In the antero-upper orbital region the interorbital wall again grows thinner down to 4 mm.

Beyond the optic nerve opening, a smaller one occurs (*o.III*), and farther dorso-anteriorly a trace of another is detectable (*o.IV?*).

The above mentioned thickness of the hind-upper part of the interorbital wall depends on the presence therein of the anterior part of the cranial cavity.

c. *Orbito-nasal wall* has been preserved on specimens no. 1 (*pl. II B*), no. 2, partly on no. 4 (*pl. IV*) and, to a smaller extent, on no. 3 (*pl. III*).

Laterally, on the boundary of the ventral side of the ethmoidal region and the orbito-nasal wall, is a triangular area (fig. 1,2). Its sides consist of the edge of the fronto-ethmoidal shield touching the lachrymal, the postero-lateral edge of the vomeral area (*ar.Vo.*) and the lateral part of the orbito-

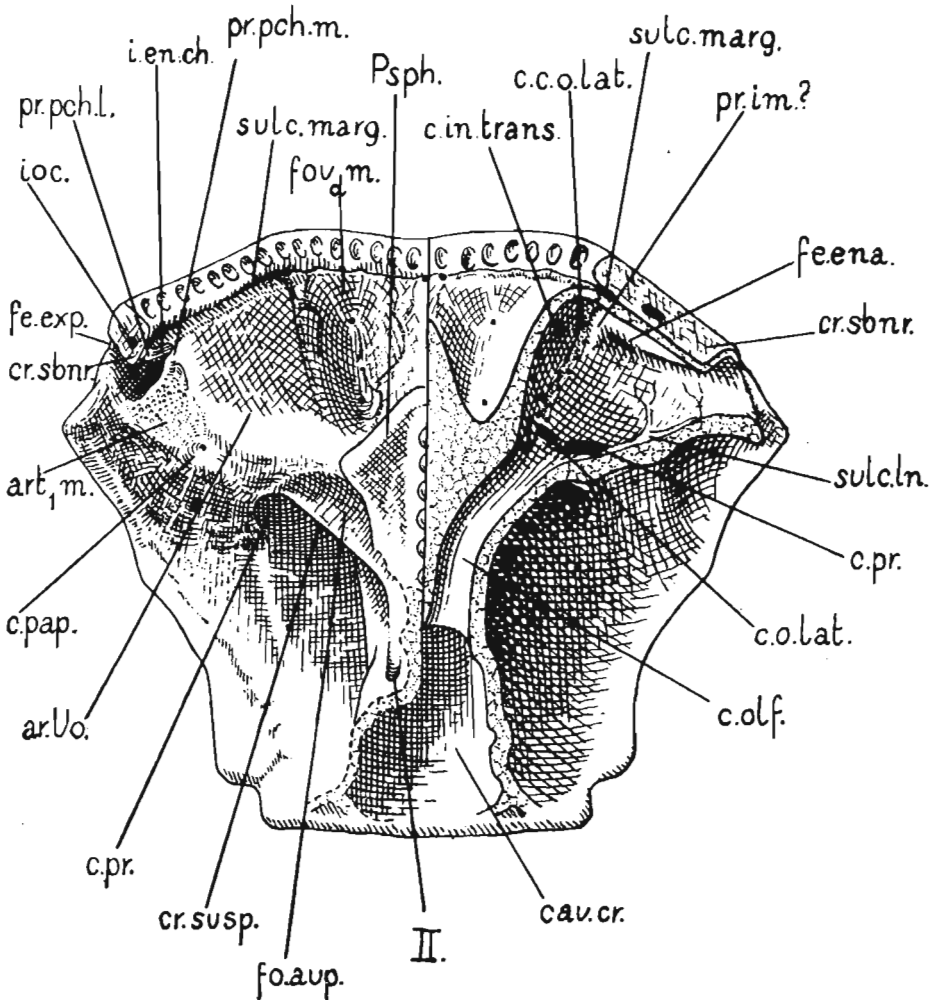


Fig. 1. — Fronto-ethmoidal shield and the ethmosphenoid, ventral view; on the left side — without basisphenoid, on the right — with removed ventral part of the ethmosphenoid

ar. Vo. vomeral area, *art₁m* surface for processus apicalis palatoquadrati, *cav. cr.* cavum cranii, *c. in. trans.* canalis internasalis transversus, *c. o. lat.* canal for N. ophthalmicus lateralis, *cc.o.lat.* canalicules for the twigs of N. ophthalmicus lateralis, *c.ol.f.* canalis olfactorius, *c.pap.* canalis paraapicalis, *c.pr.* canal for N. ophthalmicus profundus, *cr. sbnr.* crista subnarina, *fe.en.* fenestra endonarina anterior, *fe.exp.* fenestra exonarina posterior, *fo.aup.* fossa autopalatina, *fov_am.* medial depression, *inc.exch.* incisura exochoanalis, *ioc.* canalis infraorbitalis, *pr.im.* processus intermedius? *proc.pch.l.* processus parachoanalis lateralis, *pr.pch.m.* processus parachoanalis medialis, *Psph.* parasphenoideum, *sulc.ln.* sulcus lateralis narium, *sulc.marg.* sulcus marginalis, *II* outlet of N. opticus.

-nasal wall. The lateral part of this area contains the great fenestra nasalis posterior communis (fig. 1,2; pl. II B; *fe.npc.*). This is slightly elliptic, with two ventro-lateral notches, giving a subcordate outline to the whole opening. The transverse diameter of the opening in specimen no. 1 is 3 mm. Laterally it is delimited by the outer enchondral wall of the nasal cavity and the adjacent part of the fronto-ethmoidal shield. On the level just above the palatal lamina of the fronto-ethmoidal shield (*la.pal.*), the enchondral wall grows thinner owing to stronger penetration of the recess (*rec.tnp.*), whose distal end approaches to the edge of the fronto-ethmoidal shield. Ventrally the recess — *rec. tnp.* — and the notch — *i.enp.* — are delimited by the palatal list of the fronto-ethmoidal shield (*la.pal.*) and by the enchondral wall of the nasal cavity enveloping it dorsally. The medial edge of the above mentioned palatal list, together with adjacent part of the enchondral nasal cavity wall, laterally delimit another notch — *i.ench.* — of fenestra nasalis posterior communis, situated directly above the notch — *i.exch.* — within the postero-lateral margin of the vomeral area. Medially the endochoanal notch (*i.ench.*) is delimited by the small

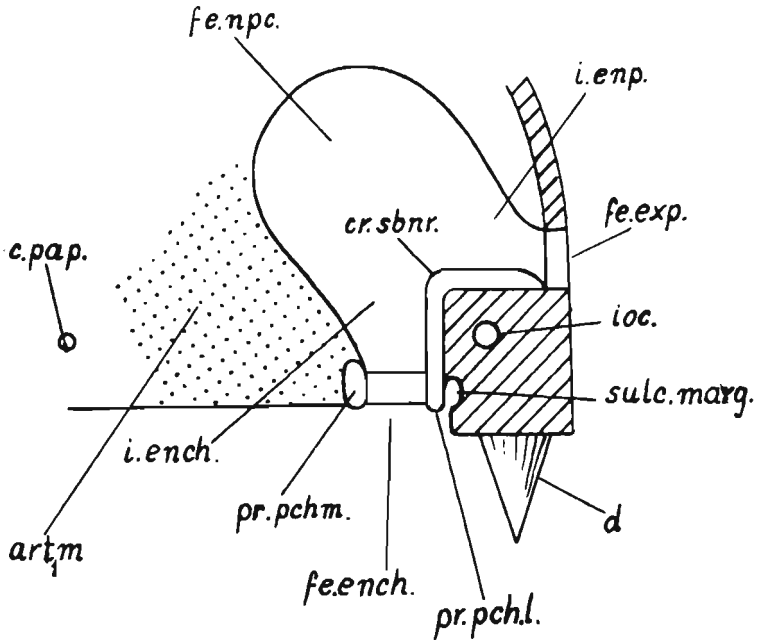


Fig. 2. — Diagrammatical drawing of the region of fenestra nasalis posterior communis

art.m surface for the processus apicalis palatoquadrati, *c.pap.* canalis paraapicalis, *cr.sbnr.* crista subnarina, *d* grasping tooth, *fe.ench.* fenestra endochoanal, *fe.exp.* fenestra exonarina posterior, *fe.npc.* fenestra nasalis posterior communis, *i.ench.* incisura endochoanal, *i.enp.* incisura endonarina posterior, *ioc.* canalis infraorbitalis, *pr.pch.l.* processus parachoanal lateralis, *pr.pch.m.* processus parachoanal medialis, *sulc. marg.* sulcus marginalis, dermal bones (fronto-ethmoidal shield) — stippled.

medial parachoanal process (pr.pch.m.), while the fenestra nasalis posterior communis is delimited by the edge of the coarse area for the processus apicalis palatoquadrati (art₁m). This area is in the shape of a trapezoid, with the longer base facing the fenestra nasalis posterior communis. In specimen no. 1 the base is 4 mm long. Farther medially from the surface for the processus apicalis, in the median angle of the triangle constituting the here described area, is a fair-sized opening of the canal entering into the nasal cavity (c.pap.). This canal runs from the rear and laterally towards the front and medially, as is readily seen in specimens nos. 1 and 3 (pl. III A). Two smaller openings are seen in the outer-upper corner of the here mentioned area in a process by Jarvik (1942), referred to as the "ventro-lateral process of the postnasal wall" (pr.vl.).

Medially of the above described triangular area, the lower part of the orbito-nasal wall forms a cavity (fig. 1; pl. II B; fo.aup.), delimited dorsally by the crista suspendens. They are arched, posteriorly passing into the interorbital wall. Above the olfactory ridge there is a depression containing a large opening at the bottom (c.pr.). A groove (sulc.o.lat.) running on the boundary line between the interorbital wall and the orbital roof is directed towards this opening, as is seen in specimens nos. 1 and 2 (pl. I). On the left side of specimen no. 1 the groove may have stretched to another somewhat smaller opening (c.o.lat.), situated more dorso-medially, similarly as on specimen no. 4 (pl. IV). No other, fairly large openings have been ascertained on the orbito-nasal wall. Only on specimen no. 4 the openings of the very minute canaliculi are detectable in the upper-lateral part of the orbito-nasal wall. Since these canalicules do not penetrate into the nasal cavity, they are to be regarded merely as foramina nutriticii.

d. *Ventral side of the ethmoidal region* (fig. 1; pl. II B; pl. III C) is trapezoidal, 14 mm high on specimen no. 1. In the same specimen the longer base, corresponding to the postero-ventral edge of the ethmoidal region, has a length of 42 mm. The opposite flank, together with the lateral sides forming the dorsal boundary of the mouth opening, is 20 mm long. This surface is delimited on the outside by the protruding, step-like, tooth-bearing edge of the fronto-ethmoidal shield (la.pal.).

In the medial part, a pair of symmetric, elliptical medial depressions (fov_dm. = "cavum internasale" of Jarvik, 1942) occurs on the ventral side of the nasal region. They are separated by a crest (cr.m. — crista mediana = "internasal ridge" of Jarvik, 1942) running in the midline. While in specimen no. 1 these depressions are nearly perfectly elliptic (with length 10 mm, width 5 mm, depth 4 mm), similarly as in *Porolepis "spitsbergensis"*, in specimens nos. 3 and 4 anteriorly they expand much farther, rather approaching *P. "brevis"* and *P. "elongata"*. In specimen no. 3 their length

is from 8 to 9 mm, while the average width is 6 mm and a depth of about 4 mm. In the distinctly larger specimen no. 4 the width is 18 mm, with depth at least 7 mm, while the moderate-sized specimen no. 5 shows a width of 7 mm. Laterally of the medial depressions (fov_m) occur the four-sided areas occupied by vomers (ar.Vo.). These are slightly roof-domed, with one plane descending to the front towards the above mentioned depressions, while the other plane is gently convex, posteriorly inclined. The vomeral areas correspond simultaneously to the bottom of nasal cavities (solum nasi). The postero-medial margin is indicated as an edge passing into a crest, arcuately directed towards the ventral margin of the interorbital wall and passes into the "suborbital ledge". In the medial part the postero-lateral edge of the vomeral area ventrally delimits the above described coarse surface of the processus apicalis palatoquadrati (art_{1m}). Farther laterally it forms a rather small semielliptic notch (i.exch.), bilaterally rimmed by the parachoanal processes (pr.pch.l. and pr.pch.m.). A somewhat larger lateral parachoanal process (pr.pch.l.) passes throughout its dorsal length into a horizontal enchondral lamina. This constitutes that part of the nasal cavity wall which rests on the dorsal side of the palatal ledge of the fronto-ethmoidal shield (la.pal.).

