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MIDDLE AND UPPER DEVONIAN POROLEPIFORMES FROM EAST GREENLAND WITH SPECIAL REFERENCE TO *GLYPTOLEPIS GROENLANDICA* N.SP.

AND A DISCUSSION ON THE STRUCTURE OF THE HEAD IN THE POROLEPIFORMES

BY

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WITH 108 FIGURES IN THE TEXT, AND 35 PLATES

С РУССКИМ РЕЗЮМЕ

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Abstract

On the basis of a large fossil material, including a grinding series of *Glyptolepis groenlandica* n.sp., the dermal bones and sensory lines of the head and shoulder-girdle, together with the main parts of the braincase and the visceral endoskeleton, have been described in the principal group of Devonian fishes since 1942 known as the Porolepiformes. All the known porolepiforms are very similar in structure and the group is characterised by a great number of specific structural features not found in any other fishes. Detailed comparisons with the Osteolepiformes and the Urodela have shown that porolepiforms agree with urodeles but differ from osteolepiforms not only in the structure of the snout and the intermandibular divison (JARVIK, 1942, 1963a, 1966) but also in the epiphysial complex, the hypophysis, the auditory apparatus, the sensory line system, etc. Because the close relationship that demonstrably exists the Porolepiformes have to be classified together with the Urodela. Consequently taxonomic units such as Sarcopterygii, Crossopterygii, Rhipidistia and Lissamphibia are to be rejected. The renaming of the dermal bones of the skull-roof of osteolepiforms and porolepiforms proposed by WESTOLL has also been rejected and the homologisation of the osteolepiform lateral rostral with the porolepiform nariodal has been disputed. The parapineal organ is retained in larvae of primitive urodeles. The hypophysis is probably paired in origin. The pars tuberalis of the adenohypophysis was well developed in porolepiforms and there were probably portal vessels and a median eminence. BJERRING's assumption (1967) that the paired subcranial muscle is homologous with the polar cartilage has been confirmed. As is now evident this muscle belongs to the 2nd cephalic metamere and is the foremost of a series of metameric basicranial muscles, backwards continuous with the myomeres of the trunk. On the basis of palaeontological and embryological data the cranial metamerism has been discussed and new interpretations of the chondrocranium in urodeles and of the median parts of the parasphenoid have been given. Also, it has been shown that the vertebral column originally continued in front of the hypophysis and that the basis cranii forwards about to the opticus canals is composed of intermetameric vertebrae separated by intrametameric vertebral joints, each spanned by a basicranial muscle. The original, regular metameric arrangement of the dorsal and ventral cranial nerves, of the derivatives of the myotomes and sclerotomes of the cephalic somites, and of the visceral arches is well shown especially in osteolepiforms, porolepiforms and larval urodeles, which groups probably include the most primitive vertebrates. Finally, it has been concluded that the common ancestor of the Acrania and the Craniata (Vertebrata) was a metameric aquatic animal in many respects suggestive of larval "*Amphioxus*".

Резюме

На основе исследований, проведенных на многочисленных экземплярах окаменевших рыб и на препарированной - отшлифованной и порезанной серии Glyptolepis groenlandica n. sp. были описаны покровные кости, сенсорные линии головы, плечевой пояс и все основные части осевого черепа, а также висцеральный эндоскелет среди главной группы рыб девона, известной с 1942г. как Поролепиформы. Все изученные До сих пор Поролепиформы очень сходны по своей структуре. Эта группа отличается большим количеством структурных особенностей, не обнаруженных ни у каких других рыб. Подробные сравнения вышеуказанной группы с Остеолепиформами и хвостатыми амфибиями показали, что Поролепиформы похожи на хвостатые амфибии, однако, отличаются от Остеолепиформ не только по строению носовой области и интермандибулярного отдела (Jarvik, 1942, 1963, 1966), но и по эпифизному комплексу, гипофизу, по слуховому аппарату, системе сенсорных линий и пр. Ввиду близкого сходства, существование которого наглядно доказуемо, Поролепиформы необходимо ставить в один ряд с хвостатыми амфибиями. Следовательно, таксономические единицы, такие как Sarcopterygii, Crossopterygii, Rhipidistia и Lissamphibia должны быть исключены и отброшены. Предложение Вэстолла о переименовании покровных костей черепной крыши у Остеолепиформ и Поролепиформ было также отклонено. Оспаривалась и гомологичность lateral rostral Остеолепиформ с nariodal Поролепиформ. Парапинеальный орган сохранился в личинках примитивных хвостатых амфибий. По своему происхождению, гипофиз, очевидно, является парной структурой. Туберальная часть аденогипофиза была хорошо развита у Поролепиформ и, иовидимому, у них имелись воротные сосуды гипофиза и существовал серединный выступ. Предположение Бьерринга (1967) о гомологичности парного подчерепного мускула с полярным хрящем было подтверждено. Как уже известно, этот мускул относится ко второй мозговой метамерии и является наиболее передним членом в серии метамерных базичерепных мускулов, проходящих сзади непрерывно в серию миомер туловища. На базе палеонтологических и эмбриологических данных велись дискуссии на тему черепного метамеризма, в результате чего по-новому были истолкованы осевой череп хвостатых амфибий и серединные отделы парасфеноида. Было также доказано, что первоначально позвоночный столбик проходил спереди за гипофиз и что основание черепа, почти вплоть до зрительных каналов, состоит из межметамерных позвонков, отделенных друг от друга внутриметамерными позвоночными суставами, каждый из которых перекрыт, как мостиком, базичерепным мускулом. Первоначальное, регулярное метамерное расположение дорсальных и вентральных черепных нервов, производных миотомов и склеротомов мозговых сомитов, црасположение висцеральных дуг хорошо заметно, в особенности у Остеолепиформ, Поролепиформ и у личинок хвостатых амфибий. По всей вероятности, в эти группы входят наиболее примитивные позвоночные животные. И наконец, сделан вывод, что общим предком Acrania и Craniata (Vertebrata) являлось метамерное водное животное, во многих отношениях напоминающее личинку "Amphioxus".

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I. INTRODUCTION

The Porolepiformes (JARVIK, 1942) are in several respects an interesting group of Devonian fishes. Like the Osteolepiformes and other fishes (Coelacanthiformes, Struniiformes) previously classified as crossopterygians they have an intracranial juncture apparatus which probably implies a retention of very primitive vertebrate characters. As to several other structural features, too, the Porolepiformes and the Osteolepiformes appear to be primitive and as recently suggested (JARVIK, 1968a, 1968b) these two groups are probably among the most primitive gnathostomes. In other regards porolepiforms and osteolepiforms, like other early fishes, have become advanced and they have certain specialised features in common for which reason they generally have been classified together as the Rhipidistia. However, in numerous respects they differ very much from each other and of particular interest is that many of the specialisations characteristic of porolepiforms are found in one group of recent tetrapods, namely the Urodela, whereas osteolepiforms in the same way agree with the Anura. On the basis of this and other evidence I have since 1942 repeatedly emphasised that urodeles are closely related to porolepiforms and descendants of primitive porolepiforms or porolepiform-like ancestors, whereas anurans (and most other tetrapods) are descendants of osteolepiforms or osteolepiform-like ancestors.

This conclusion as to a close relationship between urodeles and porolepiforms rests in the first hand on comparative anatomical analyses of two main parts of the head, viz. the snout (JARVIK, 1942, 1966) and the intermandibular division (JARVIK, 1963a; as regards the brain see also STENSIÖ, 1963b) and these parts have been described in detail in porolepiforms. With regards to other parts of the head and the exoskeletal shoulder-girdle, on the other hand, our knowledge hitherto has been incomplete (see HUXLEY, 1861; WOODWARD, 1891a; TRAQUAIR, 1895; GOODRICH, 1909; JAEKEL, 1911, 1927; WATSON & DAY, 1916; HOLMGREN & STENSIÖ, 1936; GROSS, 1936, 1941; WESTOLL, 1937a, 1937b; JARVIK, 1944b, 1948a, 1949, 1950a, 1950b, 1954, 1959a, 1960, 1962, 1963a, 1964, 1965a, 1966, 1967a, 1967b; JESSEN, 1966b, 1967; BJERRING, 1967, 1971, and others). The purpose of this paper is in the first

hand to fill out these gaps in our knowledge as far as that is possible on the basis of the fossil material at my disposal.

The external dermal bones of the head and shoulder-girdle, the sensory lines and the main dermal bones of the mouth cavity are completely or almost completely described in each of the three best known porolepiform genera (*Porolepis*, *Glyptolepis*, *Holoptychius*) and are compared with the corresponding structures in *Eusthenopteron* (JARVIK, 1937, 1942, 1944a, 1944b, 1954, 1963a; BJERRING, 1967, 1971) and other osteolepiforms (*Osteolepis*, *Thursius*, *Gyroptychius*, *Latvius*, *Glyptopomus*, *Megalichthys*, *Eusthenodon*, *Platycephalichthys*, GROSS, 1941; JARVIK, 1948a, 1949, 1950a, 1950b, 1950c, 1952, 1966; VOROBYEVA, 1962; JESSEN, 1966b, 1968a; BJERRING, 1972b; and others). The anterior part of the braincase (the ethmosphenoid) is also described in detail, whereas the posterior part of the braincase and the visceral endoskeleton, although partly well shown in the new species of *Glyptolepis*, *G. groenlandica*, from the Middle Devonian of Canning Land, East Greenland, described below, are only briefly considered. The head of one of the specimens of this new species is now being sectioned with the aid of SOLLAS' grinding method and a detailed description of the otoccipital and the visceral endoskeleton cannot be given before the grinding series has been completed and the wax-models have been made. In this connection it may be mentioned that these parts of the head have not yet been analysed in detail even in *Eusthenopteron* among the osteolepiforms which is the best known of the Devonian "crossopterygians". The brief descriptions that have been given of the posterior part of the braincase and the visceral endoskeleton in this form (JARVIK, 1954, 1963a; STENSIÖ, 1963b; BJERRING, 1967, 1971) concern special problems and a detailed comparative anatomical analysis of these parts is an urgent future task.

II. MATERIAL AND METHODS

The porolepiform material of the head and exoskeletal shoulder-girdle at my disposal includes to about equal extent specimens from the Lower Devonian, the Middle Devonian and the Upper Devonian. The material originates mainly from East Greenland, Spitsbergen and Scotland.

Lower Devonian. — Numerous specimens from various localities in the Wood Bay Series, Spitsbergen (for stratigraphy see FØYN & HEINTZ, 1943; WINSNES, et al. 1960; FRIEND, 1961; ØRVIG, 1969b). Most of this material has been collected by Norwegian expeditions (A. HEINTZ and others) and the English-Norwegian-Swedish (ENS) expedition in 1939 and a few specimens by British (P. FRIEND, Cambridge) and French (J.-P. LEHMAN, Paris) expeditions. Photographs or drawings of cranial remains of early porolepiforms from Spitsbergen have previously been published by STENSIÖ (1922, 1932), JARVIK (1942, 1950a), BJERRING (1967) and JESSEN (1967) and from other areas (the Rhineland, Poland) by GROSS (1936, 1941) and KULCZYCKI (1960; cf. JARVIK 1965a, 1966). All porolepiforms from the Lower Devonian have been referred to the genus *Porolepis* (as regards material referred to this genus from the Soviet Union, see VOROBYEVA, 1963 and ØRVIG, 1969b, p. 297).

Upper Lower Devonian or Lower Middle Devonian. — A few specimens from the upper part of the Wood Bay Series (Verdalen Member of the Stjördalen Division), Spitsbergen, referred to the new genus *Heimenia* (ØRVIG, 1969b).

Middle Devonian. — (1) Some specimens of *Glyptolepis leptopterus*, in part represented by guttapercha casts made by O. JAEKEL, from Lethen Bar and Tynet Burn, Scotland. After 1891, the year of publication of WOODWARD's Catalogue, cranial remains from these localities have been figured inter alia by JAEKEL (1911, fig. 77, 1927, fig. 86), GROSS (1936, fig. 8E, F) and JARVIK (1949, figs. 9A, D, 10B, 1950a, figs. 27B, 31C, 37).

(2) A single specimen of *Glyptolepis*? cf. *paucidens* (No. 47838, Brit. Mus., Lond.) from Thurso Bay, Scotland dissolved from the rock by

acids. A skull (No. 1964.18 RSM, Edinb.) probably from the same area has recently been figured by THOMSON (see fig. 40).

(3) Two specimens of *Glyptolepis* from unknown localities in Scotland previously figured by JARVIK (1954, fig. 19A, C, D).

(4) About twenty specimens, some showing both the head and the body, of *Glyptolepis groenlandica* n. sp. found close together in a single block and some other material from the *Asterolepis saevesoederberghi* Series in Canning Land, East Greenland (as regards stratigraphy see JARVIK, 1949, 1961). Previously figured as *Glyptolepis* or *G.* sp. by JARVIK (1962, 1963a, 1963b, 1964, 1965a, 1966), STENSIÖ (1963b) and BJERRING (1967).

(5) A fragmentary lower jaw of *Glyptolepis baltica* and a dermal bone, probably the interclavicle, of *Glyptolepis* sp. (see fig. 52D, pl. 34:5; GROSS, 1936, fig. 10G, H) from the Oredesch beds in the Baltic Devonian. Other material of *G. baltica* has previously been figured by GROSS (1936, figs. 1B, 3C, F, 7E–G, 8A, B, 9F, 10, pl. 7:1, pl. 8:6, 1941, figs. 1–5).

Material of *Glyptolepis*, *Glyptolepis* sp. or Porolepiformes indet. from the Baltic area, Norway and the Series with *Gyroptychius groenlandicus* in East Greenland has been figured by JARVIK (1944b, fig. 9A, 1949, figs. 9B, C, 10A, pl. 7:2–5, 1950a, fig. 34, pl. 24:1, 2, 1950b, fig. 3A) and of *Laccognathus panderi* ("*Dendrodus biporcatus*") from the Oredesch and Podsnetogor beds in the Baltic area by GROSS (1936, figs. 3A, B, E, 4, 5, 6, 7A–D, 8D, 9G, pl. 7:2, 1941, figs. 7–14) and JARVIK (1950a, fig. 31B).

Upper Devonian. — According to OBRUCHEV and others (see GROSS, 1956, p. 138; VOROBYEVA & OBRUCHEV, 1964) the Oredesch and Podsnetogor beds are lowermost Upper Devonian in age. This means that the genus *Glyptolepis* in the Baltic area is represented in the lowermost Upper Devonian as it is also at Escuminac Bay, where *Glyptolepis* judging from scale structure occurs together with *Holoptychius* (ØRVIG, 1957). However, the characteristic porolepiform genus of the Upper Devonian is *Holoptychius*, known by scales or other skeletal parts from many parts of the world. The following material of *Holoptychius* showing cranial remains has been available.

(1) An excellent specimen from Escuminac Bay showing both head and body (see JARVIK, 1955, fig. 2, 1959a, pl. 2:1, 1963a, fig. 10B; ØRVIG, 1957, fig. 1K).

(2) A single head (No. 1840.14.15, RSM, Edinb.) from Clashbennie, Scotland.

(3) Several specimens of *Holoptychius flemingii* from Dura Den, Scotland (see also WOODWARD, 1891a, fig. 49; TRAQUAIR, 1895, pl. 2:4; WATSON & DAY, 1916, fig. 1; HOLMGREN & STENSIÖ, 1936, fig. 274; WESTOLL, 1937a, fig. 9c, 1937b, fig. 1C; JARVIK, 1944b, fig. 8C, 1948a, figs. 33B, 34, 1950a, fig. 31D).

(4) A large collection from the Upper Devonian of East Greenland (for stratigraphy see JARVIK, 1948b, 1950b, 1961) brought home by the Danish expeditions under the leadership of Dr. LAUGE KOCH, 1929–1955. Parts of this material comes from beds, the *Phyllolepis* Series, which are about contemporaneous with the Dura Den beds but most of it originates from the overlying ichthyostegid-bearing *Remigolepis* Series. Material previously figured by STENSIÖ (1931) and JARVIK (1942, figs. 33, 34, 1950a, fig. 36, 1954, fig. 3, 1961, fig. 2C, 1963a, figs. 10A, 15A, B).

Among the available porolepiform material the specimens of *Glyptolepis groenlandica* n. sp. from Canning Land hold an outstanding position. Several of the heads show well the dermal bones and the neural endocranium which are displayed also in porolepiform material from other localities. But in addition they show the visceral endoskeleton with the visceral arches, the minute dental plates in the mouth cavity and the subbranchial series. These skulls are thus just as complete as the sectioned skull of specimen No. P. 222, Pal. sect., Stockh. of *Eusthenopteron foordi* (grinding series 2, JARVIK, 1942, p. 426, see also 1944a, fig. 1), but unfortunately they are less well preserved being somewhat compressed either dorso-ventrally or from the sides. When collected the skull chosen for sectioning with the aid of Sollas' grinding method was in two pieces (see pl. 21:2, 3) and it is possible that small fragments of the bony tissue, which generally is fragile in material from this locality, have got lost before the two pieces were glued together. The grinding started in 1959 and proceeding backwards from the tip of the snout has now reached the anterior part of the otic region. The successive grinding surfaces, which show almost perfect transverse sections through the head have been stained with alizarin and drawn in the magnification 10/1 at intervals of 100 microns. As a rule every fifth section surface has been photographed. Although not yet completed the grinding series has been utilised at several occasions and together with other material from the same block it has added considerably to our knowledge of the porolepiforms (JARVIK, 1962, 1963a, 1963b, 1964, 1965a, 1966; STENSIÖ, 1963b; BJERRING, 1967, 1971).

Several of the specimens found together with the sectioned head and numerous specimens from various other localities (Wood Bay Series, *Remigolepis* Series, etc.) have been prepared mechanically, usually with the aid of the dental mallet and sharp needles. In order to increase the

contrast between rock and fossil light refracting liquids (alcohol, xylene, etc.) and staining with alizarin have been used. In several cases imperfect or whethered fossils embedded in sandstone or other solid rocks have been removed mechanically or with the aid of acids, and casts, usually in latex, have been made of the impressions. The prepared fossils have been photographed either dry or submerged in alcohol or xylene and all photographs used as basis for drawings or published in text-figures or plates have been slightly retouched.

III. TAXONOMIC REMARKS WITH DESCRIPTION OF *GLYPTOLEPIS GROENLANDICA* N. SP.

For practical reasons it may be justified to divide the Porolepiformes into two families: the Porolepidae, generally with rhombic scales and the scales and dermal bones covered by a continous layer of cosmine, and the Holoptychiidae with cycloidal scales and ornamented scales and dermal bones. The Onychodontidae sometimes regarded as porolepiforms belong to a distinct separate group of Devonian fishes, the Struniiformes (JESSEN, 1966a, 1966b; as regards *Litoptychus* see pp. 18–19).

The Porolepidae includes two genera, *Porolepis* WOODWARD (1891b) and *Heimenia* ØRVIG (1969b). The latter is intermediate between *Porolepis* and *Glyptolepis* in scale structure.

In 1891 WOODWARD (1891b; see also ØRVIG, 1969b) described some detached scales from Woodfjorden, Spitsbergen as *Porolepis posnaniensis* (KADE). In 1942 I demonstrated on the basis of studies of the anterior cranial division (divisio cranialis anterior, JARVIK, 1937) that the porolepid fauna of the Wood Bay Series of Spitsbergen includes at least three different forms and because the scales are of a similar type throughout the Wood Bay Series none of these forms could be referred to P. *posnaniensis*. Three new specific names, *P. spitsbergensis*, P. *elongata* and *P. brevis* were introduced and holotypes were selected and figured.

Of these three species *P. spitsbergensis* (figs. 9C, D, 14, 34D, 68, 69A, pl. 11:2, 5; JARVIK, 1942, pl. 1, pl. 2:2, 3) is characterised by long and deep internasal cavities, at their deepest points extending dorsally almost to the dermal cranial roof, and the presence of a median palatal process with enlarged premaxillary teeth. Moreover the nasal cavity is longer than broad and (as in *Glyptolepis groenlandica*, fig. 12B) the side with the canal for the anterior nasal tube and the lateral recess is directed antero-laterally.

In *P. elongata* (figs. 1, 2B; JARVIK, 1942, pl. 5:1) and *P. brevis* (figs. 2A, 9A, B, 12A, pls. 2–6, pl. 7:2, 3, 4, pl. 8:1, pl. 11:1, 3, 4, 6) the internasal cavity is shallow with a fairly thick endoskeletal roof at its deepest point. Median palatal process is lacking and the antero-medial premaxillary teeth are not enlarged. The nasal cavity is broader than long and the side with the canal for the anterior external nasal tube and

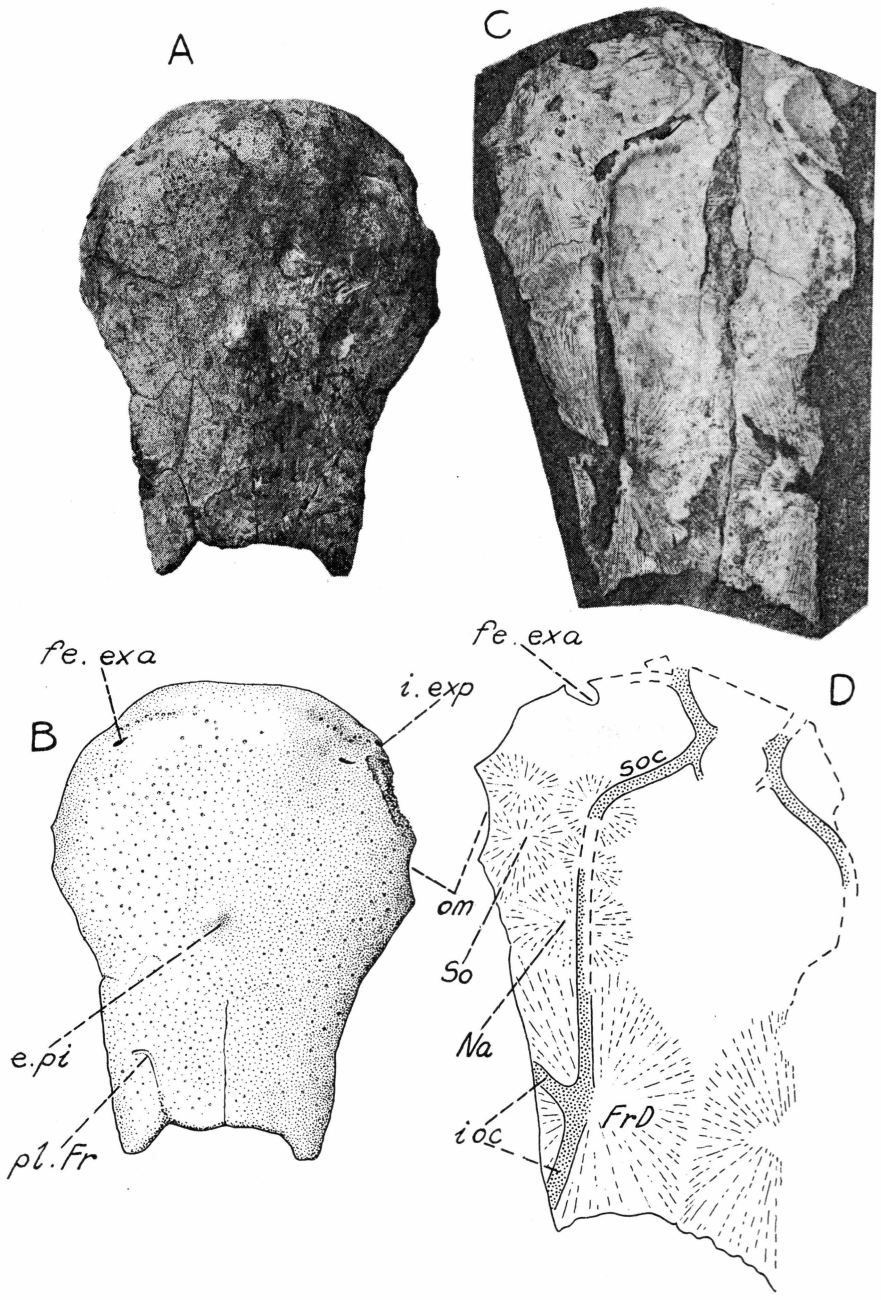


Fig. 1. *Porolepis elongata.* Photographs and drawings of fronto-ethmoidal shields of two specimens from Kronprinshøgda, Bockfjorden, Spitsbergen. Coll. ENS. exp. 1939. Lower Devonian (Wood Bay Series). *A*, *B*, No. P. 6945, Pal. Sect., Stockh. Holotype in dorsal aspect. Same specimen as figured by JARVIK, 1942, pl. 5:1. Median length 63 mm. *C*, *D*, No. A. 34038, Pal. Mus., Oslo. Ventral aspect. Median length 49 mm.