A marginal groove most readily discernible on specimen no. 3 (pl. III C), runs along the inner protruding, step-like margin of the fronto-ethmoidal shield on the ventral side of the nasal region. Some parts of this groove are closed up into a canal by the palatal lamina of the fronto-ethmoidal shield and the anterior part of the ethmosphenoid. Near the antero-lateral corner of the vomeral area (ar.Vo.) this groove gives a branch leading into a slightly smaller opening. Being now notably narrower, the groove — sulc. marg. — continues along the margin of the fronto-ethmoidal shield, anastomosing with a similar opposite groove. Along the course of the anastomosis small openings are discernible leading into the interior between the fronto-ethmoidal shield and the adjacent enchondral part. After branching off the anastomosis the groove becomes all the more shallow. It stretches along the edge of the median crest (cr.m.) forming minute ramifications directed to the bottom of the medial depression and there producing a network. The other groove ramification, branching off at the antero-lateral corner of the vomeral area (ar.Vo.), extends directly towards the medial depression. At the bottom of the depression small openings are discernible on specimen no. 3 (pl. III C), one of them at the anterior, the other on the posterior end of the depression (c,n-b?).

e. *Cranial cavity.* Casts of the anterior part of the cranial cavity are preserved on specimens nos. 1 and 2 (pl. I, II), where we can discern the lower part and the antero-upper recess. The latter is in the shape of a sac-

like chamber, with more or less uniform width. In specimen no. 1 the average width is 7 mm, with length of 20 mm. The fronto-upper recess expands somewhat more in the posterior part only, forming secondary diverticles. The anterior end is dorsally somewhat differentiated and its surface displays traces of bipartition and corrugation. In specimen no. 1 it protrudes anteriorly approx. 5 mm beyond the level of the outer optic nerve foramina, hence it does not attain to the level of the orbito-nasal wall. In specimen no. 2 it is damaged. The lower part of the cranial cavity terminated at a distance of approx. 5 mm behind the level of the external optic nerve openings, passing into two canals (c.olf.), each 3 mm in diameter. These at first run parallel to each other beneath the anterior part of the anterior-upper recess, and then diverge laterally inside the already described olfactory ridges (e.olf.), to open finally into the medio-posterior ends of the nasal cavities beneath the o.pr.foramen.

A shapeless imprint (pl. I, B, x), extending to the level of the orbito-nasal cavity (seemingly a prolongation of the cranial cavity), occurs in specimen no. 2 between the casts of olfactory canals. The ventral face of the ethmosphenoid in this specimen, however, was broken off before being covered up by sediment. Hence, the just mentioned imprint is nothing more but a trace of the damage. This is likewise suggested by its irregular surface and fusion with the olfactory canals which are distinctly bounded in specimen no. 1.

f. *Nasal cavity.* The nasal cavities, situated in the lower part of the nasal region, beneath the vomeral area (fig. 1; pl. II B; pl. III C; ar.Vo.), are onion-shaped or conical, with the apex facing postero-medially, while the base is turned antero-laterally and somewhat dorsally. The postero-lateral part of the nasal cavity elongates into a large canalis nasalis posterior communis (fig. 3, c.npc.), running postero-laterally and ventrally. It opens up as the above described fenestra nasalis posterior communis (fig. 3; pl. II B, fe.npc.). A slit-like fenestra endonarina anterior (fig. 1, 3; pl. II B, fe.ena.), leading into the anterior nasal canal, occurs in the middle of the antero-lateral nasal cavity wall. Anteriorly this fenestra is delimited by a small ridge (pr.inf.?) widening out towards the bottom. Ventrally it rims the fenestra endonarina anterior and is directed backwards, passing without distinct boundaries into a crest (cr.sbnr. — crista subnarina = "crista rostro-caudalis" of Jarvik, 1942).

This crest consists of the palatal lamina of the fronto-ethmoidal shield lined by a thin enchondral wall. It causes the differentiation of two recesses in the canalis nasalis posterior communis. The upper side recess corresponds to the i.enp.notch and may be called the recess for the posterior nasal tube. The lower medial recess leads to the endochoanal notch (i.ench.)

and represents the choanal recess. A much narrower and less conspicuous crest (*cr.or.*) stretches along the border between the antero-lateral and the ventral walls of the nasal cavity. It starts laterally to the summit of the endochoanal notch and terminates slightly below and a little to the front of the fenestra endonarina anterior.

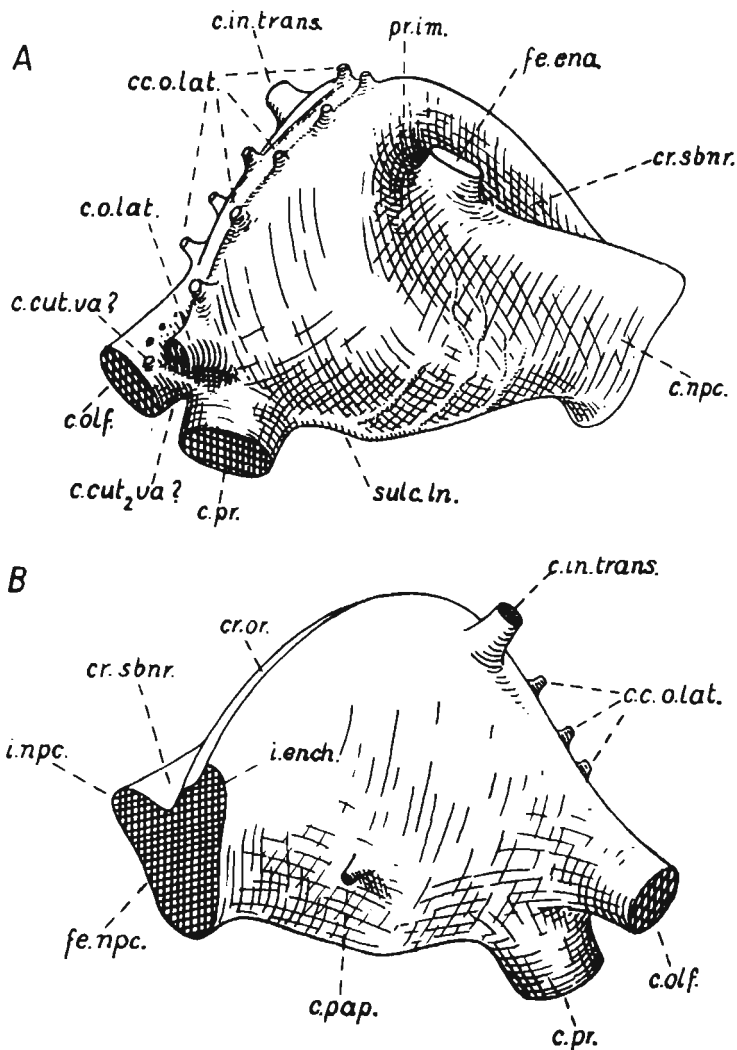


Fig. 3. — The cast of the right nasal cavity: A dorsal view, B ventral view

c.in.trans. canalis internasalis transversus, *c.npc.* canalis nasalis posterior communis, *cc.o.lat.* canalicules for the twigs of *N. ophthalmicus lateralis*, *c.cut.va.?* canal for the presumed cutaneous vein, *c.cut₂va.?* groove connecting the profundus canal with the *c.cut.va.?* opening, *c.o.lat.* canal for *N. ophthalmicus lateralis*, *c.ol.f.* olfactory canal, *c.pap.* canalis paraapicalis, *c.pr.* canal for *N. ophthalmicus profundus*, *fe.ena.* fenestra endonarina anterior, *i.ench.* incisura endochoanal, *i.enp.* incisura endonarina posterior, *ioc.* canalis infraorbitalis, *pr.im.* processus intermedius?, *sulc.in.* groove for ramus lateralis narium, *cr.or.* crista orbitorostralis.

In the medio-posterior extremity of the nasal cavity occurs a fair-sized olfactory nerve foramen (I), in specimen no. 1, with a diameter of 3 mm. Above it, somewhat to the side, is another opening with similar diameter (c.pr.), connecting the nasal cavity with the orbital. In specimens nos. 1 and 2 a groove (sulc.o.lat.) leads into that foramen, running on the boundary between the interorbital wall and the orbital roof (pl. I A). In specimen no. 4 (pl. IV) this groove penetrates by a separate opening (c.o.lat.) into the nasal cavity, medially and slightly dorsally of the o.pr. opening. From the latter opening a groove (sulc.ln.) runs laterally on the posterior nasal cavity wall; along its course it gives off numerous minute branches which in their turn ramify on the adjacent walls of the nasal cavity. The other groove (c.cut.₂va?) is directed medially above the olfactory nerve foramen, close to which one of the main groove ramifications penetrates into the nasal cavity wall through the c.cut.va? opening. Another ramification of the main groove (sulc.mn.) continues its course along the boundary between the medial and dorsal walls of the nasal cavity. Several small openings, piercing the roof of the nasal cavity, occur along that groove. They start from the c.o.lat. opening (if this is present as in specimen no. 4), or from the o.pr. opening (as in specimens 1 and 3). One of these foramens, slightly larger, occurs beneath the groove (sulc.mn.) and leads to the transverse canal connecting the two nasal cavities, as is shown in specimen no. 4 (pl. IV). In specimen no. 3 this canal apparently communicates with the c.v.n-b? opening in the domed bottom of the medial depressions (fov_dm., pl. III A).

Parasphenoid

The only preserved fragment of the parasphenoid is the anterior part resting on the suborbital ledge (specimen no. 1). As is common in *Porolepis* it is slender and narrow, the width in this case being slightly below 10 mm. The anterior end forms an angle with the anteriorly facing apex and slightly encroaches the posterior part of the ventral face of the ethmoidal region, just behind the medial depressions (fov_dm). A crest, bearing a longitudinal row of denticles, extends along the central line on the ventral face of the anterior part of the parasphenoid.

Lower jaw

Specimen no. 7 (fig. 4; pl. V A) represents a large fragment of the left lower jaw of a giant individual. On the level of the anterior end of the prear-

Fig. 4. — Latex cast of lower jaw (specimen no. 7); nat. size

*Co*₁, *Co*₂ coronoids, *d* grasping teeth, *De* dentale, *fov.v.* depressions remaining after resorption of the grasping teeth, *fo.add.* adductor fossa, *for.Meck.* foramen Meckel (s. meckelianum), *fov_d1*, *fov_d2* pits of the upper grasping teeth, *Id*₁, *Id*₂ infradentals, *o.* opening for a vein, *pl.mntm.* concave surface of the mentomandibular, *sulc.v.* groove for a vein, *Prart.* prearticulare

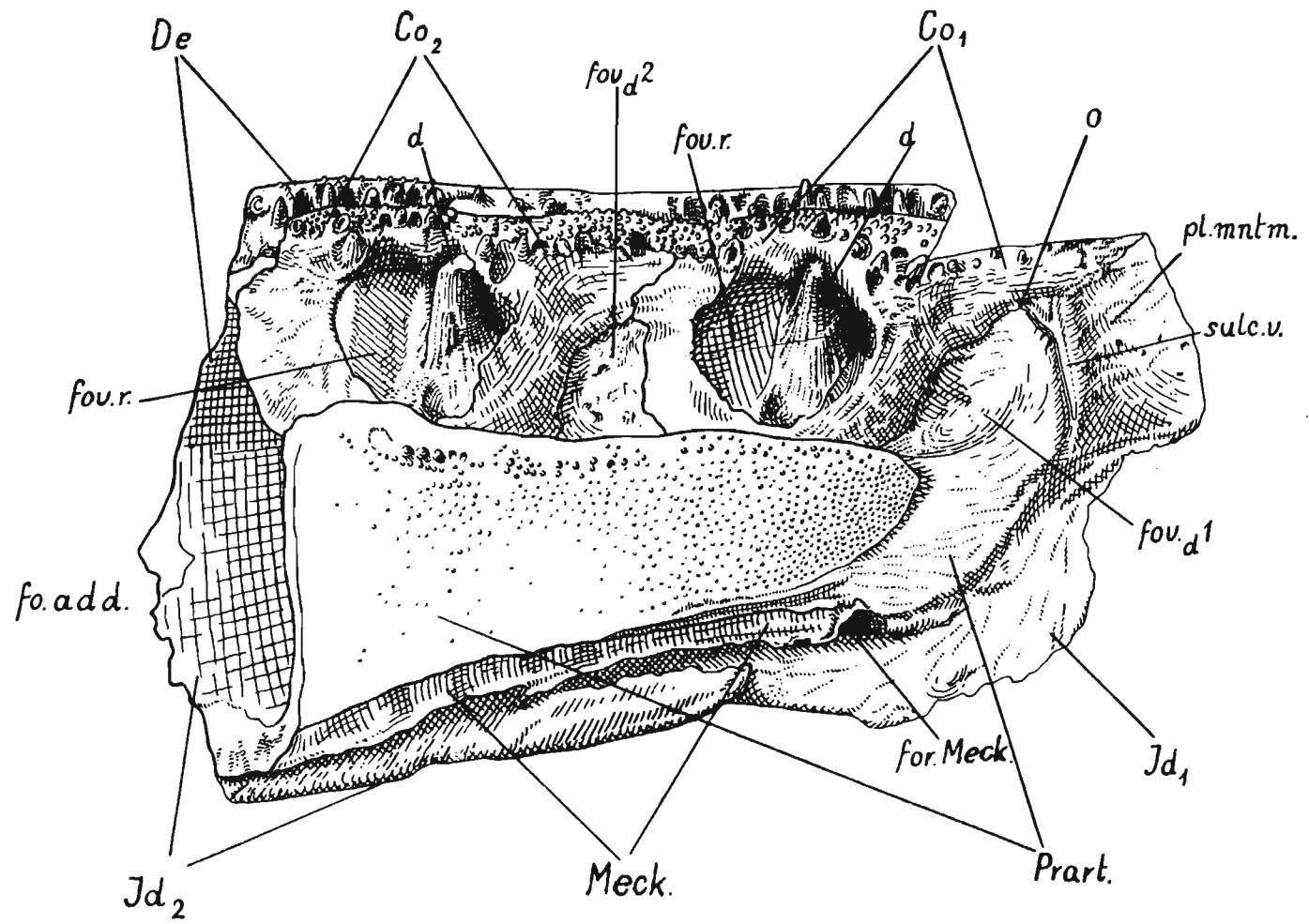


Fig. 4. — Explanation on the opposite page (bottom).

ticular its width is 73 mm, stretching 88 mm beyond the posterior margin of the intercoronoid. The whole fragment is 155 mm long. It shows the inner surface of the jaw. The lower-medial margin is formed by infradentals 1 and 2 (splenialia), whose boundaries are not visible. A more complete infradental on the smaller specimen no. 8 (pl. V B), (length 52 mm, 15 mm anterior width, 22 mm posterior width), indicates that this element stretched to the symphysis. A moderately high wall (7 mm in specimen no. 7), formed by the here uncovered lamina of the Meckelian bone (Meck.), rises steeply above the level of the infradentals. On a level just beyond the anterior end of the tooth-bearing prearticular face a large opening occurs in the Meckelian bone (with a 7 mm diameter in specimen no. 7), leading into the adductor fossa (for. Meck.). Further to the front the Meckelian bone is compressed and forms the symphyseal part, i.e. the mentomandibular. In this region it is hardly possible to distinguish the Meckelian bone from the prearticular. It seems, however, that the prearticular did not reach to the symphysis, leaving uncovered a fair sized concave surface, formed by the mentomandibular. Numerous traces of vascular branches, running to the afore mentioned groove, occur on this surface which is posteriorly bounded by a transverse groove (sulc.v.), forking laterally and penetrating by openings (o.) below the anterior procoronoid process. The free part of the mentomandibular, incomplete in specimen no. 7, is wholly visible in specimen no. 8. Here, on the anterior, bluntly truncated end, we can see the symphyseal face, suboval in outline.

The prearticular is posteriorly raised rather high (19 mm in specimen no. 7) above the medial surface of the outer maxillary wall. Anteriorly it descends gently tapering to form a tongue-like area, with minute shagreen denticles disseminated on it. A row of larger denticles stretches along its outer lateral margin. In specimen no. 7 the last denticle is over 5 mm high, with a basal diameter of 2.5 mm. Anteriorly the prearticular forms an unornamented area, gently inclined medially and steeply descending to the sides. Together with the adjacent procoronoid it forms here a depression to house the upper grasping teeth (fov₁). The bottom of this cavity, anteriorly bounded by the afore described groove (sulc.v.), seemingly represents the uncovered Meckelian bone area.

All the coronoids are ring-shaped, with the anterior process running parallel to the outer margin of the jaw. Hence the coronoids constitute an unbroken lateral boundary, along which there are rows of larger and smaller marginal denticles. In specimen no. 7 the larger ones attain a height of 5 mm, with basal diameter of 3.5 mm. Their walls display fine striation. The procoronoid meets the antero-lateral face of the mentomandibular by its anterior process, while every other process meets an anterior element.

In the remaining area the coronoids are mutually separated, bounding cavities for reception of the grasping teeth. The centres of the coronoids are occupied by pits receiving the larger grasping teeth. In specimen no. 7 they display an average height of 22 mm, and a basal width of 10 mm. They are slightly incurved. This surface is delicately striated suggesting a corrugated wall. Small circular pits (with a diameter of 7 mm in specimen no. 7) are seen on the medial side of the preserved coronoid bases. The distal ends of the dental cavities in coronoids are empty places after the lost grasping teeth. They were coated by a fine osseous layer, or even revealed the uncovered Meckelian cartilage. Specimens nos. 7 and 8 contain casts of the adductor fossa which resembles that described by Gross (1941). It differs, however, in the forward elongation stretching farther below the prearticular. Narrowing more strongly and curving medially, this fossa opens outside by the afore described aperture in the medial wall of the Meckelian bone. The width of the adductor fossa behind the intercoronoids is here 73 mm. After 90 mm of a forward course it narrows to 17 mm, whereafter it bends medially in a funnel-like terminal part. Specimens nos. 9 and 10 (pl. V C, D) do not add any new details besides those provided by specimens nos. 7 and 8. Fragments nos. 11 and 12 only show imprints of the outer surface, coated by a typical cosmine sheath.

Dentition

The described material comprises a number of detached teeth of various size (pl. VI). The grasping teeth are conical, slightly sigmoidal, with medially directed tips. The medial face of each grasping tooth, if complete, is provided with a saucer-shaped cavity, which probably represents a pressure mark, made by a tooth of the following generation. One of the grasping teeth (pl. VI, 21) attains a length of 37 mm, with a basal width (sagittally) of 23 mm. Tooth no. 14 (pl. VI, 23), with medial length of 20 mm, is equally stumpy; its outer labial length is smaller, the basal width being 12 mm. In both these teeth the dumpiness is due to the wearing off or damage of the dental tips. Tooth no. 15 (pl. VI, 22), nearly complete, is 25 mm high, with a basal width (sagittally) of 13 mm, that vertical to the sagittal being 7 mm. Since dental section in the genus *Porolepis* is usually subcircular, the difference of diameters here is probably due to compression. The true diameter is somewhere between the two figures. Other teeth, more complete and not disfigured, are rather slender though strongly expanded at the base. The outer surface of teeth is covered by flat broad ribs, separated by fine grooves, which give an appearance of longitudinal bands. In the lower portions the ribs are frequently subdivided by secondary minute grooves. The size ratio of the various tooth categories in one indi-

vidual is shown in specimen no. 7, which represents a fragmentary lower jaw. The grasping teeth here are 30 mm long medially, 16 mm labially, with a maximum sagittal diameter of 10 mm. The marginal teeth on the coronoids and on the dental attain a length of 7 mm, with a width (section diameter) of 3 mm. Similar dimensions are attained by teeth of the marginal row of the prearticular.

Scales (pl. VI)

Scales vary strongly in shape and size. All possible transition forms are encountered, from those symmetrically rhomboid to asymmetric and rounded ones. An elongated cavity may sporadically occur in the basal area, which is as a rule smooth, but an elevation or a rib may occur too. On the outer surface the free part is frequently separated from the overlapped portion by a distinct groove. The free portion of the scale is evenly coated by dentine, pierced by minute pores. At the anterior border the coating of dentine and enamel is marked all over by ribs, separated by grooves with pores. These ribs have usually a parallel arrangement, sometimes however they converge towards the centre of the proximal free surface border. Others are forked or taper forwards. The length of ribs varies too. In one specimen they occupy 1/3 of the total uncovered area, in another they are nearly altogether absent, as is commonly seen in one of the margins of asymmetric scales. The ribbing also displays a wide scale of passages, from extremely fine striation to thick, sharp and distinctly marked ribs. This is not, however, in any way correlated with the size of scales. On a large scale (pl. VI, fig. 10) the ribs may be very faint, or be strongly developed on a distinctly smaller scale (pl. VI, fig. 4). On some specimens (pl. VI, fig. 1, 12) the anterior ends of ribs are underdeveloped and replaced by tubercles resembling those in *Glyptolepis*. The behaviour of the overlapped scale area varies too. In symmetric rhomboid scales it is symmetric too, mostly broad (up to 1/3 of the overall length of scale); in asymmetric scales one area is broader and usually more strongly curved. On one specimen the overlapped area is very narrow, hardly 1/9 of the scale length. On another specimen (pl. VI, fig. 2) an embayed notch is visible on the anterior border of the free area, due to an extremely shallow course of the sensory canal. Scale dimensions in the described material range from 6 to 35 mm.

Closely indeterminate elements

Specimen in pl. VI, fig. 16, probably represents a fragmentary shoulder girdle (clavicle?). Roundish and longitudinal pits are visible on it. As compared with specimens from the Rhine province, a notably larger surface is here coated by a sheath of dentine and enamel. A similar net-work of

ribs is discernible on specimen no. 22 (pl. VI, fig. 17), whose identification is doubtful. It may represent a fragmentary gular bone. Here the dentine sheath coats a narrow marginal strip only.

DISCUSSION

a. *Ethmosphenoid*

This element is apparently short in *Porolepis* as compared with the ethmosphenoid of *Eusthenopteron*. While in the latter genus the height/length ratio is 1 : 3, that in *Porolepis* was approx. 1 : 2.

The ethmoidal area is broad, short and bluntly terminated. The ventral face of the ethmoidal region is somewhat oblique to the ventral face of the interorbital wall.

The basisphenoid (pl. II A) is short too, the processus connectens poorly developed, resembling that in *Eusthenopteron*. Large processes of processus basiptyergoideus (pr.bp.) with an ear-like area for connection with the palatoquadrate occur on the lateral surface of the body. The latter is posteriorly provided with a characteristic concavity to receive the end of the dorsal chord. The lower parts of the processes elongate downwards and forward to form the posterior portion of the suborbital ledge. In opposition to *Eusthenopteron* where the ledge narrows gradually to the front, in *Porolepis* it retains a uniform width as far as the level of the hypophysial opening (f.h.), thus forming a support for the broad posterior part of the parasphenoid. Between this support and the core of the basisphenoid occurs the process (pr.ling.), projecting from the basiptyergoid process. It bounds a groove, locally closed up into a canal (sulc.aci.) which, at the level of the hypophysial opening, gives off branches directed laterally and backward (sulc.apse.). As is suggested by the description and figure of the parasphenoid and the adjacent portion of the basisphenoid in the genus *Glyptolepis* (Gross, 1936, p. 148-151, fig. 10 A-C), the grooves (sulc.aci.) gave off a secondary branch, directed laterally to the front (sul.pal.). The two branches then united and entered the interior of the skull by openings in front of the hypophysial opening. The ventral side of the sphenoidal region of the genus *Porolepis* differs from the corresponding region in *Eusthenopteron* in that the canals, here transmitting vessels, are closed up by the parasphenoid and the adjoining part of the basisphenoid, not to speak of the presence of the broad ledge supporting the parasphenoid.

The interorbital wall is widest in the upper-hindmost quarter of the orbit, in agreement with the shape of the enclosed cavities and canals which will be discussed here below. It is just as broad on the boundary between the front-upper and the front-lower quarters, owing to the ridge-like eminences (e.olf.), which stretch here, horizontally arched, indicating

the course of the olfactory canals. The crest (*crista suspendens*), occurring on these eminences, is broken up in its distal end by a gently concave, bipartite, coarse area, doubtlessly corresponding to the attachment place of the oblique eyeball muscles (*ar.mm.obl.*). Somewhat higher up and farther backwards, on the level of the posterior end of *fossa autopalatina* (*f.aup.*) occurs the optic nerve opening (*o.II*). As compared with other crossopterygian fishes, among the *Holoptychiidae* and the *Rhizodontidae* as well as *Actinistia*, this opening is relatively small in *Porolepis*. From it a groove is directed anteriorly, with the same diameter, corresponding to the optic nerve running here immediately after being emitted from the skull and before taking a lateral course towards the eyeball. A smaller opening, most likely corresponding to the outlet of the oculomotor nerve (*o.III*), occurs behind the optic nerve opening and somewhat dorsally.

A minute aperture, not observable in the majority of *Rhipidistia*, is present a little more to the front on the olfactory eminence (*e.oif.*), above the oblique eyeball muscles area. It is certainly a natural opening; since it leads into the olfactory canal, its presumable function was to transmit the vein — *vena cerebralis anterior* (*o.vca.*). This vein has likewise persisted in *Rhizodopsis* (Säve-Söderbergh, 1930) among the *Rhipidistia*, also in *Latimeria* (Millot & Anthony, 1958) among the *Actinistia*.

The doubtful opening (*o.IV?*) in front of the oculomotor nerve outlet may have transmitted the nerve *N. trochlearis*.

In *Porolepis*, similarly as in *Latimeria* (Millot & Anthony, 1958), it has not been possible to ascertain a separate opening for the *a. ophthalmica magna*.

The pituitary vein opening (*v.pit.*) occurs quite close to the anterior border of the *basisphenoid*.

A large opening for the *N. ophthalmicus profundus* (*c.pr.*) occurs on the orbito-ethmoidal wall, above the olfactory eminence. The groove transmitting the *N. ophthalmicus lateralis* (*sulc.o.lat.*) is occasionally likewise directed into this opening. Elsewhere the latter nerve enters into the nasal cavity by its own opening (*c.o.lat.*), situated dorsally and medially in relation to the *N. ophthalmicus profundus*. In the ventro-lateral side of the just mentioned wall there is a small opening (*c.pap.*) of indeterminate function, and laterally of it, is an area (*artim*) for junction with the *processus apicalis*, which belongs to that part of the *palatoquadrate* referred to as *pars autopalatina*. The character of this area suggests a *synchondrotic* junction with the *palatoquadrate*, similarly as in *Eusthenopteron*. The small openings pitting this area are most likely nothing more but the *foramina nutriticia*, since it is impossible that any important nerves or vessels were transmitted through the joining surface. The *fenestra nasalis posterior communis* (*fe.npc.*) is placed outside the area for the *processus apicalis*. Two notches occur in the ven-

tral side of this opening. The medial one (incisura endochoanalis, i.ench.) extends ventro-medially to the palatal lamina of the ventral margin of the fronto-ethmoidal shield, and above the groove leading to the notch (i.exch.) on the postero-ventral margin of the orbito-nasal wall. This groove is rimmed by the medial and lateral parachoanal processes (pr.pch.m., pr.pch.l.). As is suggested by the position of the area for the processus apicalis, the whole fenestra nasalis posterior communis, or its greater part beyond the choanal notch, occurred above the dorsal surface of the palatoquadrate. Communication with the oral cavity was possible for the choanal notch only, by means of the just mentioned groove. Thus the internal nostrils occupied but a minor part of the fenestra nasalis posterior communis. Its lateral notch (incisura endonarina posterior, i.enp.) occurs above the palatal lamina of the fronto-ethmoidal shield, and is directed outside towards the place, where Jarvik (1942) puts the incisura exonarina posterior (i.exp.) of the fronto-ethmoidal shield.