FrD, frontodermosphenotic; *Na*, nasal; *So*, supraorbital.

e. pi, pineal elevation; *fe. exa*, fenestra exonarina anterior; *i. exp*, notch in margin of fronto-ethmoidal shield for posterior external nasal tube; *ioc*, infraorbital sensory canal; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line; *soc*, supraorbital sensory canal.

the lateral recess is almost transverse in position being directed anteriorly and only slightly laterally. *P. elongata* and *P. brevis* differ distinctly from each other in the proportions of the fronto-ethmoidal shield. In *P. brevis* that shield is about as broad as long whereas in *P. elongata* it is considerably longer, about 1.2 times as long as broad.

In this connection may be mentioned that the posterior median part of the internasal wall in the holotypes of *P. spitsbergensis* and *P. elongata* is unossified. Whether this means that the cranial cavity has an ethmoidal part occupied by the anterior part of the brain as I claimed in 1942 or if the posterior part of the internasal wall was cartilaginous (*cart*, fig. 69A) is at present impossible to say (see p. 46).

In the available porolepid material from Spitsbergen no new specimens that with certainty can be assigned to *P. spitsbergensis* have been recognised and accordingly this species is represented only by the holotype. However, in one specimen consisting of an imperfect divisio cranialis anterior that has been exposed from the ventral side (pl. 7:1) there is a median palatal process with enlarged premaxillary teeth and the internasal cavities are deep as in *P. spitsbergensis*. But the internasal ridge is more narrow than in that form and the specimen will therefore be referred to as *Porolepis* cf. *spitsbergensis*.

The material of *P. elongata* includes several specimens which, however, show only the fronto-ethmoidal shield and (in the holotype) the dorsal parts of the ethmosphenoid. The ventral parts of the anterior cranial division including the vomer and the parasphenoid are still unknown in this species as in *P. spitsbergensis*.

More or less complete anterior cranial divisions of the *brevis* type are fairly common and although variations occur indicating the presence of more than one species they have all been referred to *P. brevis* or *P.* cf. *brevis*. Only five of these specimens (pl. 2, pl. 4:1, pl. 6:1, 2, pl. 7: 3, 4) show the fronto-ethmoidal shield in association with the parietal shield and these specimens show also considerable other parts of the skull. In another specimen of *P. brevis* (pl. 11:3) the fronto-ethmoidal shield is preserved together with the anterior part of the external cheek-plate and one specimen (pl. 5) also referred to *P. brevis* shows well the main part of that plate. The remaining material from the main part of the Wood Bay Series consists of detached dermal bones or complex units (lower jaw, parietal shield). All these specimens are at present indeterminable and will be referred to as *Porolepis* sp.

Some cranial remains from localities in the uppermost part (Verdalen Member) of the Wood Bay Series that have yielded scales of the *Heimenia* type have been assigned to that genus (pl. 12:6).

Because of the incomplete knowledge of the skull in *Porolepis spitsbergensis*, *P. elongata* and *Heimenia*, the fact that the porolepid material

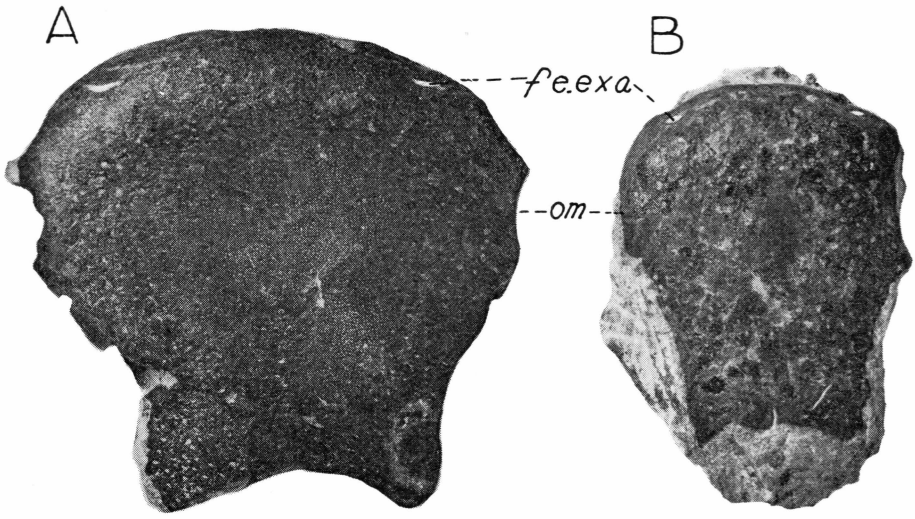


Fig. 2. Fronto-ethmoidal shields in dorsal aspects of, *A*, *Porolepis brevis* and, *B*, *P. elongata*. Both specimens from same block. Specimen No. 1964.41, Mus. de Paléont., Paris. Coll. French exp. 1964. Grønhorg, Dicksondalen, Spitsbergen. Lower Devonian (Wood Bay Series). × 2/1.

fe. exa, fenestra exonarina anterior; *om*, margin of orbital fenestra.

both from Spitsbergen and other areas (the Rhineland, Poland) consists mainly of isolated cranial remains and the remarkable uniformity in structure displayed by all porolepiforms it is at present difficult to give a definition of the family Porolepidae on the basis of cranial characters (the body is still incompletely known) and to distinguish it from the Holoptychiidæ. It may be mentioned, however, that in the five specimens of *Porolepis* showing the fronto-ethmoidal shield together with the parietal shield the fronto-ethmoidal shield is comparatively long, about 1.5 times longer than the parietal shield, whereas in the holoptychiids it is about as long as or generally, as in *Glyptolepis groenlandica*, *Holoptychius flemingii* and *H.* spp. from Escuminac Bay and East Greenland, shorter than that shield. Moreover as evidenced also by other specimens of *Porolepis* the orbital fenestra is smaller and situated farther forwards than in the holoptychiids and the postorbital is elongated, longer than high (cf. however, *Glyptolepis*? cf. *paucidens*).

Among the genera referred to the Holoptychiidae only *Laccognathus* GROSS, *Glyptolepis* Ag., and *Holoptychius* Ag., will be considered. *Hamodus* OBRUCHEV (1933; see also BYSTROW, 1939; GROSS, 1957, p. 32) and *Pseudosauripterus* WHITE (1961) are still very incompletely known and if they belong to the Holoptychiidae I would not venture to decide. The lower jaw which is the genotype of *Litoptychus* DENISON (1951) almost

certainly pertains to an osteolepiform (JESSEN, 1966b, pp. 331–333) and the view advanced by PARRINGTON (1956, p. 402) that *Elpistostege* may be a porolepiform is untenable. As indicated both by DENISON (1951, pp. 243, 247) and ØRVIG (1957, p. 394) the detached scales by them considered to belong to the genus *Sauripterus* are of a similar type as in *Holoptychius* and also for other reasons (JARVIK, 1964, p. 69) the possibility is to be taken into consideration that *Sauripterus* may turn out to be a holoptychiid. In this connection may be mentioned that the two clavicles referred to the genus *Rhizodus* by WOODWARD (1891a, pl. 12:4, 7) most likely belong to a porolepiform as well (cf. p. 129). If this be true the porolepiforms survived into the Carboniferous. That this is so is rendered likely also by the fact that *Holoptychius* is very common in the uppermost Upper Devonian strata in East Greenland and occurs also in the *Groenlandaspis* Series which forms the top of the sequence (see JARVIK, 1961, table I).

Laccognathus, *Glyptolepis* and *Holoptychius* differ clearly from each other in the ornamentation and microstructure of the exoskeleton (ØRVIG, 1957) but are at present difficult to distinguish on cranial characters. In *Laccognathus* (GROSS, 1941; "*Dendrodus biporcatus*", GROSS, 1936) the external side of the lower jaw presents three large pits thought by GROSS to be distinctive of that genus. However, such pits (*fo. Lj*) are present also in *Holoptychius* (fig. 47C, pl. 30:1–3, pl. 31) and although generally fairly small they are in one specimen almost as large as in *Laccognathus* (see p. 113). In *Glyptolepis*, on the other hand, such pits seem to be absent (as in *Porolepis* and *Heimenia*) and in this respect *Glyptolepis* differs from both *Laccognathus* and *Holoptychius*. Moreover, *Glyptolepis* differs from *Holoptychius* in the absence of a sensory canal in the prespiracular plate.

The specimens of *Glyptolepis* from Canning Land, East Greenland contained in a single block most probably belong to one species. This species which now is the best known porolepiform has been named:

Glyptolepis groenlandica n. sp.

(figs. 3, 7B, 8, 12B, 16–19, 21–23, 24E–G, 25, 27, 28, 29A,B, 30, 31, 32A1–4, 33D, E, 38, 39, 44, 66A,C, 71A, 72A, 76B, 78A,C, 79B–D, 83A,B, 85D, 87A, 92A, 101B,D, 103B, 104C, pls. 1, 15–23).

Syn. *Glyptolepis* sp., JARVIK, 1962, fig. 2, 1963a, figs. 13, 14A, B, 1964, fig. 21D, 1965a, figs. 5A, 6A, B, 1966, fig. 1; STENSIÖ, 1963b, figs. 47, 48; BJERRING, 1967, figs. 14–16.

Holotype is specimen No. P. 1488, Min. Mus., Copenhagen, from the *Asterolepis saevesoederberghi* Series, Canning Land, East Greenland (Upper Middle Devonian; see JARVIK, 1961). The specimen which meas-

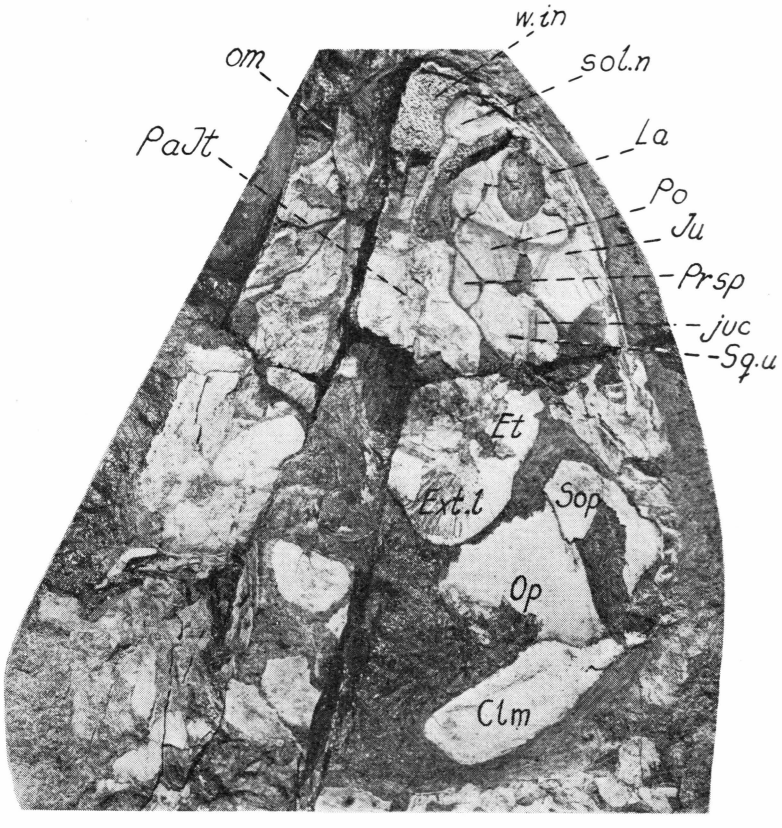


Fig. 3. *Glyptolepis groenlandica* n. sp. Holotype. Incomplete skull showing mainly dermal bones of skull-roof and external cheek-plate in inner view. Same specimen as in pl. 1. Specimen No. P. 1488, Min. Mus., Copenh. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*). × 1/1.

Clm, cleithrum; *Et*, extratemporal; *Ext. l*, lateral extrascapular; *Ju*, jugal; *La*, lachrymal; *Op*, opercular; *PaIt*, parietointertemporal; *Po*, postorbital; *Prsp*, prespiracular plate; *Sop*, subopercular; *Sq. u*, upper squamosal.

juc, jugal sensory canal; *om*, margin of orbital fenestra; *sol. n*, solum nasi; *w. in*, internasal wall.

ures about 36 cm in total length shows both the head and the body with the median fins (fig. 3, pl. 1). The paired fins are not preserved but are well shown in other specimens from the same block.

Diagnostic remarks. – *Glyptolepis groenlandica* n. sp., in which also certain other specimens from the *Asterolepis saevesoederberghi* Series are included, both in the head and body agrees well with *Glyptolepis leptopterus* which is the typespecies of the genus (WOODWARD, 1891a, p. 332). It differs from that species in the more posterior position of the median fins. In *G. groenlandica* the distance from the anterior end of the origin

of the first dorsal fin to the tip of the snout is about 1.6 but in *G. leptopterus* judging from specimens at my disposal and figures by MILLER (1875, pl. 5:2) and WOODWARD (1891a, pl. 11:2) only about 1.2 times longer than the distance to the tip of the tail. Differences in cranial characters are more difficult to find but it may be mentioned that the frontodermosphenotic in *G. groenlandica* occupies only about one third of the length of the parietal shield, whereas in *G. leptopterus* (fig. 41) it is about half as long as that shield.

Two specimens, viz. No. 47838, Brit. Mus., Lond., from Thurso Bay (pl. 14:1, 2) and No. 1964.18, RSM, Edinb. (represented only by a photograph, fig. 40) probably from the same area have been referred to as *Glyptolepis?* cf. *paucidens*. These two specimens are of special interest because they in important regards seem to agree better with *Porolepis* than with unquestionable species of *Glyptolepis* and *Holoptychius*. The fronto-ethmoidal shield is thus about as long as the parietal shield and proportionately longer than in *G. groenlandica* and the specimens of *Holoptychius* known in this regard, and moreover, as demonstrated by specimen No. 47838, it agrees as to its posterior extent in relation to the neural endocranium with *Porolepis*. Furthermore, as in *Porolepis*, the orbital fenestra is small, situated far forwards, and the postorbital is elongated.

The holoptychiid material from the *Phyllolepis* and *Remigolepis* Series (Upper Upper Devonian) in East Greenland (pl. 24:1–3, pls. 25–31, pl. 32: 1–4, pl. 33: 1, 2, 4–6, pl. 34: 1–4, pl. 35) consists mainly of isolated scales and cranial remains. Several specimens show both the fronto-ethmoidal and the parietal shields, sometimes in association with the external cheek-plate and the lower jaw, but no complete head has been found, and the body and the fins are imperfectly preserved. As regards the structure of the head the East Greenland holoptychiids agree with *Holoptychius* sp. from Escuminac Bay and *H. flemingii*. Variations occur and judging in particular from the differences in the shape of the cleithrum and the clavicle it is evident that we are concerned with several species and probably with more than one genus. However, the numerous scales that have been collected are all of the type characteristic of *Holoptychius* and all the material has therefore been referred to that genus.

IV. DESCRIPTIVE SECTION

General remarks

The porolepiforms are stout and bulky predatory fishes (fig. 4), sometimes attaining a length of two meters or more but generally of a more moderate size. The head, contained about five times in the body length, is short and broad. Judging from models of wax-plates it is nearly as broad as high and only about 1.2 times longer than high. A remarkable feature is that some specimens of *Holoptychius* show impressions of the soft parts of both the hyoidean and the mandibular gill-covers (*i. hgc*, *fl. hgc*, *fl. mgc*, figs. 5, 6A; JARVIK, 1963a, pp. 23–27). As in other fishes previously classified as crossopterygians there is an intracranial joint —

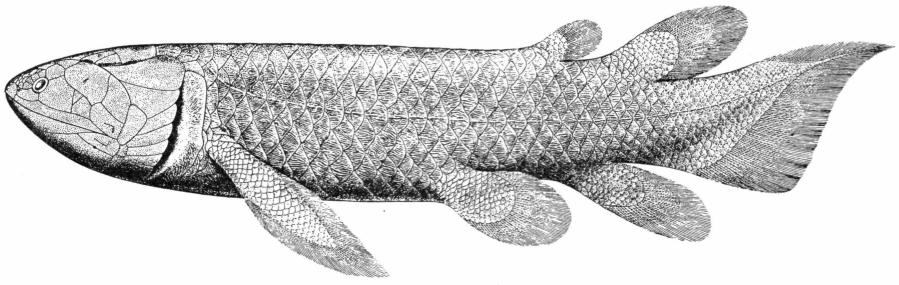


Fig. 4. Restoration of *Holoptychius*. Based mainly on specimen from Escuminac Bay, shown in figs. 6, 59B (see also JARVIK, 1955, fig. 9, 1959a, pl. 2:1); length of specimen ca 46 cm.

because of its complexity termed intracranial juncture apparatus by BJERRING (1967) — separating two complex units, the divisio cranialis anterior and the divisio cranialis posterior (JARVIK, 1937). The anterior of these divisions comprises the ethmosphenoid, the fronto-ethmoidal shield, the paired vomer and the parasphenoid. The posterior division is composed of the otoccipital (the postero-ventral part formed mainly of cranial vertebrae appears to be separate), independent arcual elements, probably one suprachordal and one subchordal arcual plate (termed zygal plates by BJERRING), the parietal shield and the extrascapular series. Laterally to these two units and intimately connected with them

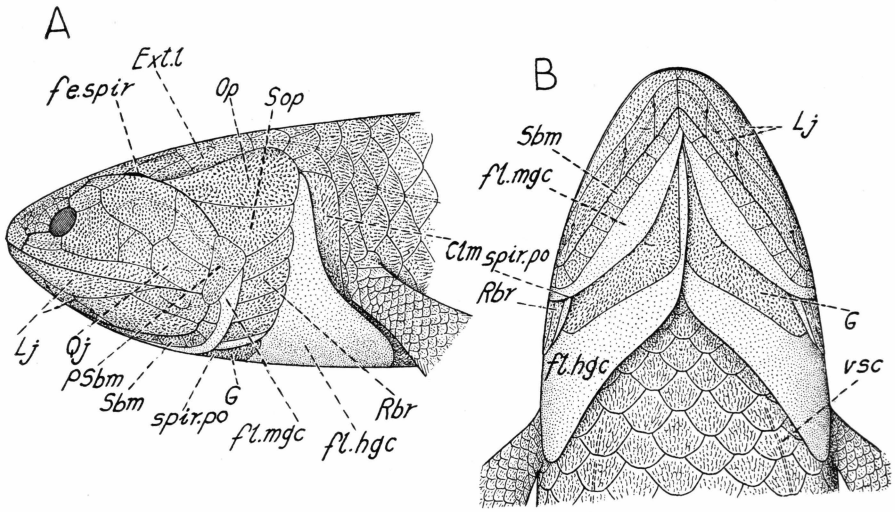


Fig. 5. Restorations of head of *Holoptychius* with soft parts of mandibular and hyoidean gill-covers in, *A*, lateral and, *B*, ventral aspects. From JARVIK, 1963a, fig. 11A, B.

Clm, cleithrum; *Ext. l*, lateral extrascapular; *G*, principal gular plate; *Lj*, lower jaw; *Op*, opercular; *PSbm*, preoperculosubmandibular; *Qj*, quadratojugal; *Rbr*, branchiostegal ray; *Sbm*, submandibular; *Sop*, subopercular.

fe. spir, spiracular fenestra; *fl. hgc*, soft flap of hyoidean gill-cover; *fl. mgc*, soft flap of mandibular gill-cover; *spir. po*, approximate position of presumed external opening of ventral division of spiracular gill-slit; *vsc*, ventral sensory canal of body.

follows another complex unit, the palatoquadrate-cheek complex, consisting of the palatoquadrate with dermal bones (dermopalatine, ectopterygoid, entopterygoid) and the external cheek-plate. In association with the two cranial divisions and to some extent with the palatoquadrate there are numerous dental plates, the upper oral dental plates (*uodp*, figs. 8C, D, 24E–G, 30), situated in the roof of the mouth cavity.