The posterior nasal tube and the choanal duct did not completely fill up the fenestra nasalis posterior communis. Hence arises the question as to the function of the remaining considerable portion of that opening. As compared with the corresponding cranial region of other Rhipidistia crossopterygians, it may be ascertained that the here considered portion of the fenestra nasalis posterior communis, owing to its position above the level of the dorsal face of the palatoquadrate, corresponded to the independent opening in the orbito-nasal wall of *Eusthenopteron*. According to Jarvik (1942), this opening corresponded to the naso-lachrymal duct and the trigeminal nerve, i.e. the ramus infraorbitalis. Apparently there is no sound reason to prevent the assignment to the same function to the major dorsal portion of the fenestra nasalis posterior communis in *Porolepis*. This differs from the corresponding opening in *Eusthenopteron* only in that it is not delimited by the skeletal bridge from the area, corresponding to the choanals and leading to the posterior external nostrils. In consequence of such an interpretation of the dorsal side of the fenestra nasalis posterior communis in *Porolepis* we must accept that the considered opening in *Eusthenopteron* cannot correspond to the posterior nostrils. It still remains to be determined, whether it actually pertained to the naso-lachrymal duct. And here again the question arises as to the position in *Eusthenopteron* of the element truly equivalent to the posterior external nostrils. This seems most likely to be the small opening in the orbito-nasal wall, by Jarvik (1942) referred to as the „opening for r. buccalis lateralis” (f.buc.). Similarly as the fenestra endonarina posterior in *Porolepis*, this opening is dorso-laterally situated in relation to the choana, above the palatal lamina of the fronto-ethmoidal shield and the palatoquadrate, and at the same time in the proximity of the lacrimale.

The central portion of the ventral face of the ethmoidal region in *Porolepis* is taken up, throughout its length, by oval medial depressions (fov_dm.), separated by a crest — crista mediana (ar.m. = „internasal ridge” of Jarvik, 1942). These cavities were originally regarded (Stensio, 1932; Holmgren & Stensiö, 1936) as dental pits to lodge the grasping teeth of the posterior coronoids. After it had been proved that teeth lying on coronoids could not reach to the just mentioned depressions, Jarvik (1942) postulated that they housed an intermaxillary gland. In *Porolepis*, similarly as in *Urodela*, this gland was supposed to be paired and to open up by numerous ducts, in opposition to that same gland in *Eusthenopteron* which was supposed to be unpaired, with one duct only, as in *Anura*.

According to Schmalhausen (1958), the unpaired intermaxillary gland is encountered in *Urodela* as well as in *Anura*. In *Anura* it occurs among the upper processes of the premaxillary bones and opens up either by numerous independent ducts (in primitive forms), or by ducts entering the transverse groove or paired pit (in more advanced forms). In *Urodela* this gland penetrates between the nasal sacs, sometimes reaching the dorsal side of the head. Numerous ducts open up on the palate within a small depression. In more advanced forms this depression is stretched into an elongated canal. In *Apoda* the intermaxillary gland consists of the glandular area in the posterior part of the palate.

In the lack of fundamental structural differences of the intermaxillary gland and in view of its complete homology, as ascertained by Schmalhausen in *Anura* and *Urodela*, this element loses its significance for the problem regarding the independent origin of stocks, to which *Porolepis* and *Eusthenopteron* are referable and, furthermore, as regards the polyphyletic or monophyletic origin of amphibians.

The dispersed type of the intermaxillary glands is doubtlessly the most primitive one and was certainly common in primitive amphibians. It is this type of glandular structure that may be expected in crossopterygians, from whom the amphibians have descended — if this gland existed there at all. It is hardly probable that cavities of such considerable size, as those encountered in the centre of the ventral side of the ethmoidal region in *Porolepis*, could have been formed for the area of dispersed glands. Even if, in *Porolepis*¹ as in *Eusthenopteron*, the medial part of the dentale did not bear teeth, surely the ancestors of these forms did possess them, since grasping teeth are encountered on the anterior end of the dentale in other representatives of the crossopterygians, e.g. in *Panderichthys*. It is not, therefore, out of the question that the cavities on the ventral face of the ethmoidal re-

¹ According to Prof. E. Jarvik's kind communication, some dental structures have been detected by him in the symphyseal part of a lower jaw in a relatively closely allied form; they will be described in one of that author's next papers.

gion — independently of their shape — may represent remnants of the original conditions. If so, Stensiö's interpretation (1932) would seem the more probable one, except that the medial depressions would then correspond not to the grasping teeth of the procoronoids, but to those in the symphyseal part of the lower jaw. The poor development of the „prenasal pits" (Jarvik, 1942) in *Eusthenopteron* would suggest their vestigial condition owing to the loss of the symphyseal teeth on the dentale. The homology of the „prenasal pits" in *Eusthenopteron* with the „internasal pits" in *Porolepis* is moreover suggested by the presence in both forms of openings, probably transmitting the same twigs of vessels and nerves (terminal twigs of r. medialis narium?).

Areas, on which the vomers are resting (ar.Vo.), occur laterally of the here discussed medial cavities. In *Porolepis* these areas are rather distant from each other, owing to the poor development of the nasal cavities, and the strong development of the medial depressions. It should be here noted that, both in *Eusthenopteron* and in *Porolepis*, the vomeral area at the same time constitutes the bottom (solum nasi) of the nasal cavities. The greater proximity of the nasal cavities in *Eusthenopteron* is correlated with the arrangement of the vomers, which meet here in the central line over a considerable length. In *Porolepis*, the distance between the vomers, as well as between the nasal cavities, is considerable. The smaller length of the vomers, as well as of the N.palatinus VII canals in *Porolepis*, is surely referable to these differences in the development and arrangement of the nasal cavities and vomers, and to the general proportions of the anterior end of the snout.

A groove, partly closed up into a canal (sulc. marg.), occurs along the lateral and anterior borders of the here adjoining fronto-ethmoidal shield. This groove merges with a similar groove of the opposite side and gives off branches, leading into the openings between the fronto-ethmoidal shield and the adjacent part of the ethmosphenoid. Several ramifications of the just described groove descend into the interior of the medial cavity, merging with the net-work of grooves at its bottom and with the opening discernible there. The marginal groove (sulc. marg.) must have transmitted the nerve twig arising at the N. maxillaris, together with the accompanying vessels.

b. Cranial cavity

The part of the cranial cavity, occupying the interior of the interorbital wall, was divided into two portions: the ventral stretching to the olfactory canals, and the antero-dorsal recess. The here studied specimens do not provide reliable suggestions as to the boundary lines of these two divisions. The delimitation of the anterior quarter of the antero-dorsal recess (rec.pin.), however, is beyond doubt. It certainly corresponded to the pineal recess, likewise encountered in *Eusthenopteron* (Jarvik, 1942, fig. 57, c.pin.). Such

an interpretation is suggested by the fact that the cast of the recess terminates in a place exactly corresponding to that of the pineal depression on the ventral face of the fronto-ethmoidal shield, and that it is ventrally attached to the remaining part of the cranial cavity. The last feature prevents the placing of the forebrain hemispheres within the posterior part of the recess. Hence it may be supposed that, in *Porolepis* similarly as in *Latimeria*, the brain fitted wholly, or in its distinctly greater part, within the cavity of the otico-occipital. This is so probably in the genus *Eusthenopteron* too, where the anterior portion of the cranial cavity is extremely narrow. The corrugated, symmetrically bipartite anterior portion of the recess suggests that in *Porolepis* the pineal apparatus was paired.

The remaining antero-ventral part of the cranial cavity terminated at some distance behind the level of the external optic nerve openings (II), and thus did not protrude anteriorly beyond the level of the orbito-nasal wall. Hence, the ethmoidal part of the cranial cavity in *Porolepis* did not differ in this respect from that in *Eusthenopteron*.

Anteriorly the antero-ventral part of the cranial cavity passed into several broad olfactory canals (c.olf.). These run parallel to each other over a long distance and, after, medially attaining the anterior orbital corner, they diverge laterally to enter the postero-medial extremities of the nasal cavities. Hence the olfactory nerves in *Porolepis* behave analogously as in *Eusthenopteron*.

c. Nasal cavity

In *Porolepis* the nasal cavity is relatively smaller than in *Eusthenopteron*. Fundamentally, however, this cavity is similar in both forms. Owing to the larger transversal dimensions of the ethmoidal region in *Porolepis*, the nasal cavity laterally extends farther, hence being relatively broader and shorter. In the centre of the antero-lateral compressed extremity occurs the slit-like fenestra exonarina anterior — fe.ena. Its front and bottom are rimmed by a thickening (pr.in.). In position it corresponds to the processus intermedius of *Eusthenopteron*, probably being its homologue. It does not, however, conspicuously project into the nasal cavity and does not cause its partition. This is most likely a consequence of the poorer development of the nasal organ in *Porolepis*, most particularly so of the greater thickness of the enchondral wall in the region of fenestra nasalis anterior, as compared with that in *Eusthenopteron*.

Downwards and laterally of the fenestra nasalis posterior communis (fe.npc.) the outer wall of the nasal cavity forms a step-like prominence or crest (cr.sbnr.), by Jarvik (1942) referred to as crista rostro-caudalis. This crest is formed by the medial border of the palatal lamina of the fronto-ethmoidal shield, transmitting the infraorbital (ioc.) canal, and by the thin

enchondral wall of the nasal cavity, repeating the configuration of the adjoining dermal element. The here considered crest separates the recesses of the posterior nasal tube recesses from the choanal recess. No supplementary recess is here present to lodge Jacobson's organ corresponding to the recessus lateralis in *Urodela*. In this connection there is no sound ground to homologize the subnarial crest (cr.sbnr.) with the crista rostro-caudalis. The former owes its origin to the penetration, progressively stronger backwards, of the nasal recess, directed to the fenestra exonarina posterior, into the partition which is thicker at its bottom owing to the presence there of the infraorbital canal.

Neither has it been possible to find in *Porolepis* an equivalent of the palatal process of Seydel. One of the parachoanal processes only could here be taken into consideration. The medial one (pr.pch.), however, lies medially to the choanal opening and, ought, therefore, to be excluded. The lateral one (pr.pch.l.) occupies a similar position in relation to the choanals as the palatal process of Seydel. However, in the absence of the lateral recess there is no fundamental criterion to homologize these two elements. A supposition that the subnarial crest (cr.sbnr.) corresponds to the crista rostro-caudalis (which has been shown to be incorrect), would place Seydel's palatal process along its prolongation, i.e. in another position than in *Urodela*.

The resulting conclusion is that *Porolepis* is not provided with equivalents of the crista rostro-caudalis and Seydel's palatal process, both so characteristic of *Urodela*, similarly as it lacks the lateral recess for Jacobson's organ. However, it would seem that the slight eminence in *Porolepis*, rimming from the front and partly from the bottom the fenestra nasalis anterior, is a homologue of the processus intermedius so strongly developed in Osteolepidae, and most particularly so in *Eusthenopteron*.

A large olfactory canal occurs in *Porolepis* in the postero-medial extremity of the nasal cavity. A smaller opening is present just in front of it on the roof of the nasal cavity. It most likely corresponds to the similarly placed canal in *Eusthenopteron* (Jarvik, 1942, fig. 57 A, C-E, c.cut.va.). Dorsally and laterally of the olfactory canal a large opening conducts to the nasal cavity of *Porolepis*, it lodged the N. ophthalmicus profundus and the accompanying vessels. As is suggested by grooves on specimen no. 4 and by the lack of additional lateral canals in the orbito-nasal wall of specimens nos. 1 and 4, the nerve and the vessels here were subdivided into the medial and lateral branches within the just mentioned opening (c.pr.), similarly as is the case in *Eusthenopteron*. The diameters of these grooves indicate that the nerve with its vessels did not fill up the whole lumen of the opening. Hence its considerable dimensions were not due to

any particularly strong development of the N. ophthalmicus profundus, but solely to the incomplete ossification of the area, on which the nerve with the accompanying vessels effected its penetration into the nasal cavity. An intermediary stage of this character in *Porolepis* and that in *Eusthenopteron foordii* will be observed in *Eusthenopteron wenjukowi*. At the place of penetration of the nervo-vascular complex the latter form (Jarvik, 1937, fig. 12, 13) displays a round depression with ossified bottom, pitted by smaller openings for the nerves and vessels. Supposing that the bottom of this depression (the orbito-nasal pit of Jarvik, 1937) remains unossified, the resultant large sized opening would fully correspond to the N. profundus canal in *Porolepis*.