These three units are connected with each other in such a way that a rigid system is formed and a remarkable fact is that the palatoquadrate in the sectioned specimen of *Glyptolepis groenlandica* has fused with the ethmosphenoid in three (left side) or four (right side) places. Judging also from the fact that the dorsal faces of the fronto-ethmoidal and parietal shields, both in specimens compressed dorso-ventrally and from the sides, are in level with each other, it is evident that the mobility at the intracranial juncture apparatus must have been inconsiderable and confined to a slight flexibility. This is only what is to be expected in immediate ancestors of tetrapods and in this respect porolepiforms agree with osteolepiforms which also have given rise to tetrapods. However, whereas in the osteolepiforms (and *Elpistostege*) the fronto-ethmoidal

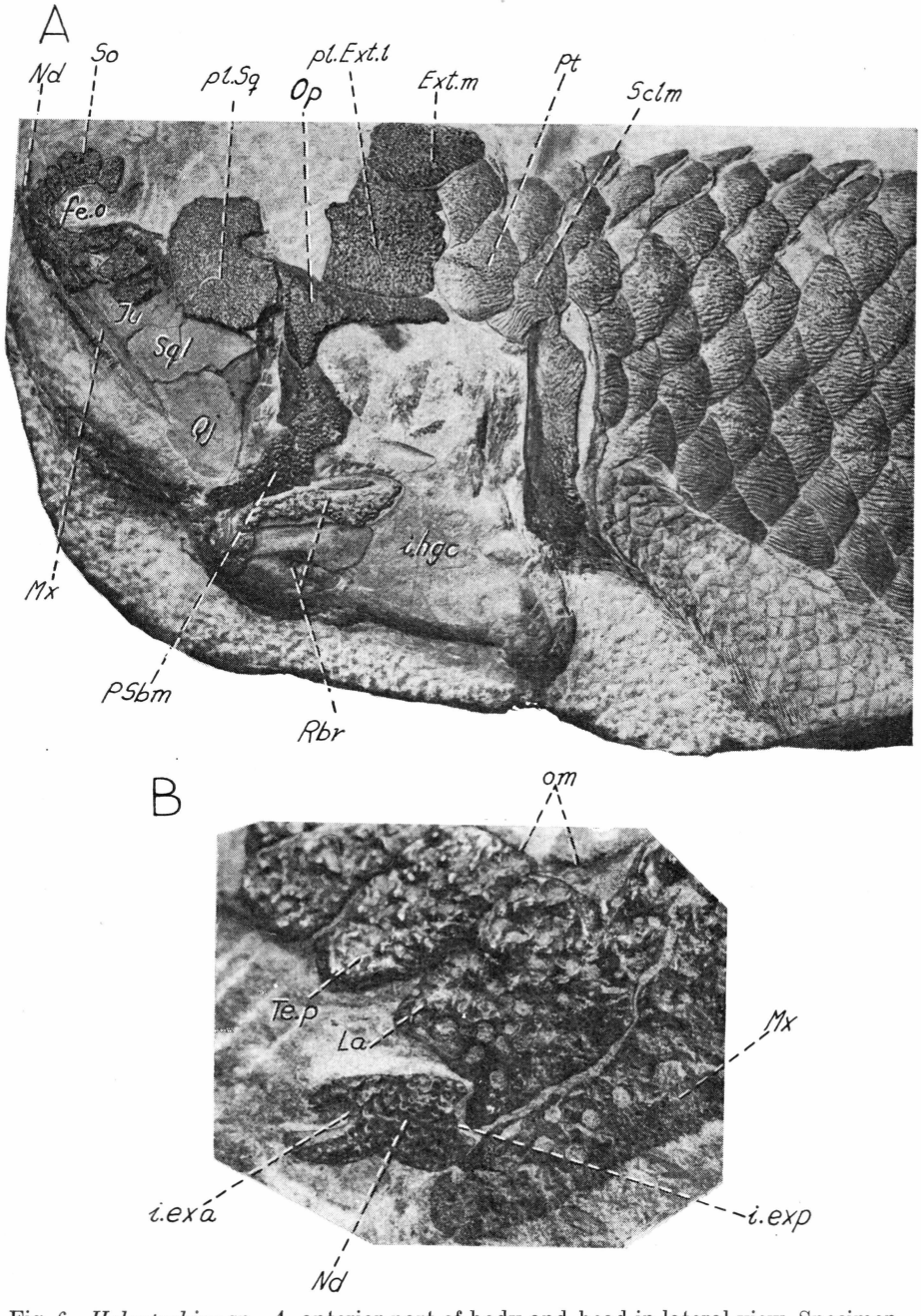


Fig. 6. *Holoptychius* sp. *A*, anterior part of body and head in lateral view. Specimen No. 38.71.10672, Dartmouth College, Hanover, N. H., U.S.A. Same specimen as in fig. 59B (see also figs. 4, 5, JARVIK, 1955, fig. 2, 1959a, pl. 2:1). Lower Upper Devonian, Escuminac Bay, Canada, × 3/4. *B*, nariodal and adjoining dermal bones of same specimen (see also fig. 62C). × 6/1.

Ext.m, median extrascapular; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Nd*,

and parietal shield sometimes have fused with each other they are in porolepiforms always separate (cf. Moy-Thomas, 1938, p. 315; Parrington, 1956, pp. 400–401) and no independent dermal bones have been found at the transition between them.

Neural endocranium

Ethmosphenoid

The ethmosphenoid and adjoining dermal bones can be studied in detail in the serial sections and other material of *Glyptolepis groenlandica* and are more or less well shown in some specimens of *Glyptolepis* from Scotland and in several specimens of *Porolepis* from Spitsbergen and *Holoptychius* from East Greenland.

The anterior part of the ethmosphenoid (the ethmoidal region and the foremost part of the orbitotemporal region) together with the dermal bones of the anterior part of the fronto-ethmoidal shield and the palate in *Porolepis* were described in 1942 and it was demonstrated that the same type of snout found in *Porolepis* characterises also *Holoptychius*. Later (Jarvik, 1954, 1962, 1964, 1965a, 1966) it was shown that this complex type of snout occurs also in *Glyptolepis* and with the aid of the serial sections a remarkable and surprisingly close agreement even as to minor structural details was demonstrated. The following account of the porolepiform snout is mainly a review of previous descriptions but presents also several new data.

However, before turning to the endoskeletal structures the principal openings in the exoskeleton of the snout will be considered.

The anterior part of the fronto-ethmoidal shield in *Porolepis* (figs. 1, 2, 7A, 11, 20A, 34, 43, pl. 6:1, pl. 7:3, 4, pls. 8, 9, 11) and *Glyptolepis* (figs. 7B, 79C, D, pl. 16:1, pl. 17:1, 2) is on each side pierced by a small oval opening, the fenestra exonarina anterior (*fe. exa*), which transmitted the anterior external nasal tube (*nta*) and probably contained the anterior external nostril (*an*). Postero-ventrally to this opening is a small but distinct notch in the margin of the fronto-ethmoidal shield (*i. exp*) bounded posteriorly by a similar notch (*i. La*) in the anterior margin of

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nariodal; *Op*, opercular; *PSbm*, preoperculosubmandibular; *Pt*, posttemporal; *Qj*, quadratojugal; *Rbr*, branchiostegal rays; *Sclm*, supracleithrum; *So*, supraorbital; *Sq. l*, lower squamosal; *Te. p*, posterior tectal.

fe. o, orbital fenestra; *i. exa*, notch in nariodal forming part of fenestra exonarina anterior; *i. exp*, notch in nariodal forming part of fenestra exonarina posterior; *i. hgc*, impression of soft flap of hyoidean gill-cover; *om*, margin of orbital fenestra; *pl. Ext. l*, pit-line of lateral extrascapular; *pl. Sq*, squamosal pit-line.

the lachrymal. The opening in the exoskeleton thus formed is the fenestra exonarina posterior (*fe. exp*) which transmitted the posterior external nasal tube (*ntp*).

In *Porolepis* the dermal bones surrounding this opening are covered with a layer of cosmine indicating that also the posterior nostril (*pn*) was situated in the exoskeletal opening. In *Glyptolepis groenlandica*, on the other hand, is a groove (*gr. La*) on the external side of the lachrymal running in a postero-dorsal direction from the fenestra exonarina posterior towards the orbital fenestra and in one specimen (pl. 17:2) it is seen to continue to or almost to the margin of that fenestra. This can only mean that the posterior external nasal tube at the passage through the fenestra exonarina posterior made a bend (*b*, fig. 79D) in a postero-dorsal direction and continued in the groove on the outside of the lachrymal to or almost to the orbital fenestra, where the posterior external nostril was probably situated. Obviously we are here concerned with a beginning transformation of the posterior external nasal tube into a naso-lachrymal duct (cf. p. 195).

In *Holoptychius* (figs. 7C, D, 36A, 37C, 45, pl. 24: 1, 4, pl. 29:3, 5, pl. 31:1) the conditions are somewhat different. In all specimens showing the area in question there is a large exoskeletal opening (*fe. ex*) like in *Porolepis* and *Glyptolepis* bounded posteriorly by a notch in the lachrymal (*i. La*) and no doubt representing the fenestra exonarina posterior. However, in contrast to conditions in *G. groenlandica* there is no groove on the external side of the lachrymal and as pointed out in 1942 (p. 407) the posterior external nostril in *Holoptychius* was probably situated in or just outside the notch in the lachrymal. Because the notch in the fronto-ethmoidal shield is larger and deeper than in *Porolepis* and there is no fenestra exonarina anterior I assumed (1942, pp. 381–382) that the large exoskeletal opening in *Holoptychius* includes that fenestra as well and is a fenestra exonarina communis. This view has now been corroborated by the excellent specimen of *Holoptychius* from Escuminac Bay. In this specimen (Fig. 6) most of the dermal bones of the snout are lacking but just at the anterior end of the lachrymal (*La*) and partly concealing that bone there is a small elongated bone, the nariodal (*Nd*, figs. 6, 7D, 20B, 62C; dermonariodal, JARVIK, 1964) with a distinct notch (*i. exp*) in its posterior end and a similar but deeper notch (*i. exa*) anteriorly. Judging from its size, shape and position the nariodal, which is ornamented but in contrast to adjoining dermal bones lacks sensory canal pores, no doubt occupied an opening corresponding to the fenestra exonarina communis (*fe. ex*) seen in the specimens of *Holoptychius* from the Upper Devonian of Scotland and East Greenland, dividing that opening into a fenestra exonarina anterior (*fe. exa*) and a fenestra exonarina posterior (*fe. exp*).

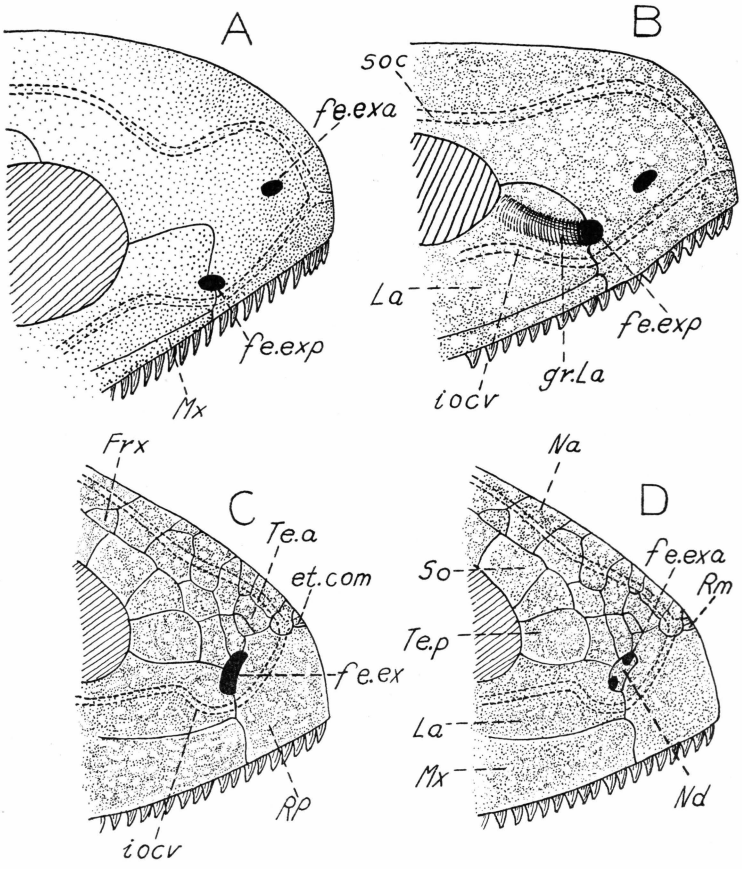


Fig. 7. Restorations of snout in lateral aspects of *A*, *Porolepis brevis*, *B. Glyptolepis groenlandica* and, *C*, *D*, *Holoptychius* sp.

Frx, independent part of frontal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *Nd*, nariodal; *Rm*, median rostral; *RP*, rostropremaxillary; *So*, supraorbital; *Te. a*, anterior tectal; *Te. p*, posterior tectal.

et. com, ethmoidal commissural canal; *fe. ex*, fenestra exonarina communis; *fe. exa*, fenestra exonarina anterior; *fe. exp*, fenestra exonarina posterior; *gr. La*, groove of lachrymal for posterior part of posterior external nasal tube; *iocv*, ventrally curving part of infraorbital sensory canal; *soc*, supraorbital sensory canal.

The ventral side of the ethmoidal region (figs. 15B, 18, 30, 31, 73A, pl. 3, pl. 17:3, pl. 22:1, pl. 25:2) is partly covered by the vomers (*Vo*) and the palatal lamina (*la. pal*) of the fronto-ethmoidal shield. Between the vomers which diverge forwards there is a large anterior palatal fenestra (*fe. pal*) bounded anteriorly and antero-laterally by the palatal lamina and posteriorly by the parasphenoid. Laterally to the vomer and bounded also by the rostropremaxillary, the maxillary and the dermopalatine lies the small fenestra exochoanalis (*fe. exch*).

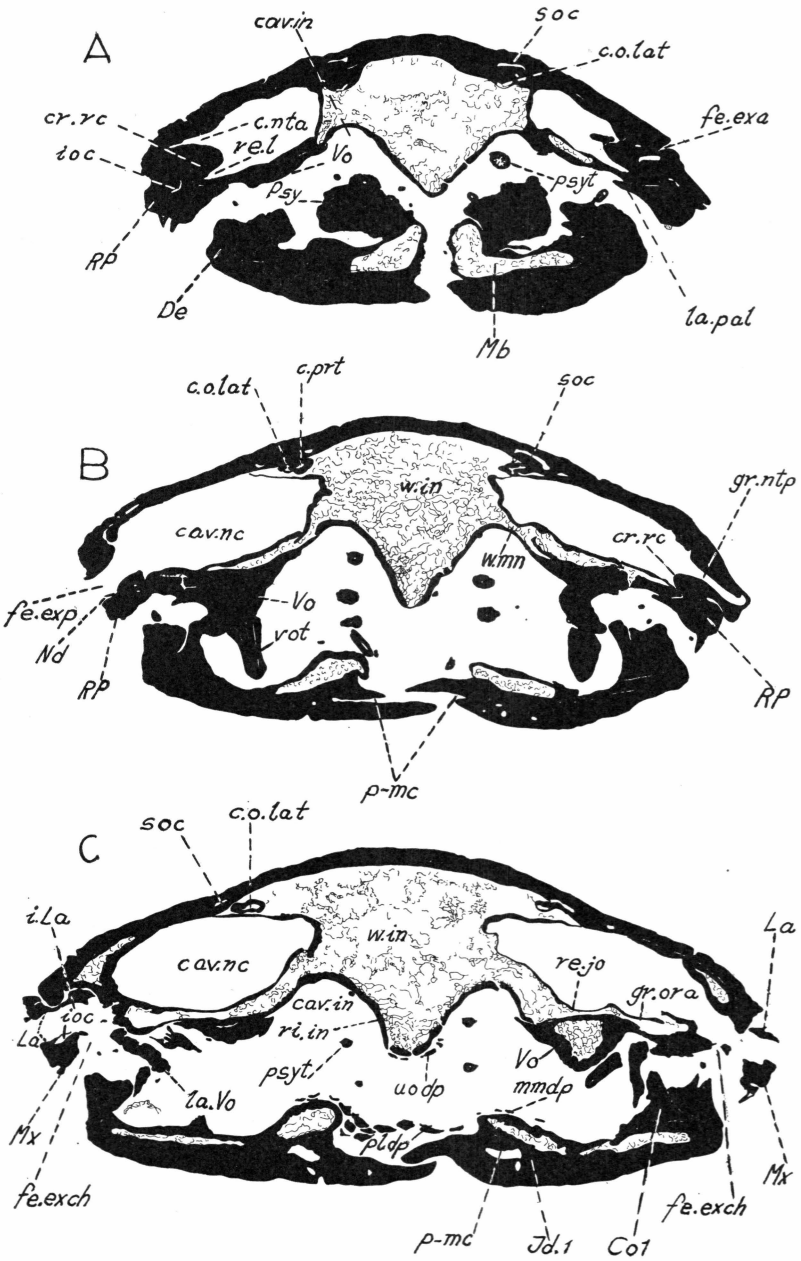

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Fig. 8 A–C.

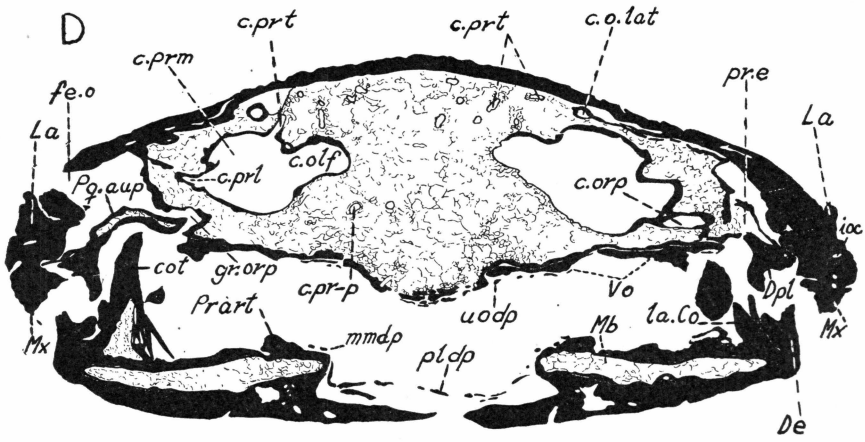


Fig. 8D.

Fig. 8. *Glyptolepis groenlandica* n. sp. Drawings of four almost transverse sections of snout. Sections Nos. 35, 50, 62 and 80 of grinding series. Other sections of snout in figs. 66C, 76B and JARVIK, 1962, fig. 2, 1965a, fig. 5A, 1966, fig. 1. × 7/2.

Co 1, coronoid 1; *De*, dentary; *Dpl*, dermopalatine; *Id. 1*, infradentary 1; *La*, lachrymal; *Mb*, meckelian bone; *Mx*, maxillary; *Nd*, nariodal; *Pq. aup*, pars autopalatina of palatoquadrate; *Prart*, prearticular; *Psy*, parasymphysial dental plate; *RP*, rostropremaxillary; *Vo*, vomer.

cav. in, cavum internasale; *cav. nc*, cavity of nasal capsule; *c. nta*, canal for anterior nasal tube; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. orp*, posterior canal of orbito-rostral passage; *cot*, coronoid tusk; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. pr-p*, canal for combined profundus-palatine nerve; *c. prt*, canals for twigs of medial terminal profundus branch; *cr. rc*, crista rostro-caudalis; *fe. exa*, fenestra exonarina anterior; *fe. exch*, fenestra exochoanalis; *fe. exp*, fenestra exonarina posterior; *fe. o*, orbital fenestra; *gr. ntp*, groove for posterior nasal tube; *gr. ora*, *gr. orp*, anterior and posterior grooves of orbito-rostral passage; *i. La*, notch in lachrymal forming part of fenestra exonarina posterior; *ioc*, infraorbital sensory canal; *la. Co*, tooth-bearing lamina of coronoid; *la. pal*, lamina palatina of rostropremaxillary; *la. Vo*, tooth-bearing lamina of vomer; *mmdp*, medial mandibular dental plates; *pldp*, prolingual dental plates; *p-mc*, preoperculo-mandibular sensory canal; *pr. e*, ethmoidal articular process of pars autopalatina; *psyt*, tusks of parasymphysial dental plate; *re. jo*, recess probably for Jacobson's organ; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *soc*, supraorbital sensory canal; *uodp*, upper oral dental plates; *vot*, tusk of vomer; *w. in*, internasal wall; *w. mn*, medial wall of nasal cavity.

The *ethmoidal region* of the neural endocranium is well ossified and is on the whole a solid structure. It contains two important paired cavities, the cavum internasale and the nasal cavity (as regards the anterior part of the cranial cavity, see p. 46).

The internasal cavities (*cav. in*, figs. 8, 9, 15, 30, 31, 76B, 77A, 78A, C, pl. 3, pl. 7:1, pl. 9:2, pl. 14:5, pl. 17:3, pl. 22:1, pl. 25:1) which receive the tips of the foremost tusks of the parasymphysial dental plates

and probably housed the internasal ("intermaxillary") gland (*gl. in*, fig. 15B; see also JARVIK, 1966, pp. 87–91) are situated between the nasal cavities, in the broad internasal wall (*w. in*). They are elongate more or less oval pits separated from each other by a median crest, the internasal ridge (*ri. in*). These pits which open ventrally and are exposed in the anterior palatal fenestra vary considerably as to size. In most specimens of *Porolepis* and *Glyptolepis* they are shallow and have a thick endoskeletal roof. In *Porolepis spitsbergensis* they are larger and deeper and the endoskeletal roof is very thin at their deepest point. In *Holoptychius* they are large and deep. In this genus the internasal ridge has become reduced into a thin septum and the vomer has developed an ascending lamina (*Vod*, fig. 77A, pl. 25:2) which covers the lateral wall of the pit. However, the internasal ridge may be fairly thin already in *Porolepis*(pl. 7:1) and a low ascending lamina of the vomer may be distinguished (fig. 73A, pl. 3).

The nasal cavities (*cav. nc*, figs. 8–14, 66A, C, 69A, 76B, 77A, 78A) are separated from each other by the broad internasal wall and lie accordingly far apart. As indicated above (see also JARVIK, 1942, p. 367) they show some variations as to shape and position but these and some other variations to be recorded below are of little importance and on the

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Fig. 9. *A*, *B*, *Porolepis brevis*. Anterior part of ethmosphenoid in ventral and posterior aspects. In *A* with certain dermal bones. *C*, *D*, *Porolepis spitsbergensis*. Restorations of ethmoidal region of neural endocranium. *C*, anterior half in posterior view. *D*, posterior half in anterior view. From JARVIK, 1942, figs. 37A, B, 39. Slightly modified.

P, parasphenoid; *RP*, rostropremaxillary; *Vo*, vomer.

art. am, anterior and posterior areas of dorsal side of floor of fossa autopalatina articulating with anterior and posterior articular areas of antero-medial lamina of pars autopalatina; *art. e*, area of postnasal wall articulating with ethmoidal articular process of pars autopalatina of palatoquadrate; *ar. Vo*, vomeral area; *cav. in*, cavum internasale; *cav. nc*, cavity of nasal capsule; *c. cut*, canal probably for cutaneous vessel and profundus branch; *co*, posterior corner of postnasal wall; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. ora*, *c. orp*, anterior and posterior canals of orbito-rostral passage; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. prt*, canals for twigs of medial terminal profundus branch and vessels; *cr. rc*, crista rostro-caudalis; *fe. ena*, fenestra endonarina anterior; *fe. ench*, *fe. enp*, divisions of fenestra ventro-lateralis representing fenestra endochoanalis and fenestra endonarina posterior; *fe. vl*, fenestra ventro-lateralis; *fo. aup*, fossa autopalatina; *gr. ntp*, groove for posterior external nasal tube; *gr. ora*, *gr. orp*, anterior and posterior grooves of orbito-rostral passage; *gr. soc*, groove for ridge housing supraorbital sensory canal; *i. enp*, notch in margin of fenestra ventro-lateralis for posterior external nasal tube; *i. exp*, notch in margin of ethmoidal shield forming part of fenestra exonarina posterior; *od. La*, area overlapped by lachrymal; *om*, margin of orbital fenestra; *pr. S*, Seydel's palatal process; *pr. vl*, ventro-lateral process of postnasal wall; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *sol. n*, solum nasi; *te. n*, tectum nasi; *te. o*, tectum orbitale; *w. al*, antero-lateral wall of nasal cavity; *w. in*, internasal wall; *w. io*, interorbital wall; *w. mn*, medial wall of nasal cavity; *w. pn*, postnasal wall.

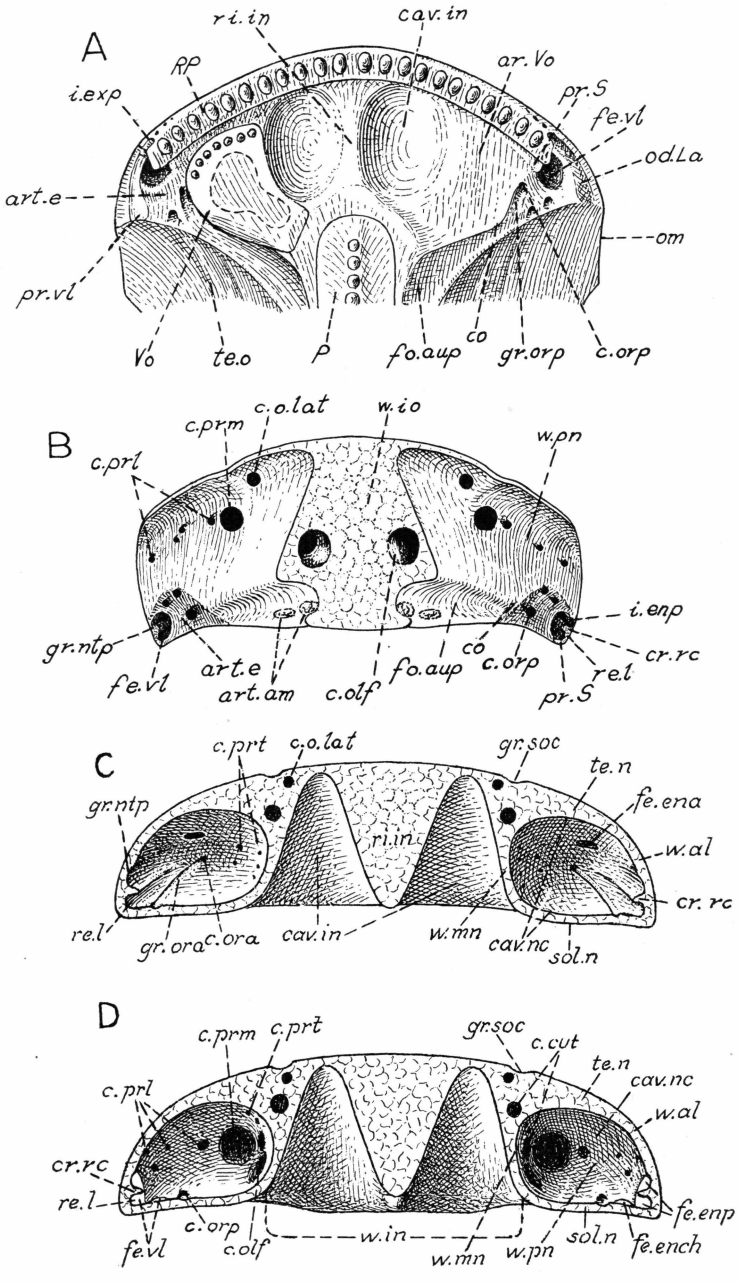

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Fig. 9.

whole the nasal cavities and their walls are very similar in all the numerous specimens of *Porolepis* and *Glyptolepis* in which they are shown.

The walls of each nasal cavity are well developed and more complete than in fishes in general. A characteristic feature is that there is a medial nasal wall (*w. mn*) which separates the nasal cavity from the internasal cavity. The walls are pierced by several canals or foramina for nerves and vessels and by two openings for nasal tubes, the fenestra endonarina anterior and the fenestra ventro-lateralis.

The fenestra endonarina anterior (*fe. ena*), which transmitted the anterior external nasal tube, is of almost the same size as the fenestra exonarina anterior outside it and is thus small. These two fenestrae form together a short canal (*c. nta*) which in *Porolepis* widens in its outer part so that a small pocket-like recess is formed antero-dorsally and a somewhat larger one postero-ventrally. My suggestion (1942, p. 370) that these recesses may have been developed for nasal muscles is supported by the conditions in *Glyptolepis?* cf. *paucidens*. In that form (fig. 10B) there is a wide groove (*gr. nta*) in the dorsal wall of the canal leading outwards from the nasal cavity to the anterior part of the fenestra exonarina anterior. This groove probably lodged the anterior nasal tube and if so there was sufficient space (*re. m. cn*) behind that tube for other structures; most likely for a muscle corresponding to the semicircular m. constrictor naris in urodeles, which (in *Salamandra*, FRANCIS, 1934, p. 304, pl. 24:82) embraces the anterior nasal tube from behind, and possibly for an external nasal gland (see also p. 193).

The fenestra ventro-lateralis (*fe. vl*, see also figs. 21A, 65B, 79B, 92A, pl. 3, pl. 7:1, pl. 9:2, pl. 14:2, pl. 25:2), situated at the postero-ventro-lateral corner of the nasal cavity, includes two small confluent openings, the fenestra endonarina posterior (*fe. enp*) in the lateral wall of the nasal cavity and the fenestra endochoanalis (*fe. ench*) which latter gave passage to the choanal tube of the nasal sac. The fenestra endonarina posterior consists of a posterior large portion closed laterally by dermal bones and a small anterior portion, the fenestra endonarina posterior proper, which transmitted the posterior external nasal tube. The latter portion is represented mainly by a notch (*i. enp*) in the lateral nasal wall situated just inside, and of about the same size as, the notch (*i. exp*) in the margin of the fronto-ethmoidal shield forming the anterior part of the fenestra exonarina posterior.

From the notch for the posterior external nasal tube (the fenestra endonarina posterior proper) in the anterior margin of the fenestra ventro-lateralis a distinct groove (*gr. ntp*) runs forwards on the inner side of the lateral nasal wall to the area of the fenestra endonarina anterior. This groove which no doubt housed the posterior external nasal tube is sometimes bounded dorsally by a slight thickening forming a low ridge

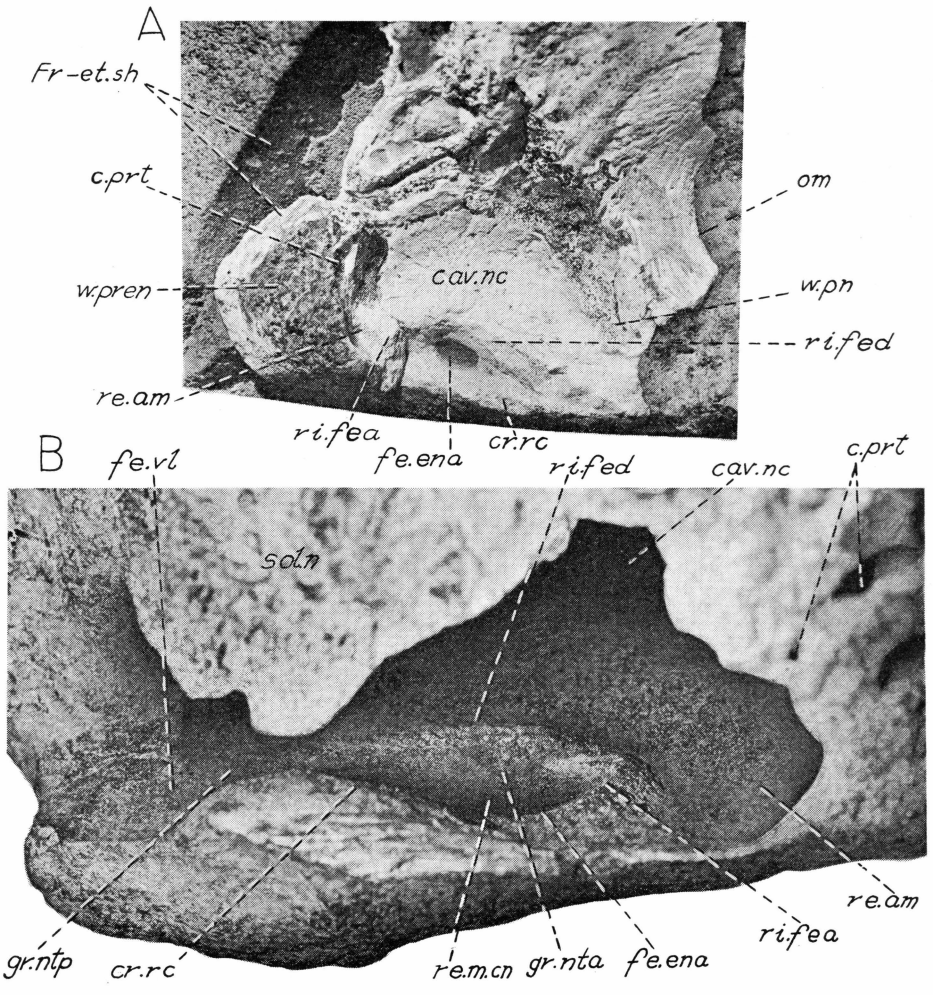


Fig. 10. *A*, *Porolepis* sp. Imperfect anterior part of divisio cranialis anterior showing mainly lateral side of right nasal capsule in medial view. Natural cast of nasal cavity of this specimen shown in fig. 13. Specimen No. A 33994, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Lykta, Dicksondalen, Spitsbergen. Lower Devonian (Wood Bay Series). × 9/4. *B*. *Glyptolepis*? cf. *paucidens*. Inner side of antero-lateral wall of left nasal cavity in antero-ventral aspect to show ridges and grooves around fenestra endonarina anterior. No. 47838, Brit. Mus., London. Same specimen as in pl. 14:1, 2. Thurso, Scotland. Middle Devonian. × 9/2.

Fr-et. sh, fronto-ethmoidal shield (partly preserved as impression).

cav. nc, cavity of nasal capsule; *c. prt*, canal for twig of medial terminal profundus branch; *cr. rc*, crista rostro-caudalis; *fe. ena*, fenestra endonarina anterior; *fe. vl*, fenestra ventro-lateralis; *gr. nta*, *gr. ntp*, grooves for anterior and posterior external nasal tubes; *om*, margin of orbital fenestra; *re. am*, antero-medial recess of nasal cavity; *re. m. cn*, recess probably for musculus constrictor narium; *ri. fea*, *ri. fed*, ridges anterior and dorsal to fenestra endonarina anterior; *sol. n*, solum nasi; *w. pn*, postnasal wall; *w. pren*, prenasal wall.

(*ri. fed*, fig. 10) not previously recorded. This thickening continues forwards dorsally to the fenestra endonarina anterior — the groove (*gr. nta*) described above in *G?* cf. *paucidens* is in its medial part situated on the ventral side of this thickening — and merges anteriorly into a ridge-like thickening (*ri. fea*) situated immediately in front of the fenestra endonarina anterior (cf. KULCZYCKI, 1960, pl. 4, *pr. im?*). Ventrally the groove for the posterior external nasal tube is bounded by a pronounced ridge, the crista rostro-caudalis (*cr. rc*), extending into the nasal cavity. By means of this crest the nasal cavity is incompletely divided into a principal chamber and a lateral recess. The principal chamber extend forwards in front of the fenestra endonarina anterior, and this anterior part, the antero-medial recess (*re. am*), may be incompletely bounded off from the main part of the principal chamber by the ridge-like thickening (*ri. fea*) in front of that fenestra. As is well shown in particular on the left side of the sectioned specimen of *G. groenlandica* there may also be a rather pronounced recess in the floor of the principal chamber. Most likely this recess (*re. jo*, figs. 66C, 76B; *el. jo*, fig. 13A) housed Jacobson's organ. The lateral recess (*re. l*) which in *P. brevis* and *P. elongata* is rather anterior than lateral in position, is bounded dorsally by the rostro-caudal crest, laterally by a part of the lateral nasal wall (*w. al*) and ventrally by the postero-lateral part of the solum nasi (*sol. n*). As evidenced by some specimen of *Porolepis* this portion of the floor of the nasal cavity is produced backwards into a small obtuse process, Seydel's palatal process (*pr. S*), situated in the antero-lateral part of the fenestra endochoanalis and obviously antero-laterally to the choana.

The shape of the cavity of the nasal capsule suggests that the nasal sac (*sac n*, figs. 15A, 70A) consisted of a main part, a ventral diverticle (Jacobson's organ) situated antero-medially to the choana, and a lateral diverticle situated partly in the lateral recess. The main part opened downwards into the mouth cavity through a short choanal tube and outwards (*an*) through an anterior external nasal tube. In front of the latter it probably sometimes formed a slight antero-medial bulge (*di. am*). The lateral diverticle (*di. l*) probably consisted of two divisions, a small dorsal (anterior) one (*di. ld*) situated close behind the anterior nasal tube, dorsally to the anterior part of the crista rostro-caudalis and one (*di. lv*) which lay ventrally to that crest in the lateral recess. The dorsal division was continued backwards by the posterior nasal tube (*ntp*, *ntpp*) which either opened outwards through a posterior external nostril (*pn*) situated in the fenestra exonarina posterior or (*G. groenlandica*, fig. 79D) made a bend (*b*) when passing that fenestra and continued (*ntps*) in the groove on the outside of the lachrymal towards the orbital fenestra. The lumen (sinus lateralis nasi) of the ventral division of the lateral diverticle was probably in open communication with the mouth cavity posteriorly by

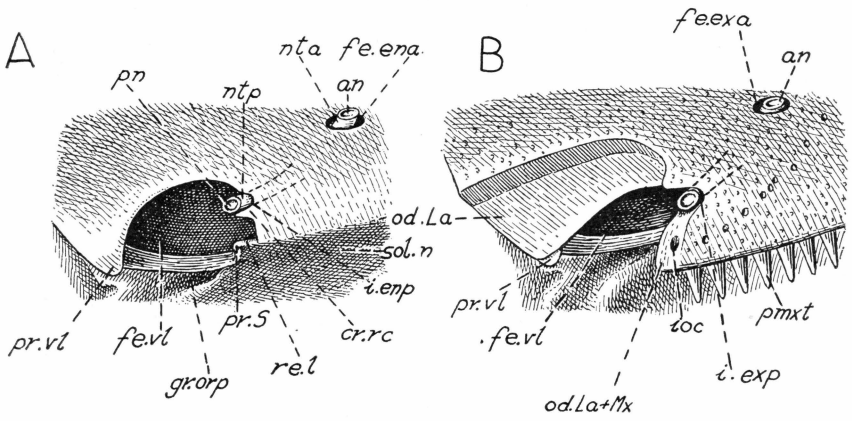


Fig. 11. *Porolepis brevis*. *A*, right ventro-lateral corner of ethmoidal region in lateral and somewhat postero-ventral aspect. *B*, same as in *A* with part of ethmoidal shield. × 7/1 approx. From JARVIK, 1942, fig. 40A, B, slightly modified.

an, anterior nostril; *cr. rc*, crista rostro-caudalis; *fe. ena*, fenestra endonarina anterior; *fe. exa*, fenestra exonarina anterior; *fe. vl*, fenestra ventro-lateralis; *gr. orp*, posterior groove of orbito-rostral passage; *i. enp*, notch in margin of fenestra ventro-lateralis for posterior external nasal tube; *i. exp*, notch forming part of fenestra exonarina posterior; *ioc*, infraorbital sensory canal; *nta*, *ntp*, anterior and posterior external nasal tubes; *od. La*, area overlapped by lachrymal; *od. La + Mx*, area overlapped by lachrymal and maxillary; *pmxt*, premaxillary teeth; *pn*, posterior nostril; *pr. S*, Seydel's palatal process; *pr. vl*, ventro-lateral process of postnasal wall; *re. l*, lateral recess of nasal cavity; *sol. n*, solum nasi.

means of a sulcus maxillo-palatinus bounded ventrally by a plica palatina supported by Seydel's palatal process (cf. JARVIK, 1965a, fig. 4A).

In *Porolepis* (fig. 9) there is postero-medially to the fenestra ventro-lateralis and medially to the ventro-lateral process (*pr. vl*) of the postnasal wall a depressed area, rather variable as to its detailed configuration. This area (*art. e*), which at the posterior end of the posterior groove (*gr. orp*) of the orbito-rostral passage is separated from the fossa autopalatina (*fo. aup*) by a pronounced corner (*co*), was described in 1942 (p. 359, *art. aup?*) and I found it reasonable to assume that the palatoquadrate anteriorly had two articular processes, one antero-lateral received by the depressed area and one antero-medial which occupied the fossa autopalatina. This assumption has been confirmed by the new material of *Glyptolepis groenlandica* (fig. 25), but in order to avoid confusion the antero-lateral process will be called the ethmoidal articular process (*pr. e*) whereas the antero-medial one will be referred to as the antero-medial articular lamina (*la. am*).

A most remarkable fact in the sectioned specimen of *Glyptolepis* (figs. 8D, 32A1) is that the ethmoidal articular process of the palatoquadrate on both sides has fused with the neural endocranium (as to

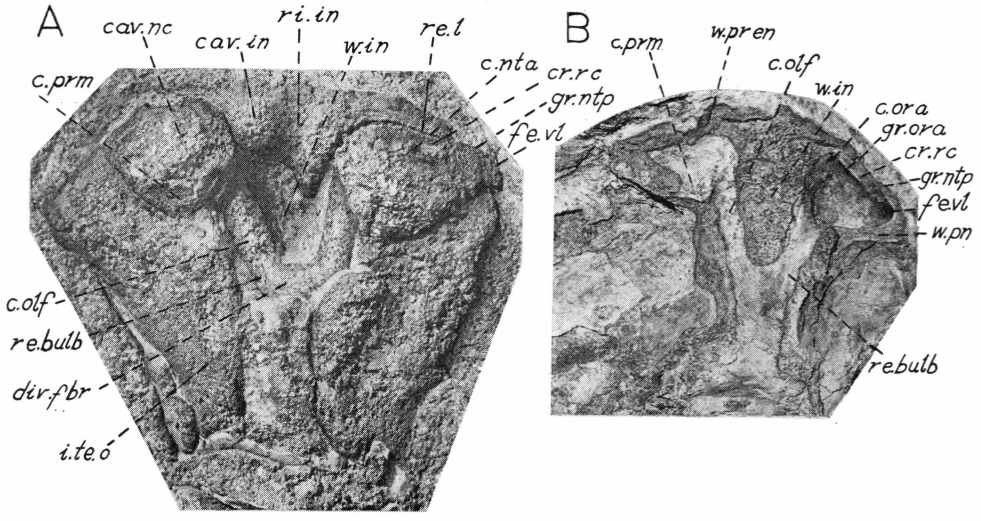


Fig. 12. Ethmosphenoid in dorsal aspect of, *A*, *Porolepis brevis* and, *B*, *Glyptolepis groenlandica* n. sp. Dorsal parts removed to show position of nasal cavities. *A*, specimen No. P. 52682, Brit. Mus., London. Coll. ENS. exp. 1939. Lykta, Dicksondalen, Spitsbergen. Lower Devonian (Wood Bay Series). × 8/3. *B*, specimen No. P. 1496, Min. Mus., Copenh. Coll. 1956; same block as holotype. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*). × 4/3.

For explanation of index letters see fig. 13.

fusion between the medial parts of the palatoquadrate and the ethmosphenoid see pp. 57–58). The area of fusion (*art. e*, fig. 21A) which faces ventro-laterally is situated laterally to the posterior canal and groove of the orbito-rostral passage (*c. orp*, *gr. orp*) and the palatoquadrate covers the most anterior part of that groove laterally and ventrally so that the groove for a short distance is converted into a canal (see JARVIK, 1966, fig. 1). If a corresponding fusion has taken place also in other porolepiforms is difficult to say. However, the fact that both the palatoquadrate and the divisio cranialis anterior are often found detached and that none of the many anterior cranial divisions of various porolepiforms that have been prepared show any traces of broken parts of the palatoquadrate indicates that the connection between the palatoquadrate and the ethmosphenoid generally was less intimate than in the sectioned specimen of *G. groenlandica*.

The ethmoidal region and the adjoining anterior part of the orbito-temporal region present numerous foramina, canals and grooves for nerves and vessels (figs. 8–15, 21A, 23, 65B, 69A, pl. 11:5, pl. 14:5, pl. 25:2). These structures are well shown in some specimens of *Porolepis* and in the sections of *Glyptolepis*, but several of them have been observed in other porolepiforms, too, and as far as may be judged at present they

are developed in fundamentally the same way in all the members of the group.

The long and wide olfactorius canal (*c. olf*, see also figs. 16A, B, 17) issues from the ventro-lateral recess (*re. bulb*) of the anterior part of the cranial cavity (see p. 48) and runs in direction antero-laterally and slightly ventrally to the nasal cavity. In the ventral wall of the most anterior part of the canal lies the dorsal orifice of a narrow descending canal (*c. a. ast*) which opens ventrally in the roof of the most anterior part of the fossa autopalatina. The importance of this and certain other but less distinct canals seen in the bony tissue ventro-medially to the olfactory canals is obscure but most likely it carried a vessel corresponding to the anastomosis between the anterior ramus of the a. carotis cerebralis and the palatine artery described by ROOFE (1935, p. 271) in *Ambystoma*.

The canal for the r. ophthalmicus lateralis (*c. o. lat*) has its posterior orifice in the foremost dorsal part of the orbitotemporal region from where it pierces the thick dorso-medial part of the postnasal wall. The posterior orifice is indistinct in the sections of *G. groenlandica* but at any rate in *G?* cf. *paucidens* it is situated in the bottom of a pit, as in *P. spitsbergensis* (JARVIK, 1942, pp. 362, 372–373). In or close to this pit or in a corresponding position there are the openings of several fine canals, in the sections situated very much as described in *P. spitsbergensis*. In *G. groenlandica*, too, there is thus a canal (see 1942, fig. 36B, *c. prd*) which comes from the posterior opening of the medial profundus canal and two canals (*c. vadl*) which accompany the main canal forwards and join that canal or run to the dorsal parts of the snout, and there are canals in the position of canals *c. prdl* (1942, figs. 36A, 43) in *P. spitsbergensis*. From its posterior orifice the canal for the r. ophthalmicus lateralis runs forwards in the ethmosphenoid dorsally to the nasal cavity and can in the sections be followed almost to the anterior end of the neural endocranium. Posteriorly it is situated ventro-medially to the supraorbital sensory canal (*soc*), but anteriorly, owing to the curvature of that canal, it runs ventrally or ventro-laterally to the sensory canal. In its course forwards it gives off several very fine canals to the sensory canal (*ct. o. lat*, fig. 23; 1966, fig. 1B). Anteriorly it is joined by a canal from the nasal cavity.