As has been mentioned here above, the N. ophthalmicus lateralis likewise sometimes penetrates the nasal cavity by the c.pr. opening. Usually, however, this has its own foramen lying medially and dorsally to the c.pr. opening. A number of minute pits (c.o.lat.), by Jarvik referred to as c.prt. (Jarvik, 1942, fig. 42 A, D, E), stretch from the N. ophthalmicus lateralis or, for lack of it, from the opening for N. ophthalmicus profundus; the pits doubtlessly transmitted to the neuromasts of supraorbital sensory canal twigs of the N. ophthalmicus lateralis, and not fibres of the N. ophthalmicus profundus.

A groove entering the c.cut.va? opening, already described and most likely corresponding to the c.cut₂va? canalicule in *Eusthenopteron*, runs on the nasal cavity wall from the opening for the N. profundus, beneath the outlet of the N. ophthalmicus lateralis. Farther anteriorly, on the medial wall of the nasal cavity, there is a fair-sized opening, conducting to the canal, which pierces transversely the internasal wall and enters the opposite nasal cavity by a similar opening. This canal (c.in.trans.) gives off a number of branches in the interior of the internasal wall and apparently communicates with the medial cavities (for_{am}.) on the ventral face of the ethmoidal region. Should this be actually so it might be regarded as an equivalent of the naso-basal canal (c.n-b) in the genus *Eusthenopteron*.

On the back wall of the nasal cavity, midway between the olfactory nerve opening (c.olf.) and the fenestra nasalis posterior communis (fe.npc.), occurs a rather small opening of a canalicule, entering the orbito-ethmoidal wall medially to the processus apicalis area. This canalicule runs from the back and side, antero-medially, approaching the wall of the nasal cavity at a nearly right angle. Its course indicates that this canalicule could not have transmitted the twig of the N. ophthalmicus profundus. Its probable function will be discussed when describing nerves and vessels. In view of its uncertain status the present writer tentatively calls it the para-apical canal (c.pap.).

d. *System of nerves and vessels* (fig. 5)

As has been shown in the beginning of this chapter, the vessel and nerve openings within the orbito-temporal region here fundamentally agree in respect to character and position with those occurring in *Eusthenopteron* and in representatives of the coelacanthids, e.g. *Latimeria*. Differences consist in the presence in *Porolepis* of a vena cerebralis anterior opening, which is missing in *Eusthenopteron*, and in the probable absence of an opening for the a.ophthalmica magna, which has been ascertained

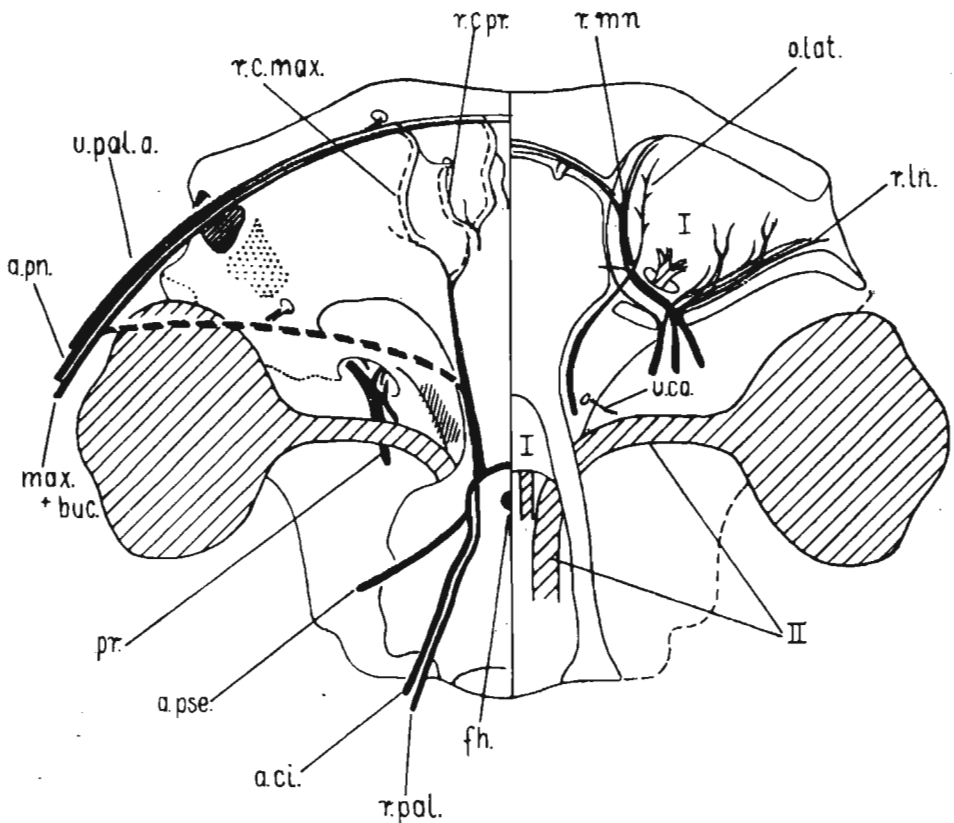


Fig. 5. — Outline sketch of the ethmosphenoid with attempted restoration of the nerves and vessels. On the left side — ethmosphenoid in ventral view, on the right — horizontal section of the same, in dorsal view

act. arteria carotis interna, a.pn. arteria palato-nasalis, a.pse. arteria pseudobranchialis efferens, f.h. fenestra hypophyseos, max.+buc. N. maxillaris and r. buccalis lateralis VII (truncus infra-orbitalis?), o.lat. N. ophthalmicus lateralis, pr. N. ophthalmicus profundus, r.a.max. ramus communicans r. palatini VII cum N. maxillare, r.a.pr. ramus communicans r. palatini VII cum N. ophthalmico profundo, r.ln. ramus lateralis narium, r.mn. ramus medialis narium, r.pal. ramus palatinus VII, v.ca. vena cerebralis anterior, I N. olfactorius, II N. opticus.

in *Eusthenopteron*, also in *Nesides* among coelacanthids. It is in the basisphenoid region in *Porolepis* and, on the whole in holoptychiids only, that the course of vessels and nerves can be traced more fully than in other crossopterygian fishes. This is so in connection with the greater posterior width of the parasphenoid and with the formation by the basisphenoid of a wide support for this element. The groove (sulc.aci.) occurring here transmitted either the ramus palatinus VII alone, or, as seems more probable, this nerve together with a.carotis interna. Exact data on the vessel system of the now living crossopterygian fish *Latimeria* have not yet been published. On the description of the skeleton (Millet & Anthony, 1958) and the attached figures, it may be supposed that in the last named form the a.carotis interna stretched more laterally, piercing the skull more vertically. Transferring these conditions into *Porolepis*, a.carotis interna ought supposedly to be placed within the sulc.a.pse. groove. In the genus *Latimeria*, however, such a course of the a.carotis interna is associated with strong development of the subcranial muscles (muscles sous-céphaliques), which occupy in this form also a medial position in relation to a considerable part of the r.palatinus VII. It is hardly possible that these muscles, maybe analogously developed in *Eusthenopteron*, could have stretched in *Porolepis*, if present at all, farther to the front, beyond the level of the basiptyergoid process. The lingual processes on the basisphenoid may possibly have been its place of attachment. In connection with the poorer development of the subcranial muscles in *Porolepis* a.carotis interna and r.palatinus VII must have been directed more medially. Hence it seems more probable that both the just mentioned nerve and the accompanying vessel were transmitted by the sulc.aci.groove, while the sulc.a.pse. groove would in that case transmit a.pseudobranchialis efferens. Farther to the front from the junction of the vessels, a twig of a.palatina probably branched off from a.carotis interna. It must have run along the r.palatinus VII to the medial cavity of the ethmoidal region, anastomosing with the artery accompanying the N.maxillaris. The a.carotis interna united with the corresponding vessel of the opposite side and entered the cranial cavity in front of the hypophysial opening.

As has been mentioned here above, the N.ophthalmicus lateralis penetrates the nasal cavity either by means of an independent opening, dorso-laterally of the N.ophthalmicus profundus, or together with the last named nerve. Thereafter it runs on the medial part of the nasal cavity roof, giving branches into the supraorbital canal.

N.ophthalmicus profundus enters the nasal cavity by a large opening, laterally and dorsally to the entrance of the N.olfactorius, with the accompanying veins and arteries, which later on ramify in agreement with the

branches of the nerve. Already during their course within the orbito-nasal wall the nerve and vessels give off lateral twigs, stretching laterally on the posterior wall of the nasal cavity (sulc.ln.), to supply the lateral portions of that wall, as well as medial ramifications, stretching on the dorso-medial wall of the nasal cavity and piercing the internasal wall. Vessels of the two sides were united within the internasal wall. Twigs of the N.ophthalmicus profundus may possibly have made their way to the ventral side of the ethmoidal region, by means of the opening at the bottom of the medial cavity, uniting with the terminations of r.palatinus VII. Their behaviour would thus have been analogous to that of twigs of r.medialis narium in *Eusthenopteron*, as reconstructed by Jarvik. The slightly different direction of their course is connected with dissimilarities in the mutual position of the nasal cavity and the medial cavities; in *Eusthenopteron* those are adjacent vertically, while in *Porolepis* horizontally.

Hence, though the course of the terminal minute twigs of the N. ophthalmicus profundus has not been quite certainly determined, it is doubtless that the larger branches (rr.mediales et laterales narium) behave analogously in *Eusthenopteron* and in *Porolepis*.

Jarvik (1942) distinguishes the following branches of the N.maxillaris in *Eusthenopteron*: 1) the ramus infraorbitalis, entering the nasal cavity through the "fenestra endonarina posterior" (this is the opening here identified as corresponding with the dorsal part of the fenestra nasalis posterior communis in *Porolepis*); 2) the postchoanal anastomose uniting within the anterior portion of the orbita with ramus palatinus VII; 3) the ramus palato-nasalis lying laterally to the choana in the canal along the medio-ventral border of the fronto-ethmoidal shield and running to the prenasal pits; it gives off branches to the maxillary and premaxillary teeth and, within the prenasal pits, uniting with the terminal twigs of ramus palatinus VII; 4) the rami cutanei.

Identical branching may have occurred in *Porolepis*. The ramus infraorbitalis may have thus entered the nasal cavity in the dorsal part of the fenestra nasalis posterior communis; behind the orbito-nasal wall there may have occurred the joining with ramus palatinus VII, through the intermediary of ramus communicans; the rami cutanei may have branched in the soft tissues of the suborbital region. The course taken by these ramifications and even their very presence is equally hypothetical in *Porolepis* as in *Eusthenopteron*, since in neither form did they leave any traces in the form of an osseous canal. The ramus communicans only in *Eusthenopteron* runs in its own groove on the dermopalatine, and farther on the boundary between the latter and the autopalatine. The corresponding bone elements in *Porolepis* have not yet been studied.

The normal development of N.maxillaris in *Porolepis* and the similar behaviour of its twigs in *Porolepis* and in *Eusthenopteron* are suggested by the presence of a groove, occasionally closed up into a canal. Its function was doubtlessly that of transmitting the ramus palato-nasalis, which is a twig of the N.maxillaris, or perhaps the truncus infraorbitalis, i.e. the nerve trunk formed together by the tissues of N.maxillaris and buccalis lateralis VII. The fibres of the N.maxillaris penetrated into the ethmoidal region ventrally to the parachoanal lateral process (pr.pch.l.), that is laterally to the choana. Farther on they stretched in a groove, or a canal, along the inner border of the ventral palatal lamina of the fronto-ethmoidal shield (sulc.marg.). Near the antero-median corner of the vomeral area (ar.Vo.) and, at the same time, near the antero-lateral corner of the medial depression, the nerve branch entered the opening between the premaxillary bone and the adjoining enchondral part. Another branch entered the medial depression probably joining with the terminal twigs of r.palatinus VII. Corresponding vessels must have certainly run along with the just described branch of N.maxillaris. Hence there is no sound evidence to suppose that N.maxillaris played a more limited part in the nervous system of the ethmoidal region in *Porolepis*, as compared with that in *Eusthenopteron*.

Ramus palatinus VII was probably transmitted in the groove sulc.aci. and farther on along the border of the parasphenoid. Upon piercing the vomer of the suitable side, it entered the medial depression on the ventral face of the ethmoidal region. Here the terminal twigs could have met the twigs of N.opthalmicus profundus and ramus palato-nasalis V. Apparently, part of the fibres of ramus palatinus VII entered the medial cavity (fov_dm.) directly beneath the anterolateral corner of the parasphenoid, without passing through the canal in the vomer. This was also probably the way followed by the artery and the vein accompanying that nerve. Before attaining the level of the orbito-nasal wall, r.palatinus VII may have anastomosed transversally with the N.maxillaris.

No particular canal is traceable in *Porolepis* for the ramus buccalis VII. The presence of an "orbito-rostral passage", described by Jarvik (1942), could not be ascertained. The para-apical canalicule (c.pap.), whose position may possibly correspond to that of the posterior part of the "orbito-rostral passage", is differently directed. On piercing the orbito-ethmoidal wall, it stretches medially to enter vertically the nasal cavity. There is nothing to suggest its farther position at the bottom of the nasal cavity, or its union with the groove bounded by the crista subnarina and crista orbitorostralis (cr.or.), postero-laterally stretching to the choana. This behaviour excludes the placement of twigs of the N.profundus and r.buccalis lateralis within the para-apical canal. This might have rather

transmitted a vessel branched off from the hypothetical arterial anastomosis, similarly as in *Polypterus*; or from a vein anastomosis, as in some amphibians; or perhaps the para-apical canal was connected with the twig of the N.maxillaris or that of ramus communicans N.maxillare cum N.palatino VII. Hence r. buccalis lateralis may only have stretched laterally of the choana, with the twig of the N.maxillaris, together possibly to form a common trunk, the tr.infraorbitalis. It should be noted here that the presence of a separate canal for r.buccalis VII is equally hypothetical in the case of *Eusthenopteron*. As has been demonstrated by tables, attached to Jarvik's monograph (1942, p. 11-13), the part supposedly corresponding to the position of r.buccalis is without a canal having its own wall, such as is encountered even in ducts for relatively small twigs, e.g. the terminal twigs of ramus medialis narium.

e. *Parasphenoid*

A cast of the anterior portion of the parasphenoid only is preserved in the Daleszyce material. According to a pattern typical of the genus *Porolepis*, it is relatively narrow and provided with a longitudinal crest, bearing a row of denticles. On the shape of the basisphenoid it may be supposed that the posterior portion of the parasphenoid did not to any great extent differ from that common in all holoptychioids. It must have been broad with an arcuate transversal groove stretching on the surface. The central course of the groove probably corresponded to the position of the hypophysial opening. In all the holoptychioids this groove runs along that part of the parasphenoid which rests on the ventral and distal face of the basiptyergoid process, and hence laterally enters the cavity lying behind the junction of the palatoquadrate with the skull, that is the spiracular cavity. If we recognize the connection of this groove with the gill-slits, it must be called spiracular. The hypothetical prespiracular groove would then stretch to the slit between the mandibular and the premandibular arches, and would open up not farther than just in front of the basiptyergoid process. The course followed by the supposed prespiracular groove would have to coincide with the boundary between the area of the derivatives of the mandibular arch and that of the derivatives of the premandibular arch. As results from the diagram drawing given by Jarvik (1954, fig. 39 C), the former is overlapped by the parasphenoid, which thus delimits the boundary of the area of the derivatives of the mandibular arch. The vomers occupy and delimit the area of derivatives of the premandibular arch. It is, therefore, hardly probable that the hypothetical prespiracular groove could transect the surface of the parasphenoid. Its position on the boundary between the parasphenoid and the vomers is much more likely.

Since the groove occurring on the parasphenoid of holoptychioids is the spiracular groove, it must be consequently recognized that, in what the gill-slits and the gill-arches are concerned, the parasphenoid of *Crossopterygii* has attained the same evolutionary stage as *Palaeoniscidae* and the *Arthrodira* (or at least the *Brachythoraci*).

Another problem is that concerning the homology of the various lateral processes on the parasphenoids of the different fish lineages. Independently of their shape and of the fact whether they are the so-called anterior ascending processes, or posterior ascending processes, or maybe both, all of them are invariably connected with the mucuous area behind the mandibular arch and with its derivatives included in the skull, that is belonging to the hyoid arch area. Thus, without taking into account the number of the component elements, the just mentioned processes would be mutually homologous, independently of their shape. The only exceptions here would be such cases, as e.g. in *Polypterus* (Jarvik, 1954), where elements belonging to other gill-arches are included into these processes. Considering that all the attempts to trace adequate criteria for homologizing the anterior and posterior ascending processes in various fishes have, so far, proved a failure, the diagnostic value of the shape of parasphenoidal processes, as well as their presence or absence, should not be over-estimated, when dealing with phyletic relations. That heed should be exercised in this respect is moreover suggested by the secondary character of the shape of these processes, i.e. that their appearance is controlled by the shape of the cranial base. Seemingly there is a correlation, though not an absolute one, between the degree of development of the lateral and ascending processes in the parasphenoid, and the width and degree of flattening of the cranial base. Thus in *Arctolepida*, with the base exceptionally broad and flat, the parasphenoid is devoid of all processes. The same applies to dipnoids, who have the cranial base considerably broader and more flat than that in actinopterygians and crossopterygians. Incipient lateral processes are observable on the parasphenoid of the *Brachythoraci*, in which the ethmosphenoidal region of the cranial base is notably narrower than in *Arctolepida*. Moreover, the development and general appearance of the parasphenoidal processes in crossopterygians are apparently affected by the behaviour of the intercranial slit, as well as by the presence and behaviour of the subcranial muscles.

f. Lower jaw

The posterior part of the lower jaw in the genus *Porolepis* is unknown. However, close structural similarities of other skeletal elements suggest that it did not differ from that common in the genus *Glyptolepis*. In the latter (Gross, 1941), a number of canals arise in the distal portion of the

lower jaw. One of the canals starts as an opening between the articular and the supra-angular, near to the dorsal face and then penetrates the infra-dental series (angulare, splenialia), stretching to the front of the jaw and opening up near the border of spleniale 1. In *Porolepis* it occurs on the level of the posterior margin of the symphyseal area of the mentomandibular. This canal, by Gross (1941) referred to as "c.m.", corresponds, in agreement with that author's interpretation, to the sensory line canal — canalis mandibularis, provided with nerves by the r. mandibularis externus VII.

The outlet of the canal, piercing the articular (canalis articularis, c.art.) and entering the Meckelian cavity, occurs near the ventral margin, below the surface for the articular, somewhat more medially. This canal probably transmitted the r.mandibularis internus VII (= chorda tympani) since in this region it is the only one answering the required conditions. Above the posterior outlet of the canalis articularis, on the margin of the prearticular, Gross ascertained in *Glyptolepis* the beginning of a canalicule (canalis prearticularis, c.pra.), running anteriorly between the prearticular and the articular. That author states that he did not discover the continuation of that canal nor its outlet into the Meckelian cavity. In view of the fairly large dimensions of that canalicule, it is hardly probable that it only transmitted the nutritive vessels for a small portion of the Meckelian bone constituting the articular, or for the prearticular. This is, however, not impossible. It is not out of the question that the lack of its prolongation may be due to the unsatisfactory state of preservation of the studied specimen. In all probability, a canal, by Gross marked with the symbol "c.z." and encountered in *Glyptolepis*, *Porolepis* and elsewhere, e.g. in *Panderichthys*, constitutes the prolongation of that canal. In *Laccognathus* it seems to reach to the symphysis. It is possible that in *Glyptolepis* and in *Porolepis* it opens up anteriorly by a foramen, by Gross marked with the symbol "ca.". This foramen occurs on the boundary between the prearticular, the mentomandibular and the splenial, approximatively on the same level as the mandibular line canal (c.m.), but somewhat more dorsally. In *Panderichthys* this canal opens up on the medial (internal) surface of the jaw, on the level of the procoronoid. At that point two grooves separate from it; one of them runs towards the dental pit on the procoronoid, while another enters, together with the above considered canal "ca.", into the depression in front of the procoronoid (fov₁), by Gross marked with the symbol Pg₁. This depression most likely lodged an important venous sinus, which crossed by means of a wide outlet the antero-lateral procoronoid process on the boundary between its tooth-bearing and toothless portions. Then it passes into a groove bounding the dental and the coronoids. In *Panderichthys* this groove is strongly deve-

loped. It communicates there with the intercoronoid depression (probably lodging the venous sinuses), this time, however, by means of a tunnel beneath the lateral processes of the adjacent coronoids. Numerous canalicules enter the groove penetrating the interior of the jaw. In *Panderichthys* two such openings are to be seen just behind the grasping teeth or behind their cavities on the boundary of the widened up part of the dentale and the antero-lateral procoronoid process. Here the groove curves medially (ventrally) and gives off branches directed anteriorly, while others stretch ventrally backwards. That whole net-work, including the "c.z." canal of Gross and probably the c.prearticularis canal, most certainly lodged vessels and venous sinuses. In holoptychioids and among them in *Porolepis*, the net of veins and corresponding canals was less developed, but, on the whole, in a similar fashion. This applies particularly to vessels and marginal canals between the dental and the coronoids, on the outer surface of all specimens, described in detail in the foregoing chapter; this applies also to the presence of the groove along the medial border of the dentale, between the latter and the Meckelian bone, discernible in specimen no. 8 after the removal of coronoids. Transversal grooves stretch from the just mentioned one; those are directed medially across the intercoronoid depressions and seemingly penetrate below the prearticular. Above such a transversal groove the lateral processes of the coronoid and the intercoronoid span in a fashion similar to that in *Panderichthys*. The anterior transversal groove runs in front of the procoronoid depression and is not covered up. The vessel transmitted by it probably united with that passing through the soft tissues along the medial ventral margin of the Meckelian bone. Laterally, the just mentioned groove gives off a branch, passing to the front, below the antero-lateral procoronoid process. The net-work of minute twigs branching off the transversal groove covers up the surface lying at the front, causing its roughness.

Besides those just mentioned, the r.mandibularis V nerve with the accompanying vessels most probably also penetrated the lower jaw through the Meckelian cavity. Within this cavity that nerve very likely forked into two major twigs, the r.alveolaris inferior, i.e. the ramus mandibularis V lateralis, and the r.mandibularis medialis, corresponding to the r.mylohyoideus, while its terminal end was the equivalent of the r.lingualis in higher vertebrates. The first mentioned of them penetrated between the dentale and the Meckelian bone, running along the a.alveolaris inferior artery and the v.alveolaris inferior s.mandibularis lateralis vein. In *Panderichthys* this vascular bundle finds its equivalent in a canal, by Gross named "c.d."; in *Porolepis* (Holoptychiidae) its corresponding elements are the just mentioned groove on the boundary of the dental, the Meckelian

bones and the coronoids. The other one of the here mentioned nerve branches extended together with a mandibularis medialis s.interna (a.mylohyoidea of higher vertebrates) and v.mandibularis superior (Hochstetter) s.meckeli (Nilsson, 1943). Passing through the Meckelian cavity this bundle stretches to the foramen Meckeli (s.meckelianum anterior) f.mylohyoideus anterior (by Gross marked with the symbol "c.b."), beyond which the terminal twigs pass to the outside. During its course in the Meckelian cavity this nerve, and the accompanying vessels probably too, give off branches to the successive coronoids, directed towards the symphysis.

CONCLUSIONS

Very close agreement of the ethmoidal region in *Porolepis* and *Eusthenopteron* are suggested by the here described materials from the Lower Devonian of Daleszyce. The existing differences mainly refer to proportions. In *Eusthenopteron* the front of the snout has undergone elongation and constriction; in *Porolepis* it has been shortened and widened out. In the latter form this, to a large extent, means the retention of primitive characters. The just mentioned differences concerning proportions, and others occurring within the ethmoidal region of both forms, are connected mainly with the degree of development of the nasal tract and with the different specialization of dentition. *Porolepis* realize a low stage of evolution of the nasal apparatus. The nasal cavities and the choana are small, the internasal wall broad, the fenestra nasalis posterior externa has persisted. To a large extent these characters likewise refer to ancestors of the genus *Eusthenopteron*, i.e. Osteolepidae (comp. Jarvik, 1942, fig. 62 B, *Thursius*?). In them the striking features are: the shortness and width of the ethmoidal region; small, widely spaced vomers; relatively short and broad parasphenoid; presence of a stout support for the parasphenoid. The far spacing of vomers and the appearance of the nasal openings, the widely spaced nasal cavities and the choanal openings — indicate considerable width of the internasal wall. In what dentition is concerned, the grasping teeth on the dentale in *Eusthenopteron* are by Jarvik said to have been lost. In this connection the pits for these teeth on the ventral surface of the ethmoidal region are vestigial. In *Porolepis*, however, they have become peculiarly specialized. The nerve and vascular systems in *Porolepis* agree perfectly with that in *Eusthenopteron*, particularly so in what the major branches are concerned. In *Eusthenopteron*, similarly as in other Osteolepoidae, the posterior external nostrils disappear in consequence of the wide communication between the oral and the nasal cavities provided by choanae.

The close similarities existing between *Eusthenopteron* and *Porolepis* suggest their relatively close relationship. The differences between them

do not, in the writer's opinion, exceed those fitting within the rank of superfamilies. Hence the here discussed forms ought to be placed within two superfamilies: Osteolepioidei and Holoptychioidei, instead of being referred to two distinct orders, the Osteolepiformes and the Porolepiformes (s. Holoptychiiformes of Berg).

The studies of Jarvik (1942) and Ørvig (1957) have shown the closest resemblances between *Porolepis* on the one hand, and *Glyptolepis* and *Holoptychius* on the other. In fact there is reasonable ground to postulate direct relationship between these three genera, which represent three successive morphologic stages of one lineage. Differences refer mainly to varying extent of the reduction of the dentine-enamel coating on the dermal bones and scales, and proportions. These differences do not surpass the rank of subfamilies. In systematics this would mean the assignment of the three just mentioned genera to the same family of Holoptychiidae. This family would comprise the subfamily of Porolepinae, characterized by the presence of cosmine on the dermal bones and scales, as well as that of Holoptychiinae, where the dentine coating has suffered disintegration in a varying degree, or has even completely disappeared. *Glyptolepis*, *Laccognathus* (differing from the former in the presence of peculiar cavities on the lower jaw), also *Holoptychius* and perhaps *Hamodus* — would thus all be referable to the Holoptychiinae. The Porolepinae at present seem to be monotypical.