One of the most conspicuous features in the porolepiform snout is the presence of a very wide medial profundus canal (*c. prm*) and one or more lateral profundus canals (*c. prl*). In front of the medial profundus canal the medial parts of the tectum nasi and the adjoining parts of the medial and anterior nasal walls are pierced by a great number of foramina or canals of different calibers (*c. prt*). All these canals, which have such a position that they no doubt transmitted branches of the n. ophthalmicus

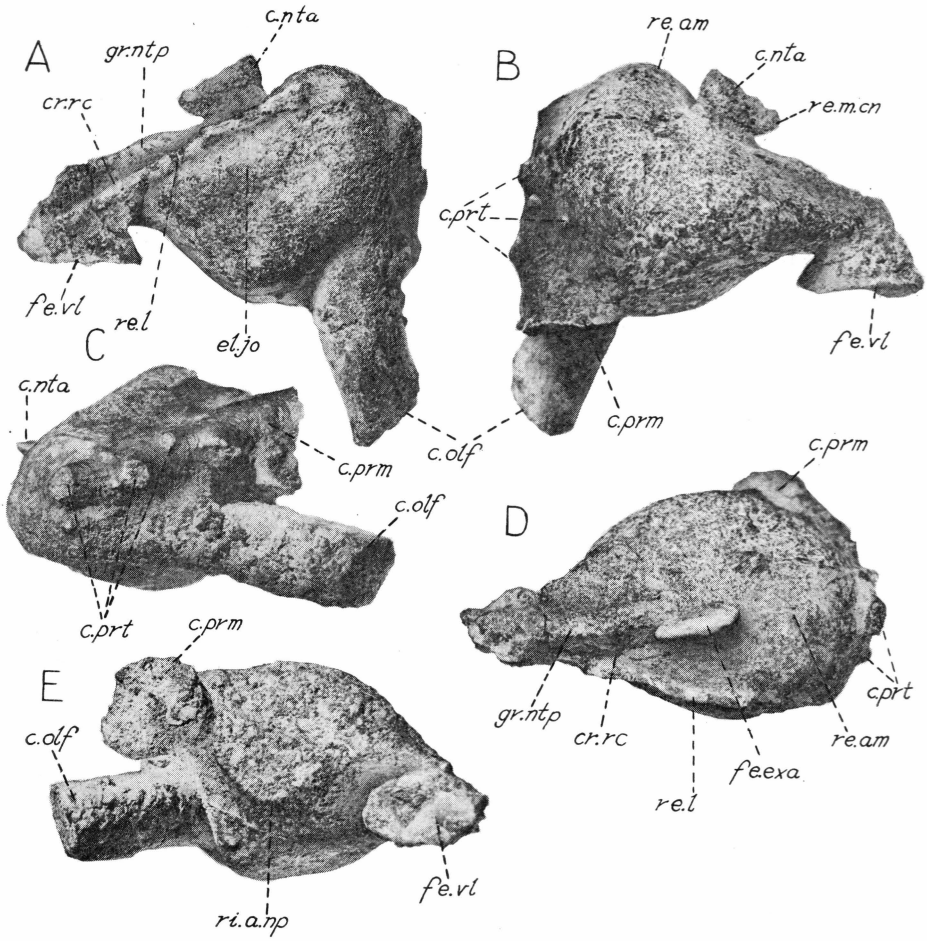


Fig. 13. *Porolepis* sp. Natural cast of right nasal cavity of specimen shown in fig. 10A in, *A*, ventral, *B*, dorsal, *C*, antero-medial, *D*, antero-lateral and, *E*, posterior aspects. Specimen No. P. 33993, Pal. Mus., Oslo. × 8/3.

cav. in, cast of cavum internasale; *cav. nc*, cast of cavity of nasal capsule; *c. cut*, canal probably for cutaneous vessel and profundus branch; *c. nta*, canal for anterior nasal tube; *c. olf*, canalis olfactorius; *c. ora*, *c. orp*, anterior and posterior canals of orbito-rostral passage; *c. prdm*, canals for dorso-medial profundus branches; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. prt*, canals for twigs of medial terminal profundus branch and vessels; *cr. rc*, crista rostro-caudalis or (in casts) groove occupied by that crest; *div. fbr*, forebrain divison of cranial cavity; *el. jo*, elevation probably occupied by recess for Jacobson's organ; *fe. ench*, *fe. enp*, divisions of fenestra ventro-lateralis representing fenestra endochoanalis and fenestra endonarina posterior; *fe. exa*, fenestra exonarina anterior; *fe. vl*, fenestra ventro-lateralis; *gr. ntp*, groove for posterior nasal tube or (in casts) ridge occupying that groove; *gr. ora*, anterior groove of orbito-rostral passage; *i. exp*, notch forming part of fenestra exonarina posterior; *i. te. o*, impression of tectum orbitale; *re. am*, antero-medial recess of nasal cavity; *re. bulb*, recess for bulbus olfactorius; *re. l*, lateral recess of nasal cavity; *re. m. cn*, recess for musculus constrictor narium; *ri. a. np*, ridge occupying groove for posterior nasal artery; *ri. in*, depression occupied by internasal ridge; *w. in*, *w. pren*, *w. pn*, internasal, prenasal and postnasal walls.

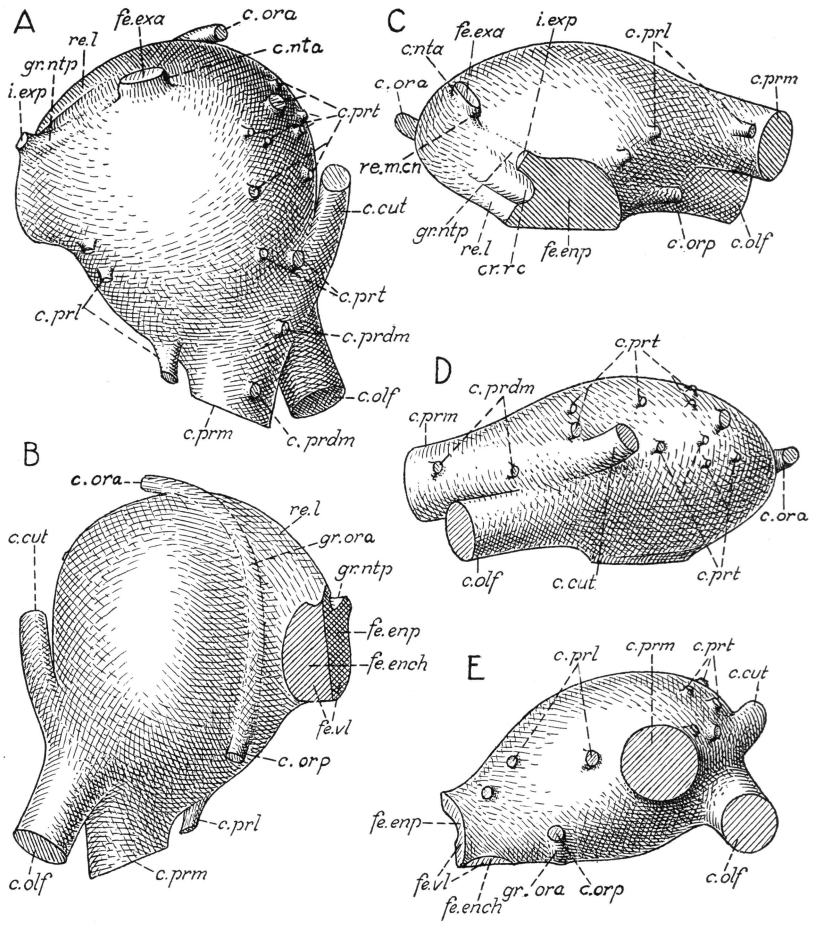


Fig. 14. *Porolepis spitsbergensis*. Restorations of cast of left nasal cavity in, *A*, dorsal, *B*, ventral, *C*, lateral, *D*, medial and, *E*, posterior aspects. From JARVIK, 1942, fig. 42. × 8/3.

For explanation of index letters see fig. 13.

profundus or of vessels accompanying that nerve, run from the nasal cavity mainly in dorsal or dorso-medial directions to the external side of the ethmoidal region. In one specimen of *Porolepis brevis* the most anterior canal (*c. prt*, fig. 10A) pierces the prenasal wall in an antero-ventral direction and the openings seen in *G?* cf. *paucidens* (fig. 10B, pl. 14:2) are probably also such more or less ventrally directed apical canals.

The natural cast of the nasal cavity of the specimen of *Porolepis brevis* referred to above (fig. 13) posteriorly presents a ridge (*ri. a. np*) which has such a position that it must have occupied a groove on the anterior face of the postnasal wall. This groove which seems to be present also in *Porolepis* sp. from Poland (KULCZYCKI, 1960, figs. 1, 3A, "*sulc. ln*")

runs from the medial side of the inner opening of the medial profundus canal in a curve towards the area of the fenestra ventro-lateralis. Most likely this groove gave passage to a vessel corresponding to the posterior nasal artery in *Salamandra* (FRANCIS, 1934, p. 204).

Another characteristic feature of the porolepiform snout is the presence of the orbito-rostral passage first described in *Porolepis* (1942, p. 369) but shown also in the sectioned and other specimens of *G. groenlandica*. The posterior part of this passage is represented by a groove (*gr. orp*) which from the pronounced corner (*co*) of the postnasal wall runs in an antero-lateral direction and which as described above in its anterior part is covered by the ethmoidal articular process of the palatoquadrate in such a way that a canal is formed. This canal is continued forwards by another short canal, the posterior canal of the orbito-rostral passage (*c. orp*), which pierces the solum nasi at the transition to the postnasal wall and enters the nasal cavity close medially or posteromedially to that part of the fenestra ventro-lateralis which gave passage to the choanal tube. Within the nasal cavity the canal is continued forwards across the dorsal surface of the solum nasi by a groove (*gr. ora*) leading to another canal (*c. ora*) which pierces the ventro-lateral part of the prenasal wall. As shown on both sides of the sectioned specimen, the latter canal gives off a fine canal (*c. buct*, figs. 21A, 75B) to the adjoining part of the infraorbital sensory canal.

Another important passage was discovered in the sectioned specimen of *G. groenlandica* (JARVIK, 1962, p. 92, 1964, p. 58, 1966, pp. 49–52). This passage is composed of a dorsal canal (1966, fig. 1c, *c. prv.*) which from the postero-medial part of the floor of the nasal cavity runs in a ventro-medial direction into the internasal wall. In the thick bony mass of that wall this canal, which almost certainly transmitted a ventral nasal branch (*r. prv*, fig. 15B) of the profundus nerve, meets a ventral canal (*c. pald*, figs. 31, 73A; 1966, fig. 1C, D, *c. pal*) which enters the neural endocranium on the ventral side in the area between the vomer and the parasphenoid and runs in a dorsal direction. This latter vertical canal which is continued backwards by a short groove on the lower side of the ethmoidal region obviously was developed for a dorsal terminal branch of the r. palatinus VII (*r. pal*, fig. 15B) and very likely an anastomosis was formed between the profundus and palatine nerves medially to the choana (fig. 75E). At the junction of the profundus and palatine canals a rather wide anterior canal (*c. pr-p*, figs. 8D, 31, 73A) is given off. This canal which must have transmitted a mixed profundus-palatine nerve (*r. pr-p*, fig. 15B) runs forwards and slightly laterally and opens into the postero-medial part of the cavum internasale. The anterior opening of that canal is discernible in specimens of *Porolepis* and *Holop-*

tychius, too, a condition which demonstrates that the profundus-palatine anastomosis was developed in porolepiforms in general. From the junction a canal issues also in a postero-lateral direction. This canal cannot be followed with certainty in the sections but most probably it opens into the anterior part of the fossa autopalatina and if so it possibly transmitted the postchoanal nerve.

The position, course and development of the various foramina, canals and grooves suggest that the snout in porolepiforms was innervated somewhat as follows (fig. 15; cf. JARVIK, 1942, pp. 378–378, 1966, pp. 45–52, fig. 2).

The r. ophthalmicus lateralis (*r. o. lat*) entered the neural endocranium in the antero-medial part of the orbit and accompanied by branches of the n. ophthalmicus profundus and vessels it passed forwards in a canal (*c. o. lat*) dorsally to the nasal cavity to or almost to the anterior tip of the snout giving off small twigs (*t. o. lat*) to the neuromasts of the supraorbital sensory canal (as regards the r. ophthalmicus superficialis V, *rd. V*, fig. 88, see JARVIK, 1942, p. 254).

The r. buccalis lateralis, as evidenced mainly by the grinding series of *G. groenlandica*, ran forwards in a groove (*gr. r. buc*, fig. 32A3; see also fig. 32A4, *c. buct*) on the ventro-medial side of the lachrymal, dorsally to the most lateral part of the palatoquadrate, divided in the anterior part of the orbit into two branches, one lateral and one anterior. The lateral branch (*r. bucl*) passed forwards laterally to the choana and dorsally to the postero-lateral part of the palatal lamina of the rostropremaxillary where a lateral twig was given off to the adjoining part of the infraorbital sensory canal (the fine canal for this twig is shown in sections Nos. 53–55). The anterior or medial branch (*r. buca*) turned medially, passed a groove (*gr. buca*, figs. 25A, 27C, pl. 19:2) on the postero-medial side of the ethmoidal articular process of the palatoquadrate and entered the orbito-rostral passage. In the most anterior part of that passage it gave off at least one twig (*buct*, fig. 15A) to the adjoining part of the infraorbital sensory canal.

The presence of a very wide medial profundus canal (*c. prm*), the fact that the canals which pierce the lateral and ventro-lateral parts of the postnasal wall—or the grooves (e.g. *gr. orp*, fig. 9A) leading to them on the posterior face of that wall—have such a direction that they must have transmitted branches of nerves (and vessels) coming from the medial parts of the orbit and, finally, the absence of distinct canals or other passages in the ventro-lateral part of the snout demonstrates conclusively that the n. ophthalmicus profundus (cf. fig. 88, *rd. Pr*) was strong, supplying also the lateral parts of the snout and that the r. maxillaris V (cf. fig. 88, *n. Pr. v*) was weakly developed and disregarding fibres

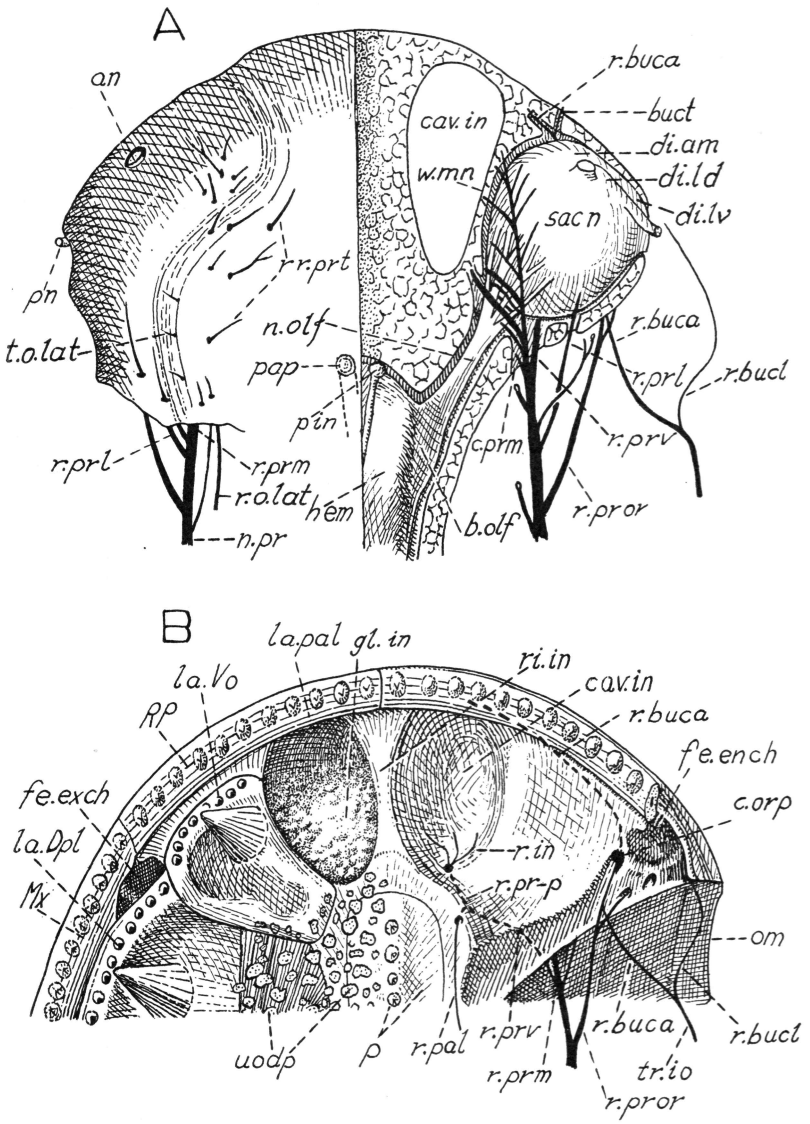


Fig. 15. *Porolepis brevis.* Restorations of nerves and certain other soft parts in snout in, *A*, dorsal and, *B*, palatal aspects. From JARVIK, 1964, fig. 20C and 1966, fig. 2A. Slightly modified.

Mx, maxillary; *P*, parasphenoid; *RP*, rostropremaxillary.

an, anterior nostril; *b. olf*, bulbus olfactorius; *buct*, twig of r. buccalis to neuromast of infraorbital sensory canal; *cav. in*, cavum internasale; *c. orp*, posterior canal of orbito-rostral passage; *c. prm*, canal for medial and ventral terminal profundus branches; *di. am*, antero-medial diverticle of nasal sac; *di. ld*, *di. lv*, dorsal and ventral divisions of lateral diverticle of nasal sac; *fe. ench*, fenestra endochoanalis; *fe. exch*, fenestra exochoanalis; *gl. in*, internasal ("intermaxillary") gland; *hem*, hemisphere of forebrain; *la. Dpl*, tooth-bearing lamina of dermopalatine; *la. pal*, palatal lamina of premaxillary; *la. Vo*, tooth-bearing lamina of vomer; *n. olf*, nervus olfac-

possibly accompanying the lateral and anterior buccalis branches did not reach the snout.

In its course forwards through the anterior part of the orbit the n. ophthalmicus profundus (*n. pr*, fig. 15) gave off at least 1) one fairly strong dorsal branch which through canal *c. prd* entered the canal for the r. ophthalmicus lateralis, 2) one ventral branch (*r. prv*) which probably entered the nasal cavity through the medial profundus canal emerging again through canal *c. prv* to anastomose with the r. palatinus VII, 3) one or more lateral branches (*r. prl*) entering the nasal cavity through the lateral profundus canals, 4) one ventro-lateral branch (*r. pror*) which together with the anterior buccalis branch passed through the orbito-rostral passage and possibly, 5) one or two ventro-lateral branches passing through canals *c. vl* described in *Porolepis* (in the sections of *Glyptolepis* no such canals have been found). After giving off these branches the strong remainder of the n. ophthalmicus profundus, the medial profundus branch (*r. prm*), went to the nasal cavity through the medial profundus canal and when passing through that canal and within the nasal cavity it broke up completely into numerous twigs (*rr. prt*) which passed through the canals in the nasal walls to supply the dorso-medial and anterior parts of the snout.

The r. palatinus VII (*r. pal*, fig. 15), as evidenced mainly by the grinding series of *Glyptolepis*, ran forwards dorsally to the small dental plates (*uodp*) which are found ventrally to the parasphenoid, continued in a short rostro-caudal groove on the ventral side of the neural endocranium between the vomer and the anterior part of the parasphenoid, then entered the vertical canal in the internasal wall and finally anastomosed with the ventral profundus branch medially and a little posteriorly to the choana. The mixed nerve thus formed (*r. pr-p*) went forwards through canal *c. pr-p* to the cavum internasale and supplied (*r. in*) the internasal gland (*gl. in*). A mixed nerve tentatively referred to as the postchoanal nerve was possibly given off in a postero-lateral direction

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torius; *n. pr*, nervus ophthalmicus profundus; *ntp*, posterior nasal tube; *om*, margin of orbital fenestra; *pap*, *pin*, parapineal and pineal organs; *pn*, posterior nostril; *r. buca*, anterior branch of r. buccalis lateralis supplying anterior neuromasts of infraorbital sensory canal; *r. bucl*, lateral branch of r. buccalis (probably including fibres of r. maxillaris V); *ri. in*, internasal ridge; *r. in*, twigs of combined profundus-palatine nerve supplying internasal gland; *r. o. lat*, r. ophthalmicus lateralis; *r. pal*, r. palatinus VII; *r. prl*, *r. prm*, lateral and medial terminal profundus branches; *r. pror*, terminal profundus branch passing through orbito-rostral passage; *r. pr-p*, combined profundus-palatine nerve; *r. prv*, ventral terminal profundus branch anastomosing with r. palatinus VII; *rr. prt*, twigs of medial terminal profundus branch; *sac n*, nasal sac; *t. o. lat*, twigs of r. ophthalmicus lateralis to neuromasts of supraorbital sensory canal; *tr. io*, truncus infraorbitalis; *uodp*, upper oral dental plates; *w. mn*, medial nasal wall.

and there is some evidence that this nerve anastomosed with a lateral palatine branch which may have entered the internasal wall in the anterior part of the fossa autopalatina.

Disregarding the groove for the posterior nasal artery on the anterior side of the postnasal wall (see fig. 13E, *ri. a. np*) no special canals or other passages for vessels have been found and it is therefore to be assumed that the arteries and veins in the main used the same passages as the nerves.

The *postethmoidal portion of the ethmosphenoid*, that is in the main the *orbitotemporal region* of the neural endocranium, is, besides in the grinding series of *Glyptolepis*, more or less well shown in several specimens of *Porolepis*, *Glyptolepis* and *Holoptychius* and although many variations occur and it may be rather different even in specimens of the same genus or on both sides of the same specimen it is clearly of the same type in all porolepiforms and distinctly different from the corresponding portion of the ethmosphenoid in osteolepiforms.

The postethmoidal portion (figs. 16, 18–21, 23, 24E, 65B, 71A, 73A, pl. 3, pl. 7:1, pls. 9,14, pl. 17:3, pl. 19:2, pl. 25; see also BJERRING, 1967, fig. 14, 1971, fig. 13) consists of a strong median interorbital wall (*w. io*) and a paired tectum orbitale (*te. o*) which latter forms a thin roof of the orbit. The internasal wall increases in height posteriorly. This is due mainly to a gradual increase in thickness of those parts of the wall that are situated ventrally to the part of the cranial cavity that contained the brain. Accordingly the floor of the posterior part of the ethmosphenoid portion of the cranial cavity which houses the hypophysial fossa is thick.

Fig. 16. *Glyptolepis groenlandica* n. sp. Three almost transverse sections through head in orbital region. Sections Nos. 119, 130 and 140 of grinding series. × 3/1.

Bb, basibranchial; *Co*, coronoid; *De*, dentary; *Dpl*, dermopalatine; *Enpt*, entopterygoid; *Etsph*, ethmosphenoid; *Fr-et. sh*, fronto-ethmoidal shield; *G*, principal gular plates; *Hh*, hypohyal; *Id*, infradentary; *Ju*, jugal; *La*, lachrymal; *Mb*, meckelian bone; *Mx*, maxillary; *Mxp*, lamina palatina of maxillary; *P*, parasphenoid; *Pq. aup*, pars autopalatina of palatoquadrate; *Prart*, prearticular; *Sbm1*, submandibular 1. *art. am2*, posterior area of fusion between posterior articular area of antero-medial lamina of palatoquadrate and dorsal side of suborbital ledge; *bbdp*, dental plates of basibranchial; *c. Mb*, canal in meckelian bone; *c. olf*, canalis olfactorius; *c. pap*, canal for parapineal nerve or tract; *c. pin*, canal for pineal nerve or tract; *div. fbr*, forebrain division of cranial cavity; *dp*, dental plates; *dplt*, tusk of dermopalatine; *fe. o*, fenestra orbitalis; *fo. aup*, fossa autopalatina; *gr. II*, groove for n. opticus; *ioc*, infraorbital sensory canal; *la. am*, antero-medial articular lamina of pars autopalatina of palatoquadrate; *la. Co*, tooth-bearing lamina of coronoid; *la. Dpl*, tooth-bearing lamina of dermopalatine; *le. so*, suborbital ledge; *mmdp*, medial mandibular dental plates; *om*, margin of orbital fenestra; *p-mc*, preoperculo-mandibular sensory canal; *re. bulb*, recess for bulbus olfactorius; *ri. Pi*, median ridge of pineal plate; *soc*, supraorbital sensory canal; *te. o*, tectum orbitale; *uodp*, upper oral dental plates; *w. io*, interorbital wall.