Remains of the genus *Porolepis*, represented by scales from erratic boulders, were first described by Kade in 1858 as *Gyroptychius posnaniensis* and *Gyrolepis posnaniensis*. Woodward, when describing scales of this form discovered in Spitsbergen, ascertained the identity of the two forms distinguished by Kade, and separated them from the genus *Gyroptychius* by establishing the new genus of *Porolepis* (1891). Later on remains of the genus *Porolepis*, chiefly in the form of scales, have been recorded from the Upper Siegenian and Lower Coblentian of the Rhine Province (Gross, 1933), from the Lower Devonian of Siberia, the Middle Devonian of the Ural (Obručev, 1957) and from the Baltic countries (Gross, 1950).

In spite of frequent occurrence and wide generic distribution and though it has been known for one hundred years, this really existing genus does not contain any well defined species. Kade's *P. posnaniensis* and Obručev's *P. uralensis* are identified on a few scales, that is on elements which cannot be considered as diagnostic for species. The species *P. siegensis* and *P. hefteri* have been established by Gross on fragments of the shoulder girdle. It is possible that *Porolepis siegensis* is merely a less complete fragment of the shoulder girdle, belonging to *P. hefteri*, if not referable to another genus. The Spitsbergen species *P. spitsbergensis*, *P. elongata* and *P. brevis*, subsequently established by Jarvik (1942), are not comparable

with the above named forms, being based on differences of proportions in the ethmoidal region. In view of the nature of differences between these three tentatively established species, their precise definition requires statistical methods, based on ample undeformed material. It is here possible that differences of proportions are due to individual variations, connected with age and sex, as well as to post-mortem deformations. This is suggested by similar variation range in material from the Holy Cross Mountains.

In this state of conditions, particularly for lack of more detailed data on the Middle Devonian form from the Baltic countries, by Gross postulated to be *P. posnaniensis*, typical of the genus, every attempt to determine the specific position of *Porolepis* from the Polish Devonian, is fruitless. Therefore, the here described specimens are by the present writer tentatively referred to the group of the forms including *Porolepis posnaniensis*. This is moreover suggested by the possibility of the occurrence of more than one species within the wide range of distribution, and the long lapse of time over which the genus *Porolepis* has been recorded. For example, very probably the Rhine and Polish forms are two distinct species (or subspecies) since, as is shown by Gross, in the former the prearticular is coated by cosmine, while in specimens from the Holy Cross Mountains, regardless of dimensions, it is strewed with shagreen denticles. Since the disintegration of the uniform dentine coating in rhipidists is of secondary character, it may be supposed that our form, displaying a more advanced evolutionary stage, if not identical with the Middle Devonian forms, will in any case be nearer to them, than are the Rhine specimens.

Independently of the specific position of the representative of the genus *Porolepis* from the Devonian of Poland, general conclusions do not lose any of their significance since they concern superspecific structural features, characteristic of the whole stock of the *Holoptychioidei* v. „*Porolepiformes*”.

Hence we may reasonably infer that the *Holoptychioidei* and *Osteolepioidei* are closely allied superfamilies, whose differentiation dates back to the early stage of development of the choanae in primitive *Rhipidistia*. At this evolutionary stage the choanae did not, most probably, fulfil any important function in the respiration process of atmospheric oxygen.

The slight dimensions of the choanal openings in *Holoptychioidei* would rather suggest that in these fishes the nasal ducts had not yet been included into the respiratory system. The poor development of the nasal apparatus, that of choanae particularly so, together with the peculiar specialization of dentition and the skeletal structure of the pectoral fins, introduce doubts as to the *Holoptychioidei* being the ancestors of any tetrapods. Moreover, the *Porolepis* material from Daleszyce has proved that *Holoptychioidei* are not provided with such structures as *crista rostro-caudalis*, *processus pala-*

talis Seydeli, recessus lateralis for Jacobson's organ, nor a well developed intermaxillary gland. N. maxillaris is equally important in the nerve system of the ethmoidal region as N. profundus. The latter is not particularly well developed. R. buccalis lateralis runs laterally of the choana. Hence there is no such element that would be a characteristic link of the Holoptychioidei with *Urodela*. Thus, the problem of the supposed polyphyletic origin of amphibians, if not completely eliminated, must at least be restricted to ascertaining that ancestors of all tetrapods are to be sought for among forms, tentatively grouped in the family of Rhizodontidae, while Holoptychioidei should be regarded as a blind branch of the stock of Rhipidistia.

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JULIAN KULCZYCKI

POROLEPIS (CROSSOPTERYGII) Z DOLNEGO DEWONU
GÓR ŚWIĘTOKRZYSKICH

Streszczenie

Wyniki badania szczątków *Porolepis* z dolnego dewonu Gór Świętokrzyskich opisanych w tej pracy prowadzą do wniosku, że pod względem budowy ethmosphenoideum rodzaj ten wykazuje daleko idące podobieństwo z rodzajem *Eusthenopteron*. Wyraża się ono: 1) w homologii zagłębienia (*fov_{dm}*) na brzusznej powierzchni okolicy nosowej; 2) w obecności u obu form synchondrotycznego połączenia między processus apicalis palatoquadrati i okolicą nosową ethmosphenoideum; 3) w braku nosowego odcinka jamy czaszkowej; 4) w takim samym przebiegu, sposobie rozgałęziania się i stopniu rozwoju nerwów N. ophthalmicus profundus, N. maxillaris, r. palatinus VII, r. buccalis VII i towarzyszących im naczyń.

Ethmosphenoideum rodzaju *Porolepis* różni się od odpowiedniego elementu u *Eusthenopteron*: a) niewielkimi rozmiarami i b) znacznym oddaleniem od siebie jam nosowych, a w związku z tym c) dużą szerokością przegrody międzynosowej; d) małymi choanami; e) zachowaniem stosunkowo długiego tylnego kanału nosowego i brakiem podziału jego na kanały wtórne; f) brakiem, lub słabym stopniem rozwoju wyrostka proc. intermedius; g) zachowaniem tylnego otworu nosowego zewnętrznego; h) obecnością w jamie nosowej grzebienia związanego z przebiegiem kanału podocz-

dołowego; i) silnym rozwojem jam przyśrodkowych; j) niekompletnym skostnieniem ściany oczodołowo-nosowej w miejscu wnikięcia *N. profundus*; k) dużą szerokością i ogólnymi kształtami basisphenoideum (oraz tylnej części parasphenoideum); l) zachowaniem się *v. cerebialis anterior*.

Cechy *a*, *b*, *c*, a także *f* oraz *k*, które należy uważać za pierwotne, spotyka się również u Osteolepidae. Punkty *d*, *e*, *l* dotyczą cech prymitywnych, właściwych zapewne wszystkim przodkom Rhipidistia i zachowanych przez *Porolepis* i bliskie mu formy, a utraconych przez Osteolepidae i Rhizodontidae. Wreszcie punkt *i* odnosi się do swoistej specjalizacji *Porolepis* i jemu podobnych.

Przyjmując powyższą ocenę różnic i biorąc pod uwagę znaczne podobieństwo (punkty 1-4) między *Porolepis* i *Eusthenopteron* — autor stoi na stanowisku naturalności szczepu Rhipidistia.

Obecność u *Porolepis* grzebienia homologicznego z *crista rostr-caudalis* i podniebiennego wyrostka Seydela, charakterystycznych dla płazów ogoniastych, a nie występujących u innych kręgowców czworonożnych, okazała się co najmniej problematyczna. Jednocześnie z przyjęciem nowej interpretacji szczegółów morfologicznych rodzaju *Porolepis*, oznaczonych nazwami *crista rostr-caudalis*, *processus palatalis* Seydela i *cavum internasale*, oraz ze stwierdzeniem podobnego zachowania się nerwów i naczyń u *Porolepis* i Osteolepidae (= Osteolepiformes Jarvik, 1942; Berg, 1950; Bertin & Arambourg, w Grassé, 1958), znikają rzekome podobieństwa między Holoptychioidei (= Porolepiformes Jarvik, 1942; Bertin & Arambourg, 1958; = Holoptychiiformes, Berg, 1950) i *Urodela*. W konsekwencji, przypuszczenie o polifiletycznym pochodzeniu płazów — o ile nie powinno być całkowicie odrzucone — musi ulec znacznemu ograniczeniu przez uznanie, że przodkowie czworonogów wywodzą się nie z dwóch odrębnych rzędów, lecz co najwyżej z członków jednej rodziny ryb kwastopłetwych, a mianowicie z Rhizodontidae.

Co się tyczy nieparzystej kości skórnej podstawy czaszki — parasphenoideum, to znajdujący się na niej rowek otwiera się z tyłu za wyrostkiem *processus basiptyergoideus*, czyli do jamy spirakularnej. Jeżeli więc związek tego rowka ze szczelinami skrzelowymi jest rzeczą istotną, musi być uznany za spirakularny i w konsekwencji stwierdzić musimy, że parasphenoideum u *Crossopterygii*, *Palaeoniscidae* i *Placodermi* (a przynajmniej u *Brachythoraci*) znajduje się na jednym i tym samym stadium rozwojowym rozpatrywanego elementu.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 70)

Tarcza czołowo-nosowa i ethmosphenoideum, od strony brzusznej; z lewej strony — bez basisphenoideum i tylnej części parasphenoideum (wg okazu no. 1), z prawej — przekrój na poziomie kanałów nerwów węchowych i jam nosowych.

Fig. 2 (p. 71)

Rysunek diagramatyczny okolicy wspólnego tylnego otworu nosowego (*fe.enpc.*).

Fig. 3 (p. 75)

Odlew prawej jamy nosowej od strony grzbietowej (A) i brzusznej (B).

Fig. 4 (p. 77)

Fragment szczęki dolnej (z lateksowego odlewu okazu no. 7); w.nat.

Fig. 5 (p. 89)

Rekonstrukcja przebiegu niektórych naczyń i nerwów u *Porolepis*. Z lewej strony — ethmosphenoideum od strony brzusznej, z prawej — od strony grzbietowej, po usunięciu sklepienia.

Pl. I

Odciski etmosfenoidów od strony grzbietowej: A okaz no. 1, B okaz no. 2; $\times 2$.

Pl. II

A odlew lateksowy basisphenoideum, od strony brzusznej, w.nat.; B odlew lateksowy etmosfenoidu (okaz no. 1), od strony brzusznej, $\times 1,5$.

Pl. III

Okaz no. 3: A okolica nosowa, od tyłu; B to samo, po usunięciu odlewu lewej jamy nosowej; C odlew lateksowy od strony brzusznej; $\times 1,5$.

Pl. IV

Odlew lateksowy okazu no. 4: A strona brzuszna, B od tyłu; $\times 1,5$.

Pl. V

Dolne szczęki: A okaz no. 7 $\times 0,5$; B okaz no. 8, $\times 1,5$; B' odlew lateksowy tegoż okazu; C, D odlewy lateksowe okazów no. 9 i 10, $\times 1,5$.

Pl. VI

Odlewy lateksowe łusek (fig. 1-15), zębów (fig. 18-23) i dwóch nieoznaczalnych fragmentów kostnych (fig. 16, 17) rodzaju *Porolepis*; w. nat.

ЮЛИАН КУЛЬЧИЦКИ

POROLEPIS (CROSSOPTERYGII) ИЗ НИЖНЕГО ДЕВОНА
СВЕНТОКРЖИСКИХ ГОР

Резюме

Изучение остатков *Porolepis* из нижнего девона Свентокржиских Гор, описанных в настоящей работе приводит к заключению, что по строению этмосфеноида род этот обнаруживает далеко идущее сходство с *Eusthenopteron*. Выражено оно: 1) в гомологии углубления (fov_{am} = „cavum internasale” = = „prenasal pits”) на брюшной поверхности носовой области; 2) в наличии у обеих форм синхондротического сочленения между processus apicalis palatoquadrati и обонятельной областью этмосфеноида; 3) в отсутствии этмоидального участка черепной полости; 4) в таком же расположении нервов

(*N. ophthalmicus profundus*, *N. maxillaris*, *г. palatinus VII*, *г. buccalis VII*) и сопутствующих сосудов.

Этмосфеноид рода *Porolepis* отличается от свойственного роду *Eusthenopteron*: а) небольшой величиной и б) значительным удалением друг от друга носовых полостей, а в связи с этим и в) большой шириной межносковой перегородки; г) небольшой величиной хоан; д) сохранением относительно длинного заднего носового канала и отсутствием подразделения его на вторичные каналы; е) слабо развитым отростком *processus intermedius*; ж) сохранением заднего наружного носового отверстия; з) присутствием в носовой яме гребня *crista subnarina*, связанного с прохождением подглазничного сейсмодатчика канала и заднего носового канала; и) сильно развитыми углублениями *foveam*; к) неполным окостенением глазнично-носовой стенки в месте входа *N. profundus*; л) большей шириной и общей формой базисфеноида (а также задней части соседствующего парасфеноида); м) сохранением *v. cerebralis anterior*.

Признаки а, б, в, а частично и ж, л, которые следует считать примитивными, встречаем тоже у *Osteolepidae*. Также примитивными являются признаки г, д, м, которые были повидимому свойственны предкам всех *Rhipidistia* и сохранились у *Porolepis*, но исчезли у большинства *Osteolepidae* и *Rhizodontidae*. Наконец признак и связан со своеобразной специализацией семейства.