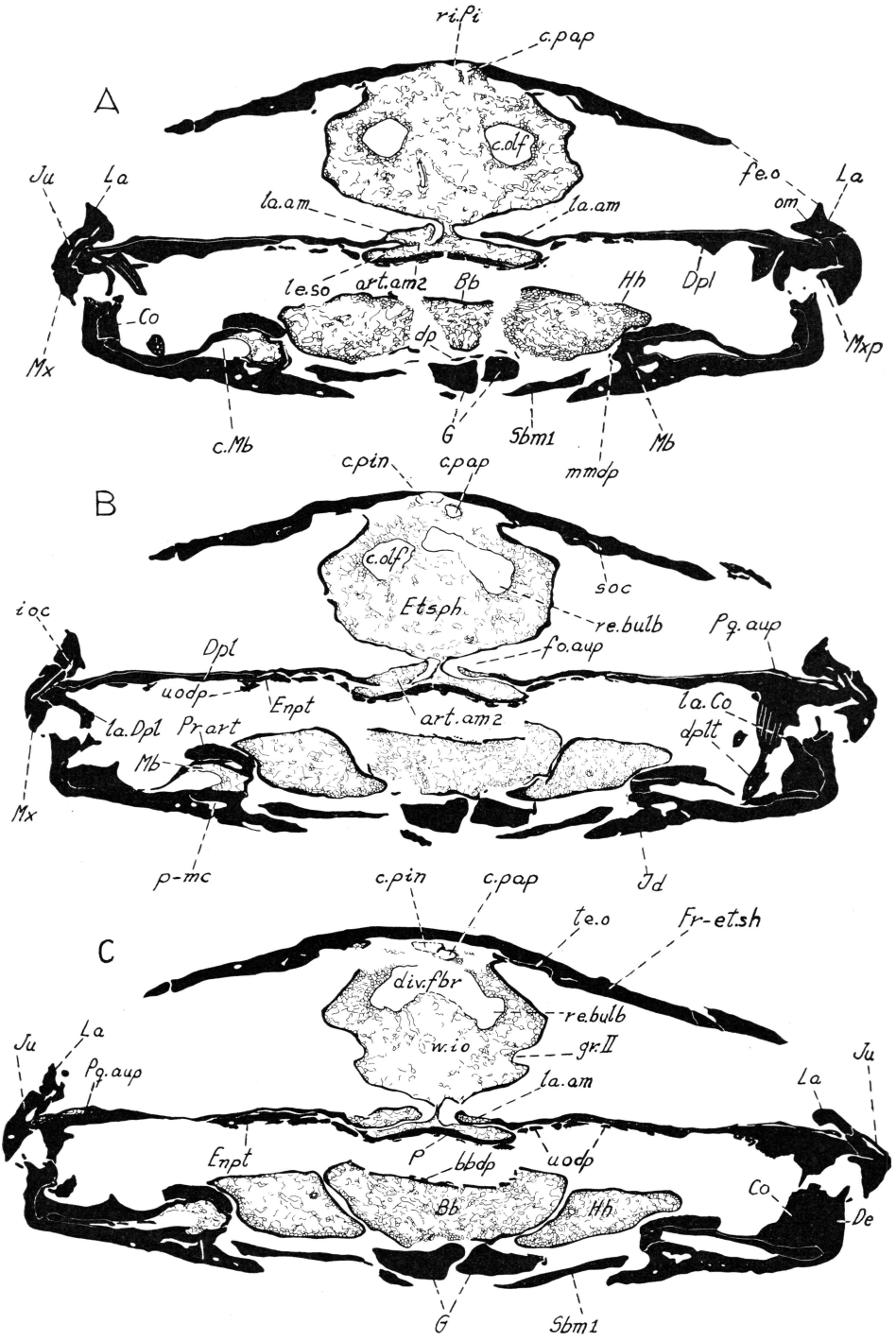

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la.Co
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Prart
art.am2
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Mx
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C
te.o
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Fig. 16.

The endoskeletal roof of this part of the cranial cavity, most posteriorly formed by the anterior part of the otoccipital, is thin and the brain was situated high up in the interorbital wall, close below the dermal cranial roof, which is formed by the fronto-ethmoidal shield and most posteriorly by the anterior part of the parietal shield.

The ethmosphenoid portion of the cranial cavity (see also figs. 17, 72A) is well shown in particular in the grinding series of *Glyptolepis* and is in its broad features developed as follows. Anteriorly it ends well behind the transverse line running through the posterior margin of the wide medial profundus canal and accordingly in *G. groenlandica* it has no ethmoidal part. This in contrast to the two specimens, viz. the holotypes of *Porolepis spitsbergensis* and *P. elongata*, which were the only specimens showing this detail available to me in 1942. In both these specimens (p. 17) the cranial cavity in the fossil state of preservation extends far forwards into the ethmoidal region (see *cart* fig. 69A; JARVIK, 1942, pl. 1:1, pl. 2:3, pl. 5:1, *eth. cr*) and in the holotype of *P. elongata* this ethmoidal part of the cranial cavity contains a detached dermal bone which must mean that there was a cavity during the process of fossilisation. Accordingly there was no reason to doubt that the cranial cavity in porolepiforms had an ethmoidal part although this, as was pointed out (1942, p. 381), in *Holoptychius* must have been small (cf. 1965a, pp. 112–113, 1966, p. 53). However, in specimens of *P. brevis* that have been prepared after 1942 and in *Glyptolepis?* cf. *paucidens* the cranial cavity as to its anterior extent agrees well with that in the sectioned and other specimens of *G. groenlandica* and most probably the cranial cavity in porolepiforms in general ends in the anterior part of the orbitotemporal region. This, however, does not exclude the possibility that the forebrain

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Fig. 17. *Glyptolepis groenlandica* n. sp. Graphical restorations after serial sections of cast of anterior part of cranial cavity with fossa hypophyseos in, *A*, lateral, *B*, dorsal, and, *C*, ventral aspects (cf. STENSIÖ, 1963b, figs. 47, 48). × 6/1.

FrD, frontodermosphenotic; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Ptr*, postrostral.

c. a. ast, canal probably for anastomosis between anterior cerebral artery and a. palatina; *c. a. cer*, *c. a. ci*, *c. a. om*, *c. a. pal*, canals for a. cerebralis, a. carotis interna, a. ophthalmica magna and a. palatina; *c. bhd*, *c. bhs*, canals for right and left buccohypophysial ducts; *c. olf*, canalis olfactorius; *c. pap*, *c. pin*, canals for parapineal and pineal tracts; *c. port*, canal probably for portal vessels; *c. p. tub*, canal for pars tuberalis of adenohypophysis; *c. v. pit*, canal for pituitary vein; *c. vx*, canal probably for vessel; *c. II*, *c. III*, *c. IV*, canals for n. opticus, n. oculomotorius and n. trochlearis; *div. fbr*, *div. mes*, forebrain and mesencephalon divisions of cranial cavity; *fo. hyh*, *fo. hyv*, anterior, horizontal and posterior, vertical portions of fossa hypophyseos; *gr. cr. m*, groove for median hypophysial crest; *gr. v. o*, groove for orbital vein; *re. bulb*, recess for bulbus olfactorius; *re. inf*, recess for infundibulum of diencephalon; *re. lhy*, lateral recess of fossa hypophyseos for lateral lobe of adenohypophysis; *re. pin*, pineal recess.

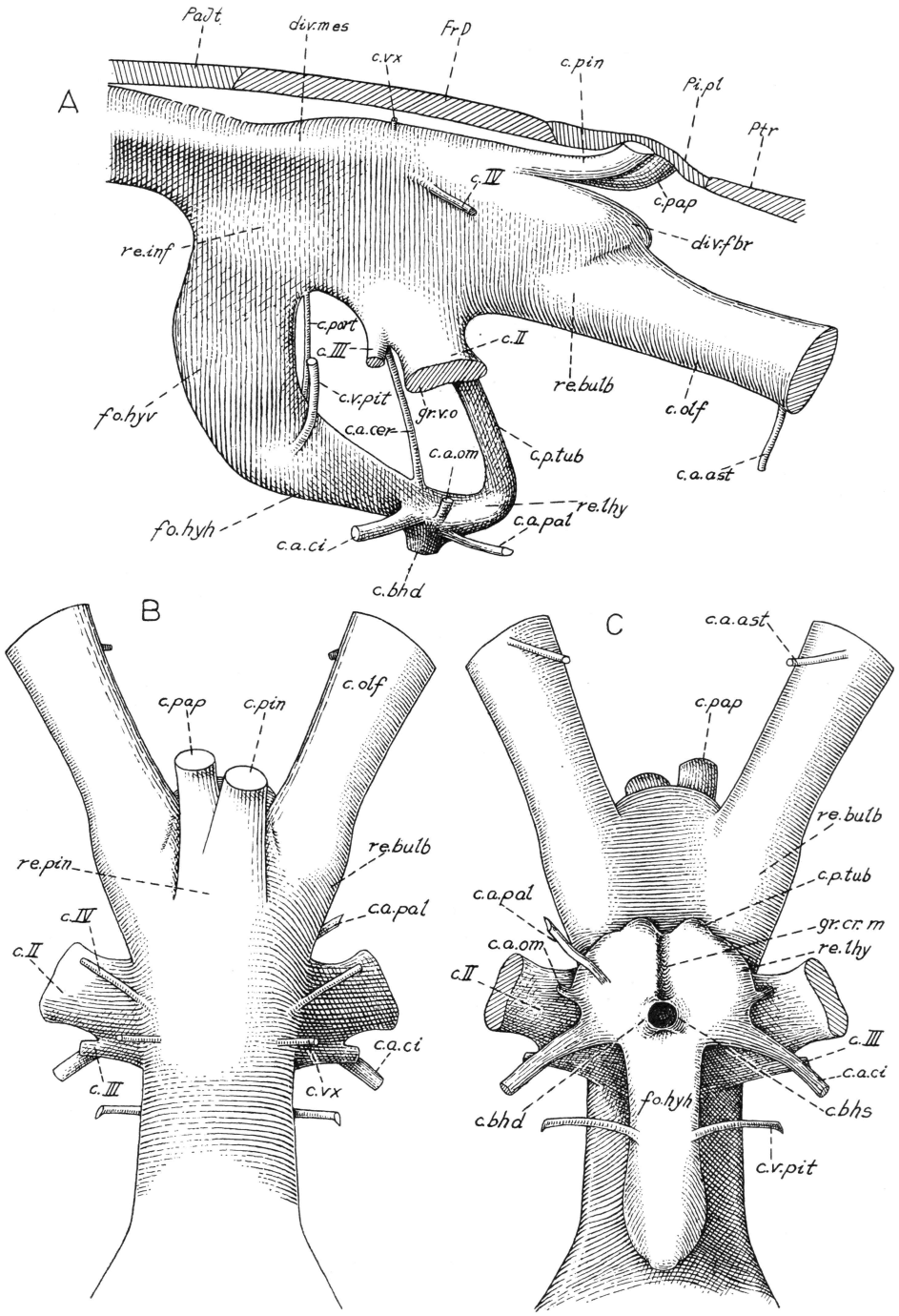

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c.vx
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fo.hyv
c.v.pit
gr.v.o
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c.III
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fo.hyh
c.bhd
c.bhs
c.v.pit

Fig. 17.

in some early forms (*P. spitsbergensis*, *P. elongata*) may have retained its larval position between the nasal sacs.

The ethmosphenoid portion of the cranial cavity is in its anterior part comparatively broad. In this broad part three main divisions may be distinguished, the paired ventro-lateral recess, the forebrain division, and the pineal recess (fig. 17). The ventro-lateral recess (*re. bulb*), which also in *P. spitsbergensis* and *P. elongata* is found in the anterior part of the orbitotemporal region, is situated ventro-laterally to the forebrain division and is dorsally bounded from that by a distinct ridge on the inner side of the wall of the cranial cavity. The ventro-lateral recess is continued forwards by the canalis olfactorius (*c. olf*) and as discussed in 1942 (p. 363; see also 1965a, pp. 112–113; STENSIÖ, 1963b) it in all probability housed the bulbus olfactorius (*bulb*, fig. 83A). The forebrain division (*div. fbr*) is both dorsally and ventrally indistinctly divided by median elevations into right and left halves indicating the position of the hemispheres. The median pineal recess (*re. pin*) which besides the proximal portions of the pineal and parapineal stalks probably contained dorsal parts of the paraphysis is situated postero-dorsally to the forebrain division and is narrower than that division. Antero-dorsally it is continued by two canals, one posterior (*c. pin*) situated close the right of the median line, and one anterior (*c. pap*) emerging close to the left of the median line. These canals which obviously transmitted the pineal and parapineal stalks diverge slightly forwards and open on the dorsal face of the ethmosphenoid about straight dorsally to the anterior end of the forebrain division (figs. 17, 18, 23). Dorsally to these openings lies the pineal plate (*Pi. pl*) of the fronto-ethmoidal shield. As is well shown, in particular in some specimens of *Holoptychius* (fig. 37A, B, pl. 29:1.2), the dorsal face of this plate is slightly domed (*e. pi*) and it rises a little above the adjoining parts of the external face of the fronto-ethmoidal shield. The ventral face of the pineal plate shows a corresponding depression. In *Holoptychius* (pls. 27, 28) there are no traces of a subdivision of this pit and in 1942 (p. 362) I therefore claimed that it contained the pineal organ only. However, in the sectioned and other specimens of *Glyptolepis groenlandica* the pit is divided by a median ridge (*ri. Pi*, figs. 16A, 72A) into two small pits (*p.p.*, *p.pp*, pl. 20:2) situated dorsally to the openings of the pineal and parapineal canals respectively. These pits or canals are found in other specimens of *Glyptolepis* and in *Porolepis* (pl. 7:2) and both the parapineal and the pineal organs (*pap*, *pin*, figs. 15A, 83A; see also JARVIK, 1967b, fig. 2C) were certainly developed in porolepiforms in general and were situated close below the dermal cranial roof. In the grinding series of *Glyptolepis* (fig. 16A, B) the roof of each of the pits of the pineal plate is very thin but as far as I can find there is no foramen and judging also by numerous other specimens both pineal and parapineal ("parietal") foramen are lacking in porolepiforms.

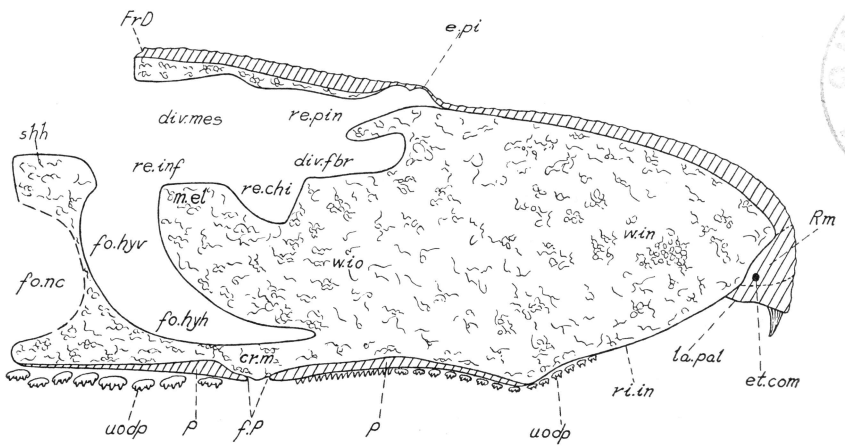


Fig. 18. *Glyptolepis groenlandica* n. sp. Divisio cranialis anterior in median section. Restoration after grinding series. × 4/1.

FrD, posterior margin of frontodermosphenotic; *P*, parasphenoid; *Rm*, approximate position of median rostral.

cr. m, median hypophysial crest; *div. fbr*, *div. mes*, forebrain and mesencephalon divisions of cranial cavity; *e. pi*, pineal elevation; *et. com*, ethmoidal commissure of infraorbital sensory canals; *fo. hyh*, *fo. hyv*, anterior horizontal and posterior vertical portions of fossa hypophyseos; *fo. nc*, fossa for anterior end of notochord; *f. P*, foramen in parasphenoid for common opening of paired buccohypophysial duct; *la. pal*, palatal lamina of rostropremaxillary; *m. el*, median elevation in floor of diencephalon portion of cranial cavity; *re. chi*, chiasma recess; *re. inf*, recess for infundibular portion of diencephalon; *re. pin*, pineal recess; *ri. in*, internasal ridge; *shh*, horizontal shelf; *uodp*, upper oral dental plates; *w. in*, *w. io*, internasal and interorbital walls.

The posterior part of the ethmosphenoid portion of the cranial cavity (figs. 17–19, 24E; Bjerring, 1971, fig. 13) is a little narrower than the anterior one. Dorsally, behind the pineal recess, a division well bounded posteriorly by a thickening on the inner side of the roof of the cranial cavity may be distinguished. This division (*div. mes*) no doubt housed the mesencephalon (*mes*, fig. 83A). Posteriorly to this division, at the transition between the ethmosphenoid and the otoccipital the cranial cavity widens and in this part, below the dorsal boundary between the anterior and posterior cranial divisions, the anterior broad part of the medulla oblongata and the cerebellum were probably situated. In the roof of the mesencephalon division there is on both sides of the sectioned specimen a short narrow canal (*c. vx*) which opens on the dorsal side of the ethmosphenoid. The importance of this canal is unknown but probably it transmitted a vessel. The lateral wall of the mesencephalon division is pierced by the canal for the n. trochlearis (*c. IV*) which runs in an antero-lateral direction and is continued backwards by a groove (*gri. IV*, fig. 19D) on the inner side of the lateral wall of the cranial cavity

running towards the posterior end of the mesencephalon division. Ventrally to the posterior part of that division there is an elevation on the inner side of the lateral wall of the cranial cavity. Below that elevation (*el*, fig. 24E) the cranial cavity widens slightly and forms a median space extending ventrally to the dorsal opening of the fossa hypophyseos. This space, the infundibular recess (*re. inf*), probably housed the infundibulum of the diencephalon and the neurohypophysis. Antero-ventrally to that recess, in front of the dorsal opening of the fossa hypophyseos, the floor of the cranial cavity rises and forms a pronounced median elevation (*m. el*) bounded laterally on each side by a longitudinal groove. Anteriorly the dorsal side of the median elevation, which is convex as seen both in transverse and longitudinal sections, slopes down into a rather deep median depression in the floor of the cranial cavity. This depression, the chiasma recess (*re. chi*), is situated between the inner openings of the wide opticus canals (*c. II*) and in its lateral part the dorsal opening of a strong, paired, vertical canal (*c. p. tub*) coming from the antero-ventral end of the fossa hypophyseos is found. This canal which very likely carried the pars tuberalis of the adenohypophysis (see fig. 83A) is continued backwards by a groove (*gr. p. tub*) on the antero-lateral side of the median elevation. A little behind the posterior end of that groove, in the groove between the median elevation and the lateral wall of the cranial cavity, lies the inner opening of the oculomotorius canal (*c. III*). Medially to that opening, on the dorso-lateral side of the median elevation, the dorsal opening of another paired vertical canal (*c. a. cer*) connecting the cranial cavity with the fossa hypophyseos is found. This canal which is narrower than the canal for the pars tuberalis probably conveyed the ascending cerebral artery. From the dorsal opening of canal *c. a. cer* a short almost transverse groove, presumably for the a. centralis retinae (*a. cr*, fig. 83), runs to the dorsal opening of the oculomotorius canal. In addition to the two paired vertical canals (*c. p. tub*, *c. a. cer*) now described there is another paired canal (*c. port*) connecting the cranial cavity and the fossa hypophyseos. This canal is found close in front of the vertical portion of the fossa (*fo. hyp*) and judging from its position it seems likely that it transmitted vessels of the hypophysial portal system.

The fossa hypophyseos (figs. 17–19, 24E, 72A, pl. 14:2) which is situated in the solid ventral part of the interorbital wall consists of a posterior, vertical (*fo. hyp*) and an anterior, ventral and almost horizontal (*fo. hyh*) portion.

The dorsal opening of the vertical portion which forms the entrance to the fossa is oval in shape and fairly narrow. Below the opening the fossa becomes wider and ventrally to this widened part which is situated close in front of the pit (*fo. nc*) for the anterior end of the notochord the

vertical portion decreases slightly in width, curves forwards and merges into the horizontal portion. At the transition between the two portions an important canal is given off from the fossa in a dorso-lateral direction. This canal (*c.v.pit*) which almost certainly is the canal for the pituitary vein opens on the external side of the ethmosphenoid close dorsally to the basipterygoid process, where it is continued backwards by a distinct groove. At some distance in front of the inner opening of the canal for the pituitary vein the horizontal portion receives canal *c.a.cer* described above. In front of the entrance of that canal the horizontal portion broadens considerably and anteriorly it consists of a median canal-like part and a low paired lateral recess (*re.lhy*). The median part is divided ventrally by a strong median crest (*cr.m*, *gr.cr.m*; see also BJERRING, 1971, fig. 13, *exch.b*) into right and left halves and each of these halves is continued forwards and upwards by the strong canal for the pars tuberalis (*c.p.tub*).

In addition to these canals no less than four paired canals open into the anterior broad part of the horizontal portion of the fossa hypophyseos (figs. 17, 19, 83, pl. 14:2).

Three of these canals pierce the parasphenoid or are formed partly by grooves on its dorsal face. One of these canals is the bucco-hypophysial canal and a remarkable fact is that it is paired (*cd.bhy*, *cs.bhy*). This canal which is very short and somewhat funnelshaped runs from the ventral side of the median canal-like part of the horizontal portion in a ventro-medial direction and is bounded medially by the posterior part of the median crest (*cr. m*). It then pierces the parasphenoid (*f. P*) and opens on the ventral side of that bone together with the corresponding canal of the other side. The two other canals related to the parasphenoid are given off from the low lateral recess. The strongest of these canals (*c.a.ci*) which no doubt is the canal for the a. carotis interna runs in a postero-lateral direction, pierces the parasphenoid and opens on its ventral side (figs. 31, 39) close in front of the dorsal end of the groove for the prespiracular gill-slit, where it is continued backwards by a short groove on the ventral side of the parasphenoid and the adjoining part of the basipterygoid process. The third canal (*c.a.pal*) given off from the lateral recess runs in an antero-lateral direction to open on the lateral side of the parasphenoid where it is continued forwards by a groove (*gr.a.pal*). This canal which in the sectioned specimens is developed only on the right side (*cd. a. pal*, fig. 19) no doubt conveyed the a. palatina.