Автор имеет возможность убедиться, что у *Porolepis* нет ни *recessus lateralis* для якобсонова органа, ни каких нибудь образований, которые могли бы соответствовать *processus palatalis Seydela*. Гомология же гребня *crista subnarina* с *crista rostro-caudalis*, также как и наличие уже у кистеперых рыб высоко дифференцированной межжелюстной железы, является крайне сомнительной. Из выше изложенного явствует, что между *Holoptychiidae* и хвостатыми амфибиями нет никакого особенного сходства. Если даже считать приведенные факты недостаточными для полного опровержения гипотезы полифилетического происхождения амфибий, так во всяком случае заставляют ограничить предков всех тетрапод до одного семейства — *Rhizodontidae*.

Что касается непарной покровной кости основания черепа — парасфеноида, так находящийся на нем желобок открывается позади *processus basipterygoideus*, т. е. в полость спиракулярную. Ввиду этого, если считать существенными соотношения с жаберными щелями, так упомянутый желобок следует звать спиракулярным. Если это верно, так парасфеноиды кистеперых палеонисцид и панцирных рыб (по крайней мере *Brachythoraci*) находились бы на одной и той же стадии развития рассматриваемого элемента.

EXPLANATIONS OF PLATES

Pl. I

Imprints of ethmosphenoids in dorsal view: *A* specimen no. 1, *B* specimen no. 2; $\times 2$ *c.cut.va?* canal, probably for cutaneous vessels, *c.olf.* canalis olfactorius, *c.pr.* canal for *N. ophthalmicus profundus*, *cav.cr.* cavum cranii, *cav.nas.* nasal cavity, *fov_{dm}*. medial depression, *la.pal.* palatal lamina of the fronto-ethmoidal shield, *rec.pin.* recessus pinealis, *sulc.o.lat.* groove for *N. ophthalmicus lateralis*, *te.orb.* tectum orbitae, *x* trace of damage.

Pl. II

A latex cast of basisphenoid, in ventral view; nat.size.
B latex cast of ethmosphenoid (specimen no. 1), in ventral view; 1.5
ar.mm.obl. area for oblique eye muscles, *ar.Vo.* vomeral area, *c.pap.* canalis paraapicalis, *art_{1m}* autopalatine articular area, *c.pr.* canal for *N. ophthalmicus profundus*, *cr.m.* crista mediana, *cr.sbnr.* crista subnarina, *cr.susp.* crista suspendens, *f.h.* fossa hypophyseos, *fe.ench.* fenestra endochoanalis, *fe.npc.* fenestra nasalis posterior communis, *fe.exp.* fenestra exonarina posterior, *fo.aup.* fossa autopalatina, *fo.nt.* pit for anterior end of notochord, *la.pal.* palatal lamina of the fronto-ethmoidal shield, *o.vca.* opening for *v. cerebralis anterior*, *pr.ling.* tongue-shaped process, *pr.bp.* processus basipterygoideus, *Psph.* parasphenoideum, *sulc. aci.* groove for *a. carotis interna*, *sulc.apse.* groove for *a. pseudobranchialis efferens*, *sulc.marg.* sulcus marginalis.

Pl. III

Specimen no. 3: *A* ethmoidal region in posterior view, *B* the same after removal of the left nasal cavity cast, *C* latex cast in ventral view; $\times 1.5$
c.olf. canalis olfactorius, *c.pap.* canalis paraapicalis, *c_vn-b?* canal probably corresponding to the ventral ramification of the canalis naso-basalis in *Eusthenopteron*, *c.pap.* canalis paraapicalis, *c.pr.* canal for *N. ophthalmicus profundus*, *cav.nas.* cavum nasale, *fov_{dm}*. medial depression, *ioc.* infraorbital sensory canal.

Pl. IV

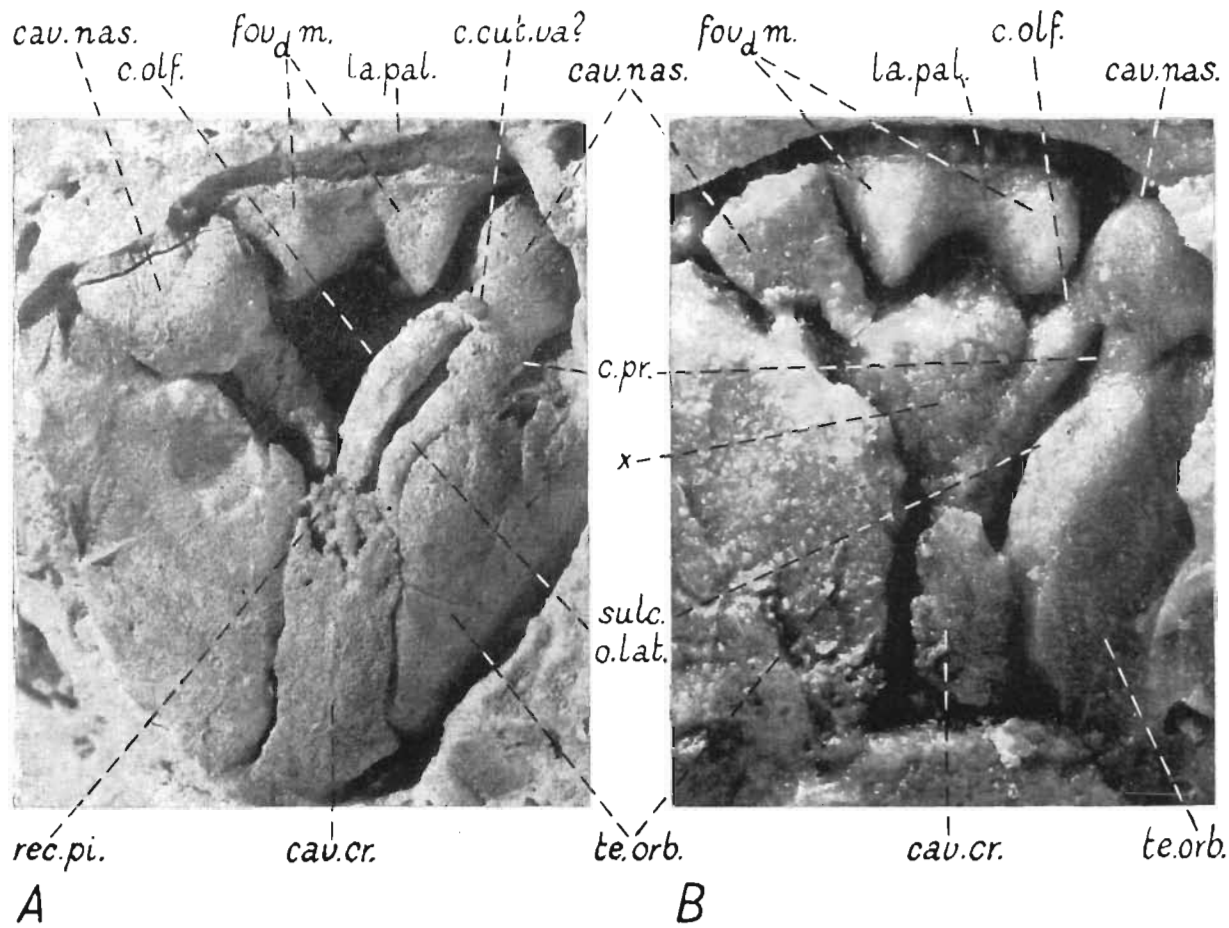
Latex cast of the specimen no. 4: *A* in ventral view, *B* in posterior view; $\times 1.5$
c.in.trans. canalis internasalis transversus, *c.o.lat* canal for *N. ophthalmicus lateralis*, *c.olf.* canalis olfactorius, *c.pr.* canal for *N. ophthalmicus profundus*, *cr.m.* crista mediana, *cr.sbnr.* crista subnarina, *d* denticle, *fe.ena.* fenestra endonarina anterior, *for.nutr.* foramina nutritii, *fov_{dm}*. medial depression, *la.pal.* palatal lamina of the fronto-ethmoidal shield, *pr.im.?* processus intermedius? *sulc.ln.* sulcus lateralis narium and their branches.

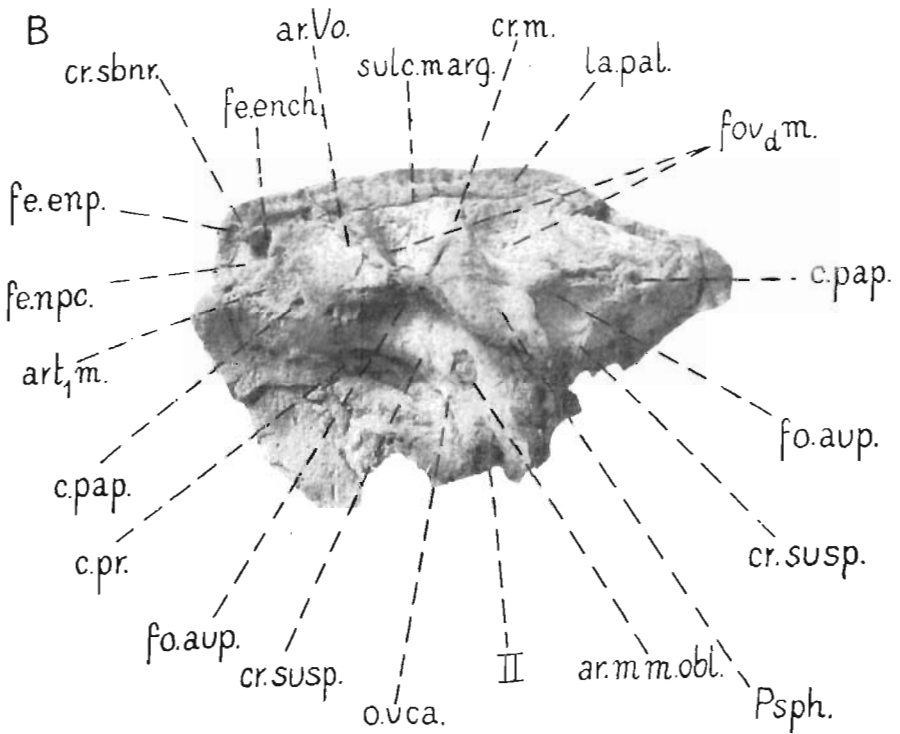
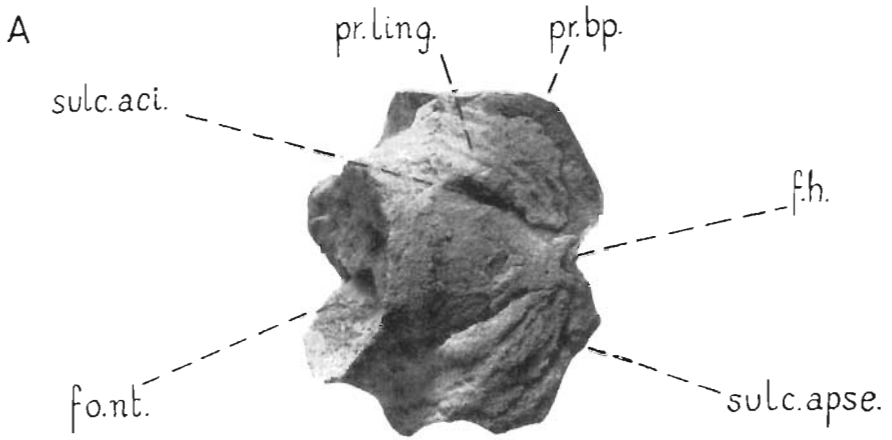
Pl. V

Lower jaws: *A* specimen no. 7, $\times 0.5$; *B* specimen no 8, $\times 1.5$; *B'* latex cast of same; *C*, *D* latex casts of specimens no. 9 and 10, $\times 1.5$.

Pl. VI

Latex casts of scales (fig. 1-15), teeth (fig. 18-23) and two undetermined bone fragments (fig. 16, 17) of *Porolepis*; nat.size.







A

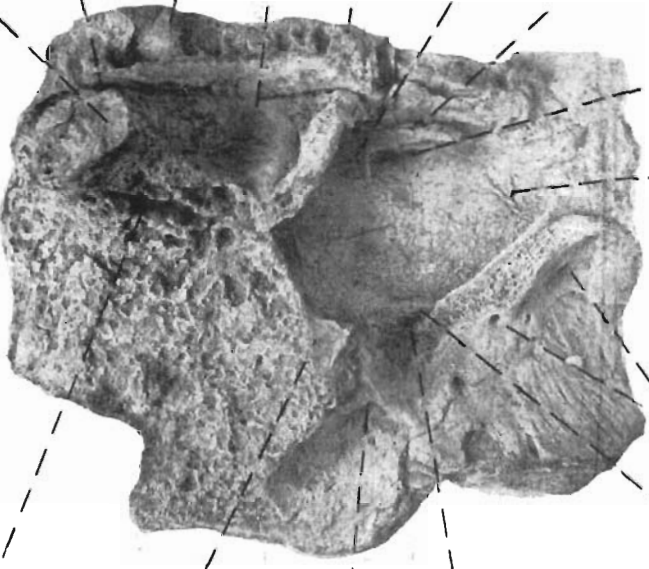
fe.ena. c.o.lat.



cr.sbnr. pr.im.? cr.m. c.in.trans.

B

cr.m. sulc.marg. fov_dm. la.pal. pr.im.? cr.sbnr.



fe.ena.
sulc.ln.
for.nutr.
sulc.ln.

c.in.trans. c.olf. c.o.lat. c.pr.