The last of the four canals to be described also issues from the lateral recess but it runs in a dorsal direction and opens on the lateral side of the ethmosphenoid close dorsally to the thick suborbital ledge. It may be suggested that this canal (*c. a. om*) which is short and wide transmitted the a. ophthalmica magna. That this is so is supported by the fact that

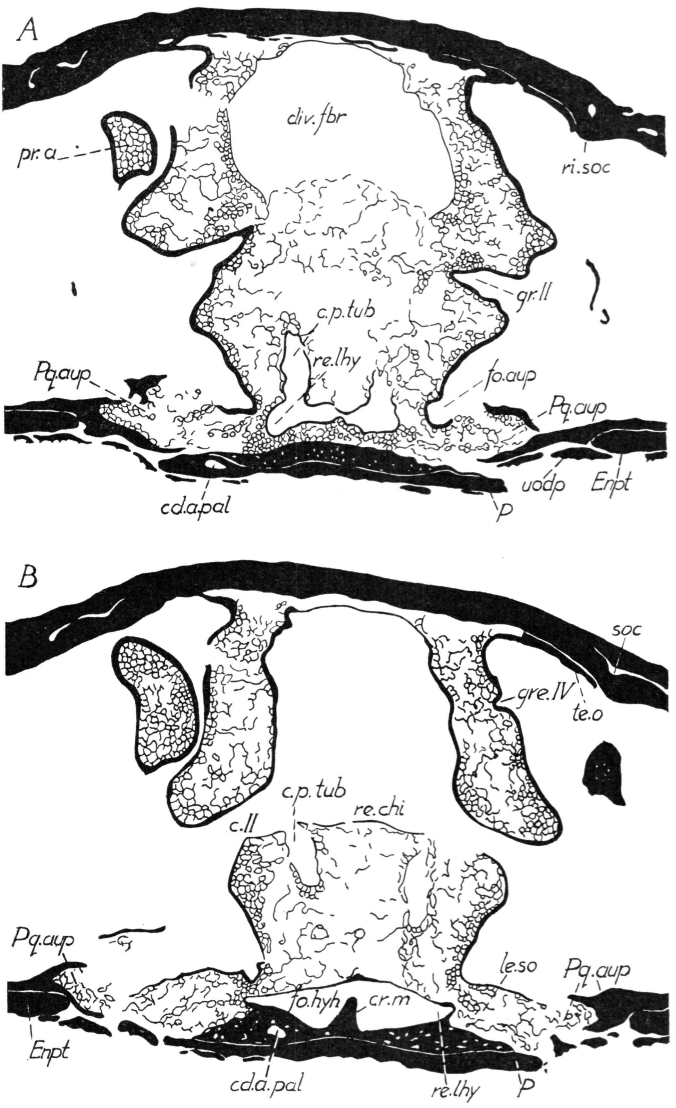
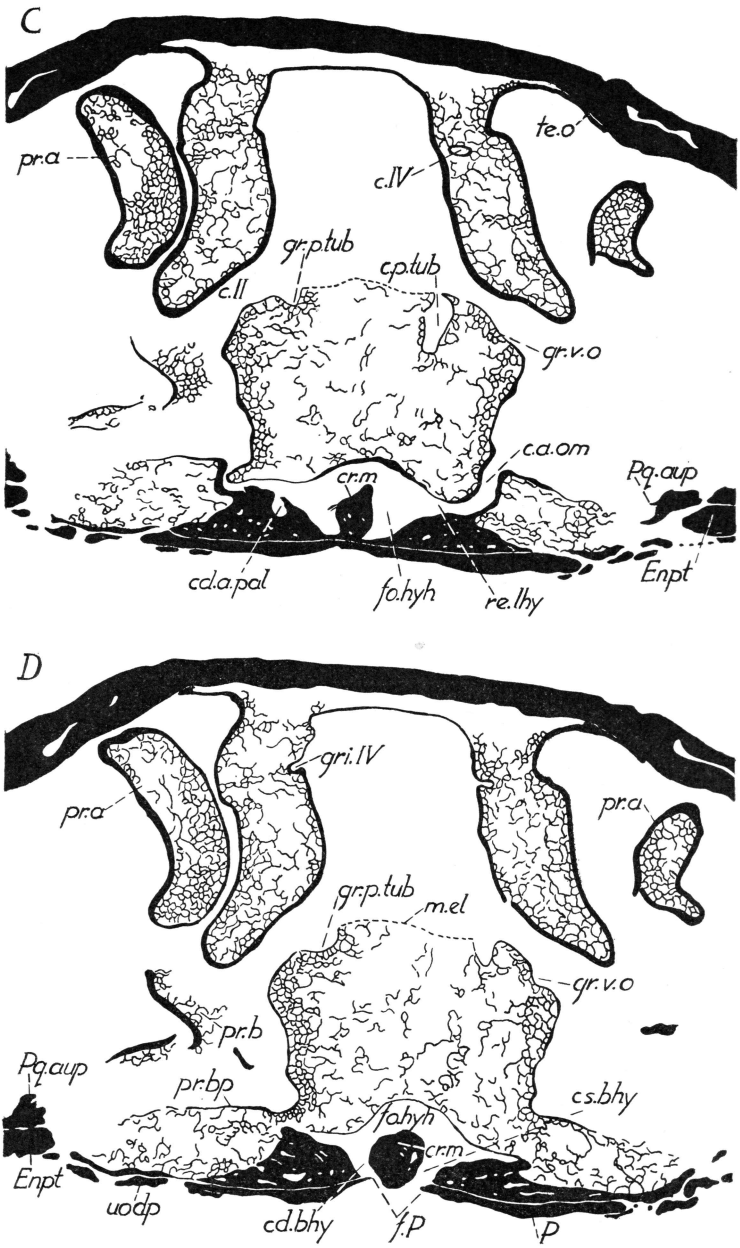


Fig. 19. *Glyptolepis groenlandica* n. sp. *A–D*, four almost transverse sections through divisio cranialis anterior in region of anterior horizontal portion of fossa hypophyseos. Parts of sections Nos. 157, 166, 171 and 174 of grinding series. × 6/1.

Enpt, entopterygoid; *P*, parasphenoid; *Pq. aup*, pars autopalatina of palatoquadrate.

c. a. om, canal for a. ophthalmica magna; *cd. a. pal*, canal of right side for a. palatina; *cd. bhy*, canal for buccohypophysial duct of right side; *c. p. tub*, canal for pars tuberalis of adenohypophysis; *cr. m*, median hypophysial crest; *cs. bhy*, canal for buccohypophysial duct of left side; *c. II*, *c. IV*, canals for n. opticus and n. trochlearis; *div. fbr*, forebrain division of cranial cavity; *fo. aup*, fossa autopalatina; *fo. hyh*, anterior horizontal portion of fossa hypophyseos; *f. P*, foramen in parasphenoid for common opening of buccohypophysial ducts; *gr. p. tub*, groove for pars



tuberalis of adenohypophysis; *gr. v. o*, groove for vena orbitalis; *gr. II*, *gre. IV*, *gri. IV*, grooves for opticus and trochlearis nerves; *le. so*, suborbital ledge; *m. el*, median elevation of floor of diencephalon division of cranial cavity; *pr. a*, processus ascendens of palatoquadrate; *pr. b*, processus basalis of palatoquadrate; *pr. bp*, basipterygoid process; *re. chi*, chiasma recess; *re. lhy*, lateral recess of fossa hypophyseos for lateral lobe of adenohypophysis; *ri. soc*, ridge of fronto-ethmoidal shield caused by supraorbital sensory canal; *soc*, supraorbital sensory canal; *te. o*, tectum orbitale; *uodp*, upper oral dental plates.

the canal in *Glyptolepis?* cf. *paucidens* (pl. 14:1) is continued by a distinct groove which on the external side of the interorbital wall runs in an antero-dorsal direction towards the external opening of the opticus canal.

One more canal may be described in this connection. This canal (*c. a. cib*), which is paired and fairly narrow, runs backwards from the bony tissue behind the lateral recess, pierces the parasphenoid and opens on its ventral side posterior to the groove for the prespiracular gill-slit. As will be demonstrated below (p. 209) this canal probably transmitted a medial branch of the a. carotis interna.

The five canals now described (*c. bhy*, *c. a. ci*, *c. a. pal*, *c. a. om*, *c. a. cib*) and the canal for the pituitary vein (*c. v. pit*), or at any rate their external openings, have been observed in specimens of *Porolepis* (figs. 20A, 73A, pl. 7:1, pl. 9), *Glyptolepis* (figs. 21, 31, 39, 72A, pl. 14, pl. 17:3; as regards *G. baltica* see GROSS, 1936, pp. 148–151, fig. 10, *hc*, *x*, *y*, *z*) and *Holoptychius* (fig. 20B, pl. 25) and although variations occur they are on the whole developed very much in the same way in all porolepiforms. The external openings of the trochlearis (*c. IV*), oculomotorius (*c. III*) and opticus (*c. II*) canals, too, have a similar position in all the specimens of *Porolepis*, *Glyptolepis* and *Holoptychius* in which they have been observed. The opening of the opticus canal often lies in the bottom of a deep pocket and from this pocket a groove (*gr. II*), sometimes short and wide, sometimes long and narrow, carried the n. opticus forwards to the eye. Another groove (*gr. v. o*) is sometimes found in the posterior part of the pocket. This groove which is short and broad and runs in a ventro-lateral direction was probably developed for the optic vein (see p. 208; JARVIK, 1966, p. 64).

Antero-dorsally to the opening of the opticus canal, at some distance behind the opening of the canal for the r. ophthalmicus superficialis lateralis, there is in one specimen (*Glyptolepis?* cf. *paucidens*, pl. 14:1) the external aperture of a distinct canal (*c. v. ca*) which appears to come from the most anterior part of the cranial cavity. If so this canal probably represents the canal for the vena cerebralis anterior which I previously have searched in vain in porolepiforms (see JARVIK, 1942, pp. 378–379, 1966, pp. 62–64) and which is absent in the sectioned specimen of *G. groenlandica*.

Ventrally to the opticus foramen and the groove for the n. opticus, between the basipterygoid process behind and the postnasal wall in front, the internasal wall presents a large elongated fossa, the fossa autopalatina (*fo. aup*), bounded ventrally by the suborbital ledge (figs. 9A, B, 16, 19–21, 65B, 71A, pl. 3, pl. 9:1, pl. 14:1, 2, 5; pl. 25:3, 6). This ledge (*le. so*) which posteriorly merges into the basipterygoid process is ventrally supported by the broad parasphenoid. In the specimens of *Porolepis* available in 1942 the fossa autopalatina is fairly shallow and

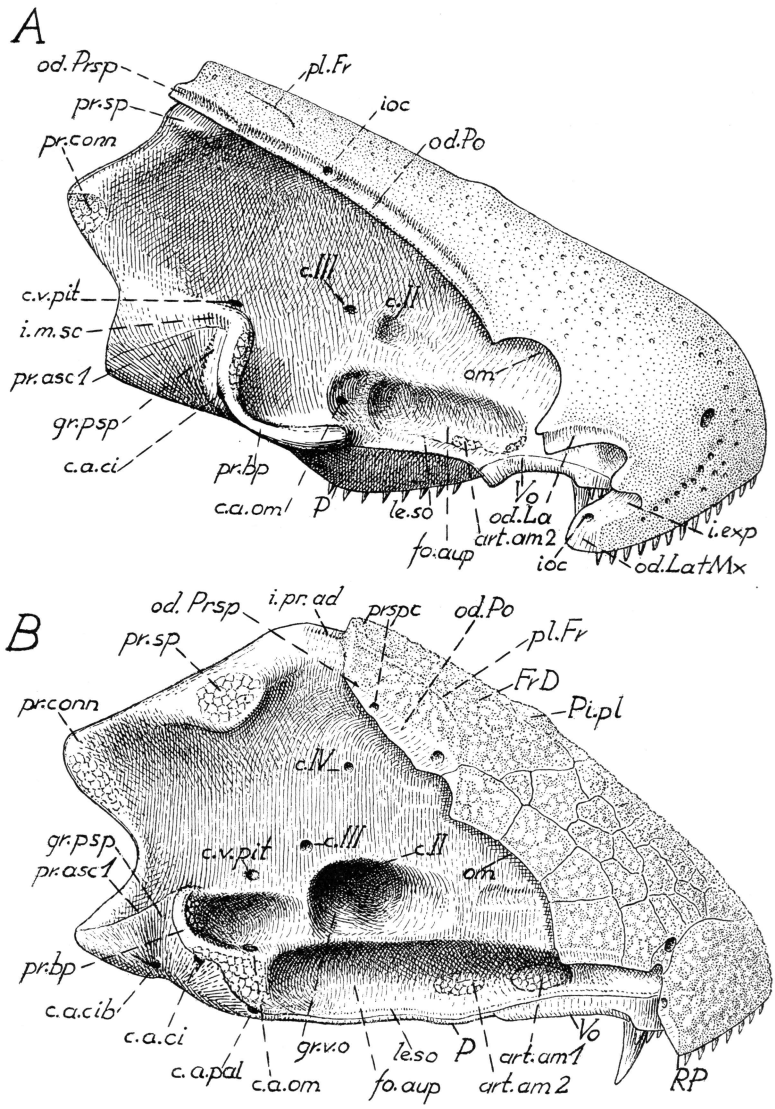


Fig. 20. Restorations of divisio cranialis anterior in lateral aspects of, *A*, *Porolepis* and, *B*, *Holoptychius*.
For explanation of index letters see fig. 21.

although it was clear that it must be developed for an antero-medial articular lamina of the pars autopalatina of the palatoquadrate I was unable to find any articular areas devoid of periostal lining in the fossa. In a large specimen of *Porolepis* (pl. 9) recently prepared the fossa is much deeper and agrees well with that in *Glyptolepis* and *Holoptychius*. In the latter the fossa is very deep, at its deepest point separated from that of the other side by a low thin median septum only (fig. 16) and

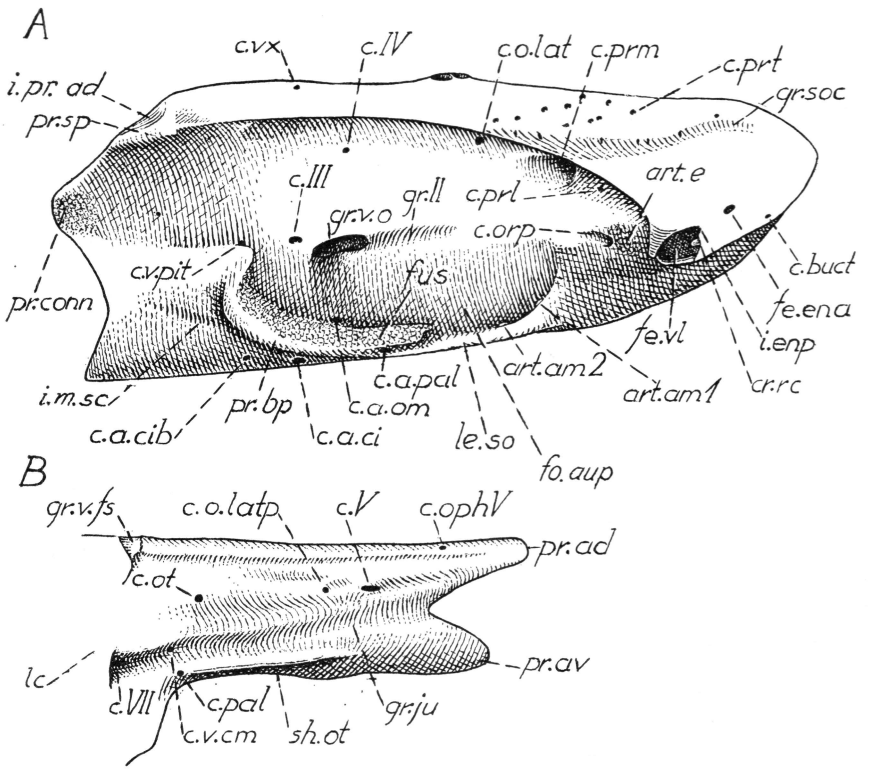


Fig. 21. *Glyptolepis groenlandica* n. sp. Tentative restorations of, *A*, ethmosphenoid and, *B*, anterior part of otoccipital in lateral aspects. Graphical restorations after grinding series. × 4/1.

FrD, frontodermosphenotic; *P*, parasphenoid; *Pi. pl*, pineal plate; *RP*, rostro-premaxillary; *Vo*, vomer.

art. am1, *art. am2*, areas articulating with antero-medial articular lamina of palatoquadrate; *art. e*, area of fusion with ethmoidal articular process; *c. a. ci*, canal for a. carotis interna; *c. a. cib*, canal for medial branch of a. carotis interna; *c. a. om*, *c. a. pal*, canals for a. ophthalmica magna and a. palatina; *c. buct*, canal for anterior twig of r. buccalis lateralis; *c. o. lat*, *c. o. latp*, canals for r. ophthalmicus lateralis; *c. ophV*, canal probably for r. ophthalmicus superficialis of n. trigeminus; *c. orp*, posterior groove and canal of orbito-rostral passage; *c. ot*, canal for r. oticus lateralis; *c. pal*, canal for r. palatinus VII; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. prt*, canals for twigs of medial terminal profundus branch; *cr. rc*, crista rostro-caudalis; *c. v. cm*, canal possibly for v. cerebralis media; *c. v. pit*, canal for pituitary vein; *c. vx*, canal probably for vessel; *c. II*, *c. III*, *c. IV*, *c. V*, *c. VII*, canals for n. opticus, n. oculomotorius, n. trochlearis, n. trigeminus and n. facialis; *fe. ena*, fenestra endonarina anterior; *fe. vl*, fenestra ventro-lateralis; *fo. aup*, fossa auto-palatina; *fus*, area of fusion; *gr. ju*, groove for jugular vein; *gr. psp* groove for pre-spiracular gill-slit; *gr. soc*, groove for ridge housing supraorbital sensory canal; *gr. v. fs*, groove for v. facialis superior; *gr. v. o*, groove for orbital vein; *gr. II*, groove for n. opticus; *i. enp*, *i. exp*, notches for posterior nasal tube; *i. m. sc*, depression for insertion of subcranial muscle; *ioc*, infraorbital sensory canal; *i. pr. ad*, depression for antero-dorsal articular process of otoccipital; *lc*, lateral commissure; *le. so*, suborbital

moreover it extends forwards into the ventral part of postnasal wall (JARVIK, 1966, fig. 1C, D). An interesting fact is that the antero-medial articular lamina of the palatoquadrate in the sectioned specimen of *Glyptolepis* has fused to the dorsal face of the thin and laminar suborbital ledge in two places and accordingly we may distinguish two areas of fusion, one anterior (*art. am1*) situated partly in the postnasal wall and developed on both sides of the specimen (fig. 71A), and one posterior (*art. am2*) present only on the right side (fig. 16A, B; see also fig. 25B). In other specimens of *Glyptolepis*, in the large specimen of *Porolepis* referred to above and in *Holoptychius* the areas of fusion are represented by areas of articulation, devoid of periostal lining, on the dorsal face of the suborbital ledge and in most cases there seems to be two such areas situated very much as the anterior and posterior areas of fusion on the right side of the sectioned specimen.

Another remarkable fact is that the palatoquadrate in the sectioned specimen of *Glyptolepis* seems to have fused to the neural endocranium also farther to the rear (*fus*, fig. 21A), in front of and at the basipterygoid process. Unfortunately the specimen (in particular the palatoquadrate) in this part is damaged by crushing on both sides (see fig. 19) and the conditions could therefore not be made out quite safely. However, as appears to be clear the medial margin of the palatoquadrate has fused to the lateral side of the internasal wall antero-dorsally to the external opening of the canal for the a. palatina and dorsally to the most posterior part of the fossa autopalatina. In this area the palatoquadrate lies dorsally to the suborbital ledge and forms the lateral wall of a small pocket which represents the postero-medial part of the fossa autopalatina. Posteriorly the suborbital ledge increases in breadth and thickness and merges into the ventral horizontal portion of the basipterygoid process which laterally without any traces of a boundary is continued by the palatoquadrate. Still farther to the rear the palatoquadrate, or more precisely the processus basalis, seems to be joined (synchondrotically?) to the lateral part of the anterior face of the posterior vertical portion of the basipterygoid process.

The basipterygoid process (*pr. bp*) which as indicated consists of a posterior vertical and an anterior or ventral horizontal portion is shown

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ledge; *od. La*, area overlapped by lachrymal; *od. La + Mx*, area overlapped by lachrymal and maxillary; *od. Po*, area of fronto-ethmoidal shield overlapped by postorbital; *od. Prsp*, area overlapped by prespiracular plate; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line; *pr. ad*, antero-dorsal articular process of otoccipital; *pr. asc1*, processus ascendens anterior of parasphenoid; *pr. av*, antero-ventral articular process of otoccipital; *pr. bp*, basipterygoid process; *pr. conn*, processus connectens; *pr. sp*, suprapterygoid process or crest; *prspc*, prespiracular sensory canal; *sh. ot*, otical shelf.

also in several other porolepiforms (figs. 20, 65 B, pl. 3, pl. 7:1, pls. 9, 14, 25). The anterior face of the vertical portion generally lacks periostal lining in its lateral part forming an articular area for the basal process of the palatoquadrate. The medial part of that face, on the other hand, has such a lining and forms the posterior wall of a pocket which extends forward dorsally to the horizontal portion and conceivably is the area of insertion of the m. retractor bulbi (cf. *Eusthenopteron*, BJERRING, 1968, fig. 4). The horizontal portion of the basipterygoid process and the adjoining parts of the neural endocranium are subject to rather strong variations. Most often this portion forms a fairly thin shelf which may be separated from the suborbital shelf by a notch (pl. 14:5) and it has an antero-lateral or anterior and almost transverse free margin. Along this margin there is an antero-dorsally facing articular area without periostal lining corresponding to the area of fusion (*fus*, fig. 21 A) in *G. groenlandica*. In specimen No. 478 of *Holoptychius* (pl. 25:3; see also fig. 20 B) in which the horizontal portion is thick and forms the posterior wall of the fossa autopalatina there is a similar but higher area. Judging from several specimens it thus appears as if the palatoquadrate in the region of the basal process articulates with the basipterygoid process in two places, one anterior situated at the antero-lateral or anterior margin of the horizontal portion and one posterior on the lateral part of the anterior face of the vertical portion. However, because of the variations and because the basal process is still imperfectly known in porolepiforms the mode of articulation cannot be quite safely made out and possibly, as indicated by the sectioned and certain other specimens, these areas of articulation (or fusion) may sometimes be confluent.

Behind the basipterygoid process there is in the sectioned specimen a somewhat groove-like depression (*i.m.sc*, figs. 21 A, 24 E) running along the dorsal margin of the ascending process of the parasphenoid. As suggested by BJERRING (1967) this depression, which, although it varies somewhat as to its position and shape, has been observed also in other porolepiforms, probably represents the area of insertion of the subcranial muscle (cf. pp. 227–228). Postero-dorsally to this depression the ethmosphenoid protrudes backwards into the paired processus connectens (*pr. conn*). The articular area for the otoccipital is situated on the posterior part of the process and is directed ventro-laterally. Antero-dorsally to this process the suprapterygoid process (*pr. sp*) is found. This process is in the specimen of *Holoptychius* shown in pl. 24:3 (see also fig. 20 B) a distinct structure with an area devoid of periostal lining at its lateral truncate end. A similar area is discernible also in another specimen of *Holoptychius* (pl. 24:6) and appears to be present also in one of the Scottish specimens of *Glyptolepis* (pl. 14:5). On the basis of this evidence I have assumed (1954) that the processus ascendens of the

palatoquadrate articulates with the lateral end of the suprapterygoid process forming an articulation corresponding to the suprapterygoid articulation in osteolepiforms. However, in the sectioned specimen of *Glyptolepis groenlandica* both the suprapterygoid process which is less distinct and represented by a crest (*pr. sp*, figs. 21A, 24E) and the adjoining part of the processus ascendens (*pr. a*) have complete periostal linings and it therefore is likely that in this species, in *Porolepis* (fig. 20A), and perhaps in porolepiforms in general there was only a ligamentous connection at this place.

The posterior face of the ethmosphenoid in porolepiforms as in osteolepiforms (fig. 93C) and coelacanthiforms presents a wide shallow pit (*fo. nc*) for the anterior end of the notochord. Dorsally to this pit which is separated from the vertical portion of the fossa hypophyseos by a thin wall (fig. 18) there is a backwards protruding horizontal shelf (*shh*, fig. 18, pl. 19:2, pl. 25:1, 5, 6; cf. fig. 93C, *Apld*) formed by the posterior part of the ethmosphenoid. This shelf which in its median parts forms the floor of the posterior part of the ethmosphenoid portion of the cranial cavity and laterally extends to and includes the posterior end of the processus connectens, is, as is clearly seen in some specimens of *G. groenlandica* that have been prepared (pl. 19:2, pl. 22:1), covered with a distinct periostal layer and at any rate in these specimens the shelf has not been capped with cartilage (cf. BJERRING, 1967, fig. 14B). Dorsally to the lateral part of this shelf, laterally to the dorsal part of the cranial cavity, there is a distinct depression (*i. pr. ad*) which as described by BJERRING (1967) is occupied by the antero-dorsal articular process of the otoccipital.

Otoccipital

The otoccipital (hitherto generally called otico-occipital) is shown in all the three porolepiform genera (*Porolepis*, pls. 3, 10; BJERRING, 1967, pl. 3:A; *Glyptolepis*, figs. 21B, 22, 23, 24F, G, 31, 39, 92A, 104C, pl. 18:2, pl. 19, pl. 20:1, pl. 21, pl. 22:1; *Holoptychius*, pl. 24:2) but is imperfectly preserved and cannot be described in detail. However, as far as it is known it in most respects agrees well with that in *Eusthenopteron* (fig. 93D, E; JARVIK, 1954) and appears to be of the same general type as in osteolepiforms.

The dorsal face of the otoccipital is shown in several specimens of *Glyptolepis groenlandica* and could be studied in the sectioned specimen (pl. 21:2, 3) before the two pieces were glued together. This face (figs. 23, 104C; pls. 19–21) presents some interesting features. In contrast to *Eusthenopteron* (fig. 104A) there is a large fontanel (*font*) in the roof of the cranial cavity in front of the otic capsules. This fontanel which seems to be absent in *Porolepis* and *Laccognathus* (GROSS, 1936, fig. 4B)

is bounded anteriorly by a thin transverse bar which forms the anterior margin of the otoccipital and at the lateral end of that bar there is on each side a small articular process (*pr. ad*) which fits into the depression (*i. pr. ad*) at the posterior end of the ethmosphenoid. The posterior part of the fontanel is divided into right and left halves by a short pointed taenia tecti medialis (*t. tm*). Postero-laterally to the fontanel there is on each side a broad but shallow groove covered dorsally by the parietal shield so that a canal is formed. This groove or canal (*gr. v. fs*), which most probably transmitted a vein corresponding to the v. facialis superior in Urodeles (DRÜNER, 1901, pl. 28:26, pl. 29:37; FRANCIS, 1934, p. 225) begins postero-laterally at the lateral margin of the roof of the medial part of the fossa bridgei (*fo. br*), runs first in a medial direction to a point not far from the median line where it makes a sharp bend forwards and continues in an antero-lateral direction to the margin of the otoccipital. At some distance from its antero-lateral end a wide short antero-medial branch is given off to the posterior paired part of the fontanel and at the sharp medial bend a short transverse groove in some specimens connects the grooves of both sides.

The grooves (canals) in *Glyptolepis* now described are suggestive of the anterior part of the groove (canal) for the occipital artery in *Eusthenopteron* (*gr. a. occ*, fig. 104A, see also JARVIK, 1954, fig. 1, 1967b, pp. 194–196) together with the strong lateral branch of that canal which pierces the roof of the medial part of the fossa bridgei and the transverse commissure medially to the lateral branch. However, the canal for the occipital artery in *Eusthenopteron* has an important posterior part (*c. a. occ*) which posteriorly is wholly enclosed in the neural endocranium and opens on the posterior face of the otoccipital (fig. 86B) medially to the posterior opening of the fossa bridgei and dorso-laterally to the foramen magnum. As far as known this posterior part has no equivalent in *Glyptolepis* and if this be true there is an important difference between porolepiforms and osteolepiforms in this respect (see p. 282 No. 32).

The anterior part of the otoccipital (figs. 21B, 22, 23, 24F, G, 31, 92A, pls. 3, 10, pl. 19:2, pl. 22:1, pl. 24:2) forms the roof, the lateral walls and parts of the floor of the myelencephalic division (*div. myc*) of the cranial cavity. Ventrally there is a large opening, the basicranial or ventral fenestra (*fe. bc*), bounded anteriorly by the ethmosphenoid. Behind this fenestra the ventro-medial parts of the otoccipital in the sectioned specimen are unossified and also in the specimens of *Porolepis* and *Holoptychius* (pl. 3, pl. 24:2) showing this detail there is a median gap in the corresponding place (cf. *Eusthenopteron*, fig. 93). Each lateral wall of the cranial cavity antero-ventrally projects forwards into an articular process. This process (*pr. av*) which lacks periostal lining on its medial side articulates with the processus connectens of the ethmos-

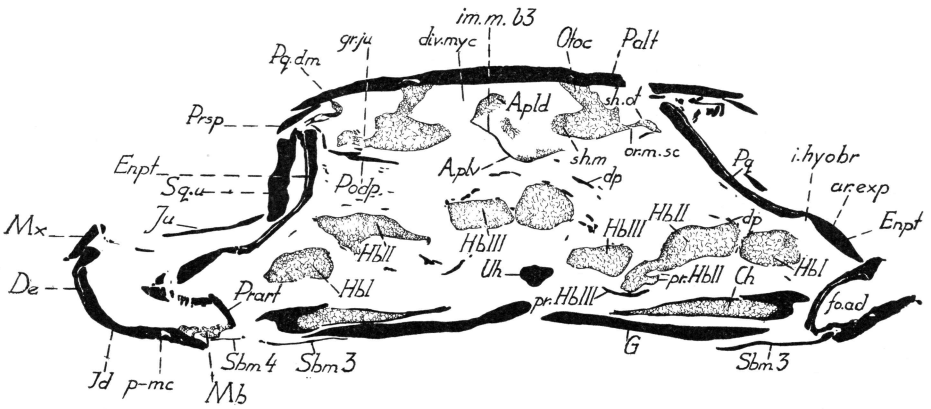


Fig. 22. *Glyptolepis groenlandica* n. sp. Transverse section through middle part of head. Section No. 310 of grinding series. × 2/1.

Apld, *Aplv*, suprachordal and subchordal arcual plates; *Ch*, ceratohyal; *De*, dentary; *Enpt*, entopterygoid; *G*, gular plate; *HbI*, *HbII*, *HbIII*, hypobranchials I, II and III; *Id*, infradentary; *Ju*, jugal; *Mb*, meckelian bone; *Mx*, maxillary; *Otoc*, otoccipital; *PaIt*, parietointertemporal; *Podp*, paraotic dental plate; *Pq*, palatoquadrate; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate; *Prart*, prearticular; *Prsp*, prespiracular plate; *Sbm3*, *Sbm4*, submandibulars 3 and 4; *Sq. u*, upper squamosal; *Uh*, urohyal.

ar. exp, exposed area of entopterygoid; *div. myc*, myelencephalic division of cranial cavity; *dp*, dental plates; *fo. ad*, adductor fossa of lower jaw; *gr. ju*, groove for jugular vein; *im. m. b3*, impression probably for basicranial muscle 3; *i. hyobr*, depression probably for lateral side of hyobranchial apparatus; *or. m. sc*, area of origin of subcranial muscle; *p-mc*, preoperculo-mandibular sensory canal; *pr. HbII*, *pr. HbIII*, articular processes of hypobranchials II and III; *sh. m*, medial shelf; *sh. ot*, otical shelf.

phenoid. Behind the articular process the ventral part of the lateral wall is thickened and projects medially into a shelf (*sh. m*) which increases in breadth posteriorly and forms the lateral part of the floor of the cranial cavity. The medial margin of this shelf which bounds the basicranial fenestra laterally lacks periostal lining, too, and conceivably this margin was capped with cartilage and joined to the cartilaginous lateral margin of the suprachordal arcual plate (*Apld*, fig. 24F, G) which probably formed the median part of the floor of this part of the cranial cavity. Laterally the thick ventral part of the lateral wall projects into a prominent otical shelf (*sh. ot*). On the ventral side of this shelf there is an elongate depression (*or. m. sc*) which no doubt was occupied by and probably formed the area of origin of the subcranial muscle. The otical shelf is in *Glyptolepis groenlandica*, *Holoptychius* (pl. 24:2) and one specimen of *Porolepis* (pl. 10) thin and laminar, whereas it in another specimen of *Porolepis* appears to be thicker. Dorsally to that shelf the lateral wall is pierced by several canals and there are grooves for nerves and vessels

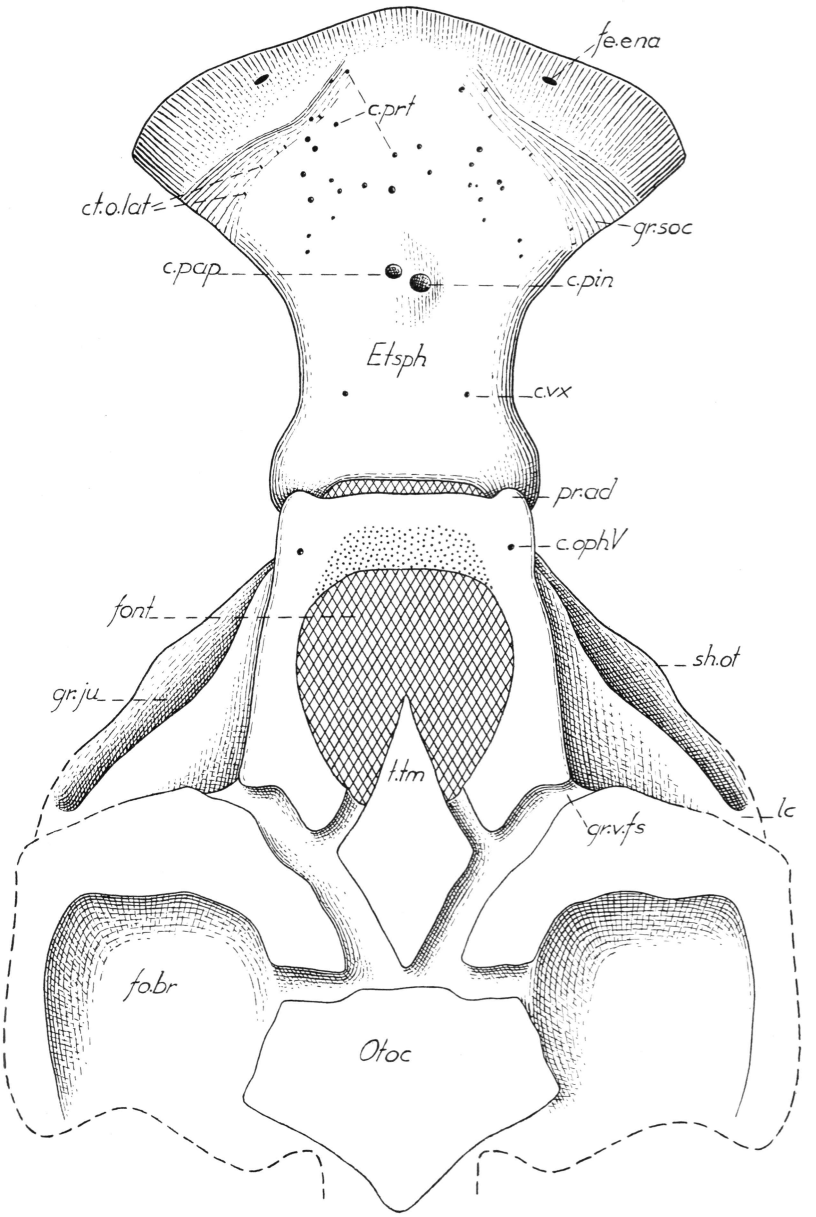


Fig. 23. *Glyptolepis groenlandica* n.sp. Neural endocranium in dorsal aspect. Graphical restoration after grinding series. × 3/1.

Etsph, ethmosphenoid; *Otoc*, otoccipital.

c. ophV, canal for r. ophthalmicus superficialis of n. trigeminus; *c. pap*, *c. pin*, canals for parapineal and pineal tracts; *c. prt*, canals for twigs of medial terminal profundus branch; *ct. o. lat*, canals for twigs of r. ophthalmicus lateralis to neuromasts of supraorbital sensory canal; *c. vx*, canal for vessel; *fe. ena*, fenestra endonarina anterior; *fo. br*, fossa bridgei; *font*, fontanel in roof of myelencephalic division of

both on its external and internal sides. One fairly short and wide groove (*gr. prof*, fig. 24F) runs forwards on the inner side of the most anterior part of the lateral wall. Judging from its position it most likely was developed for the n. ophthalmicus profundus which if this be true passed out of the cranial cavity in the slit between the ethmosphenoid and the otoccipital. The foremost of the canals in the otoccipital observed in the sections of *G. groenlandica* is given off from the dorsal part of the cranial cavity. This canal (*c. oph V*) which runs in an antero-dorsal direction to the dorsal side of the otoccipital possibly transmitted the r. ophthalmicus superficialis V. From its inner opening a short groove leads backwards on the inner side of the lateral wall of the cranial cavity towards the inner opening of another but much wider canal (*c. V*) which no doubt is the trigeminus canal. From the external opening of this canal a groove leads forwards and upwards on the lateral side of the wall, and a similar groove is found a little farther back coming from the external opening of another canal (*c. o. latp*) which very likely is the canal for the r. ophthalmicus superficialis lateralis. At some distance behind that canal the lateral wall is pierced by a fairly long canal (*c. ot*) which probably transmitted the r. oticus lateralis, and postero-dorsally to that lies the opening of the canal, which as described above is formed by a groove (*gr. v. fs*) on the dorsal side of the otoccipital and the overlying dermal cranial roof. On the dorsal side of the otical shelf and in front of that, on the lateral side of the lateral wall of the cranial cavity, there is a groove (*gr. ju*) for the jugular vein continued backwards by the jugal canal. In the bottom of the posterior part of that groove, close in front of and partly inside the lateral commissure (*lc*) which bounds the jugal canal laterally, lies the opening of the facial canal (*c. VII*). The palatine canal (*c. pal*) is given off from the distal part of that canal, runs in an antero-ventro-lateral direction and opens on the lateral side of the otical shelf. Another canal (*c. v. cm*) given off from the facialis canal runs in a lateral direction and opens in the dorso-medial part of the groove for the jugular vein, dorsally to the opening of the palatine canal. The importance of this canal is obscure, but it may be tentatively suggested that it is developed for the v. cerebralis media secundaria (BERTMAR; v. cerebralis media vera, VAN GELDEREN) which according to BERTMAR (1965, pp. 121–122) joins the jugular vein between the trigeminus and facialis ganglia.

The posterior part of the otoccipital has not yet been sectioned and also because it is imperfectly preserved in the specimens of various poro-

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cranial cavity; *gr. ju*, groove for jugular vein; *gr. soc*, groove for ridge housing supra-orbital sensory canal; *gr. v. fs*, groove probably for superior facial vein; *lc*, lateral commissure; *pr. ad*, antero-dorsal articular process of otoccipital; *sh. ot*, otical shelf; *t. tm*, taenia tecti medialis.

lepiforms (figs. 23, 92A; pls. 3, 10, pl. 19:2, pl. 24:2) that have been prepared only a few remarks will be given. Behind the lateral commissure the dorsal articular area (*hyd*) for the hyomandibula is discernible whereas the ventral one could not be identified with certainty. However, judging from the shape of the proximal part of the hyomandibular both these areas seem to be situated somewhat as in *Eusthenopteron* (*hyd*, *hyv*, fig. 93D) and as in that form the jugal canal is continued backwards by a groove for the jugular vein bounded dorso-laterally by a distinct ridge (*ri. ju*). This ridge ends posteriorly on the ventral side of the postotical process (*pr. po*) and dorso-laterally to that process lies the posterior opening of the large fossa bridgei (*fo. br*; cf. fig. 86). Postero-medially to that the dorsal part of the otoccipital projects backwards into a median process suggestive of that in *Eusthenopteron* (fig. 104A).

The postero-ventral ossification (see JARVIK, 1954, p. 7) is incompletely preserved or lacking in all the prepared specimens. In one specimen of *Glyptolepis groenlandica* there is a detached cylindrical but somewhat compressed piece of bone pierced by a wide canal which no doubt is the canal for the notochord. This piece which carries remains of the lateral walls of the neural canal on its dorsal side obviously corresponds to the posterior ventro-median part of the postero-ventral ossification in *Eusthenopteron* that forms the walls of the notochordal canal (fig. 93B, D, E). However, in one specimen of *Porolepis* (pl. 3) which as may be noticed in passing shows the aorta grooves (*gr. a. dl*) and a notch which presumably represents the ventro-medial boundary of the fenestra ovalis (*fe. ov*, "vestibular fontanelle"), the ventral wall of the notochordal canal behind the basicranial fenestra (*fe. bc*) seems to be divided into right and left halves by a median suture or unossified tract. A more distinct ventral median gap or suture is found behind the basicranial fenestra in a specimen of *Holoptychius* (pl. 24:2; see also fig. 92A). In that specimen the margins of the ventral fenestra, in contrast to conditions in *Eusthenopteron* and other osteolepiforms, do not meet posteriorly and a little farther back there seems to be an independent square paired plate (*Apv*), behind which there is space for a cylindrical piece corresponding to that found in *G. groenlandica*. These conditions indicate that the arcual elements of the cranial portion of the vertebral column (see below) which form the main part of the postero-ventral ossification are less intimately fused to each other in porolepiforms than in osteolepiforms, and if not simply broken parts the square plates in *Holoptychius* may possibly be subchordal arcual plates comparable to the posterior subchordal plate in *Latimeria* (cf. *Eusthenopteron*, fig. 99, *CV* 3 + 4).

Arcual plates

In a previous paper (1959a, see also 1960) I suggested that the vertebral column has a cranial portion extending forwards to the area of the hypophysis, and that embryonic elements that in various vertebrates have been observed along the cranial portion of the notochord (somitic part of trabecula, polar cartilage, pila antotica, parachordalia, etc) may represent arcual elements of cranial vertebrae. This view was supported by the discovery of independent endoskeletal elements associated with the cranial portion of the notochord in *Latimeria* (MILLOT & ANTHONY, 1956, pp. 167–168, pl. 2; 1958, pp. 21–22, 25, fig. 5, pls. 3, 17, 18, 20, 24, 25, 31), and which STENSIÖ (1963b, fig. 44, *Daf*, *Vaf*, *Vagl*) interpreted as metameric arcual bones. In *Latimeria* there are three principal such arcual plates as they may be called because they are cartilaginous or only partly ossified: one dorsal, the suprachordal arcual plate (pièce préoccipitale suschordale, MILLOT & ANTHONY) and two ventral, the anterior and posterior subchordal arcual plates (pièces préoccipitales souschordales). These arcual plates (*Apld*, *Aplv*, fig. 24B) are at least partly embedded in the fibrous sheet (*tis. conn*) of the notochord and also the conditions in recent Amphibia support the view that they are vertebral elements. In recent Anura (*Xenopus*, fig. 24C, D; SMIT, 1953; see also SCHAUINSLAND, 1905, pp. 501–502) the trunk vertebrae present subchordal and suprachordal cartilages (*cart. sub*, *cart. sup*) situated very much in relation to the notochord as the arcual plates in *Latimeria* and of great interest is that similar cartilaginous elements, or we may say arcual plates (epichordal and hypochordal cartilaginous commissures, SMIT, 1953, pp. 113–114), are developed also in relation to the cranial portion of the notochord (see also EEDEN, 1951, p. 51).

Arcual plates are present also in Devonian coelacanthiforms and other groups (osteolepiforms, porolepiforms) with an intracranial joint. In connection with his studies of this joint, by him called the intracranial juncture apparatus, BJERRING (1967) recorded such arcual plates (called zygal plates) in various Devonian "crossopterygians". In particular he paid attention to the suprachordal plate which at any rate in *Latimeria* articulates with the processus connectens of the ethmosphenoid forming an important part of the juncture apparatus and on the basis of the conditions in *Latimeria* he restored that plate in *Nesides*, *Eusthenopteron* and *Glyptolepis* considering also the soft parts. The suprachordal arcual plate is well shown in the grinding series of *Nesides* and a wax-model of it was made at an early date by STENSIÖ (cf. BJERRING, 1967, figs. 5, 6C, D, *Zypd*). As demonstrated by BJERRING (1967, pl. 1B) it is also well shown in another Devonian coelacanthiform (*Diplocercides*). In the serial sections of *Eusthenopteron* this and other arcual plates are

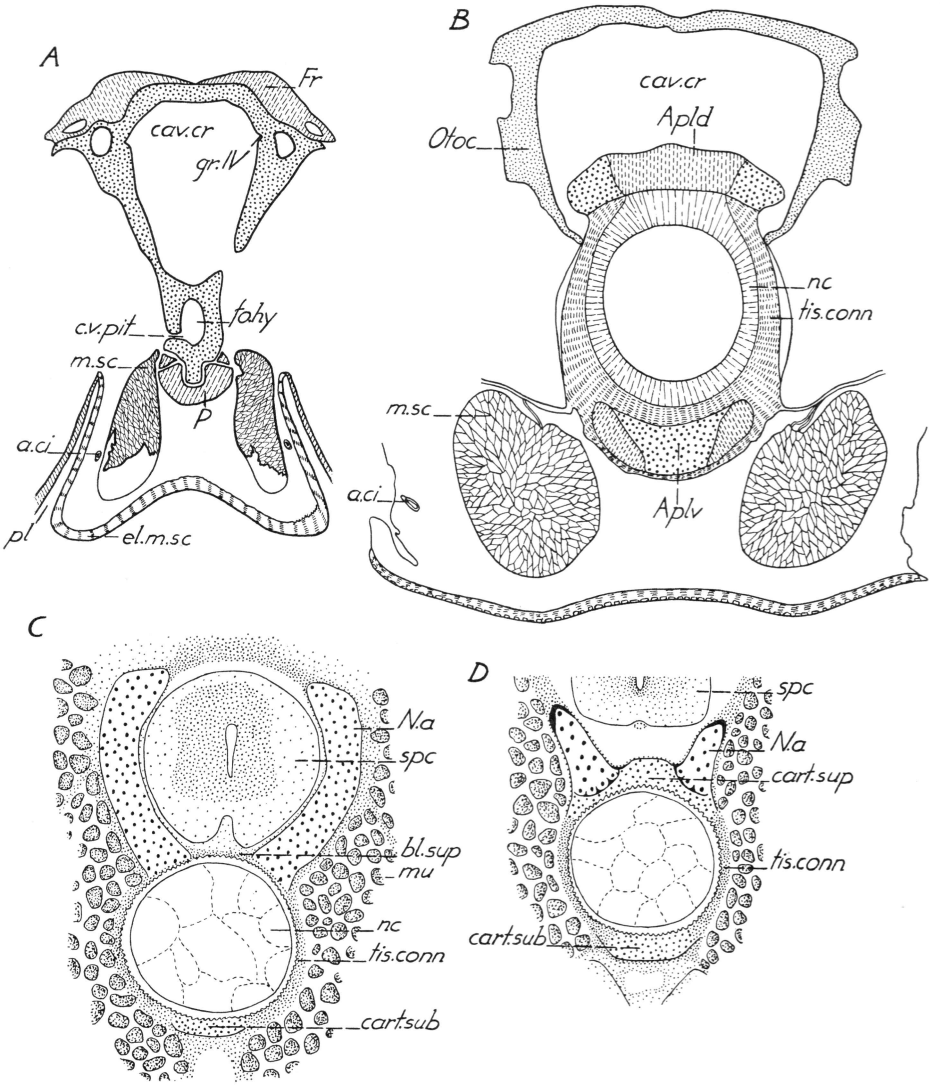
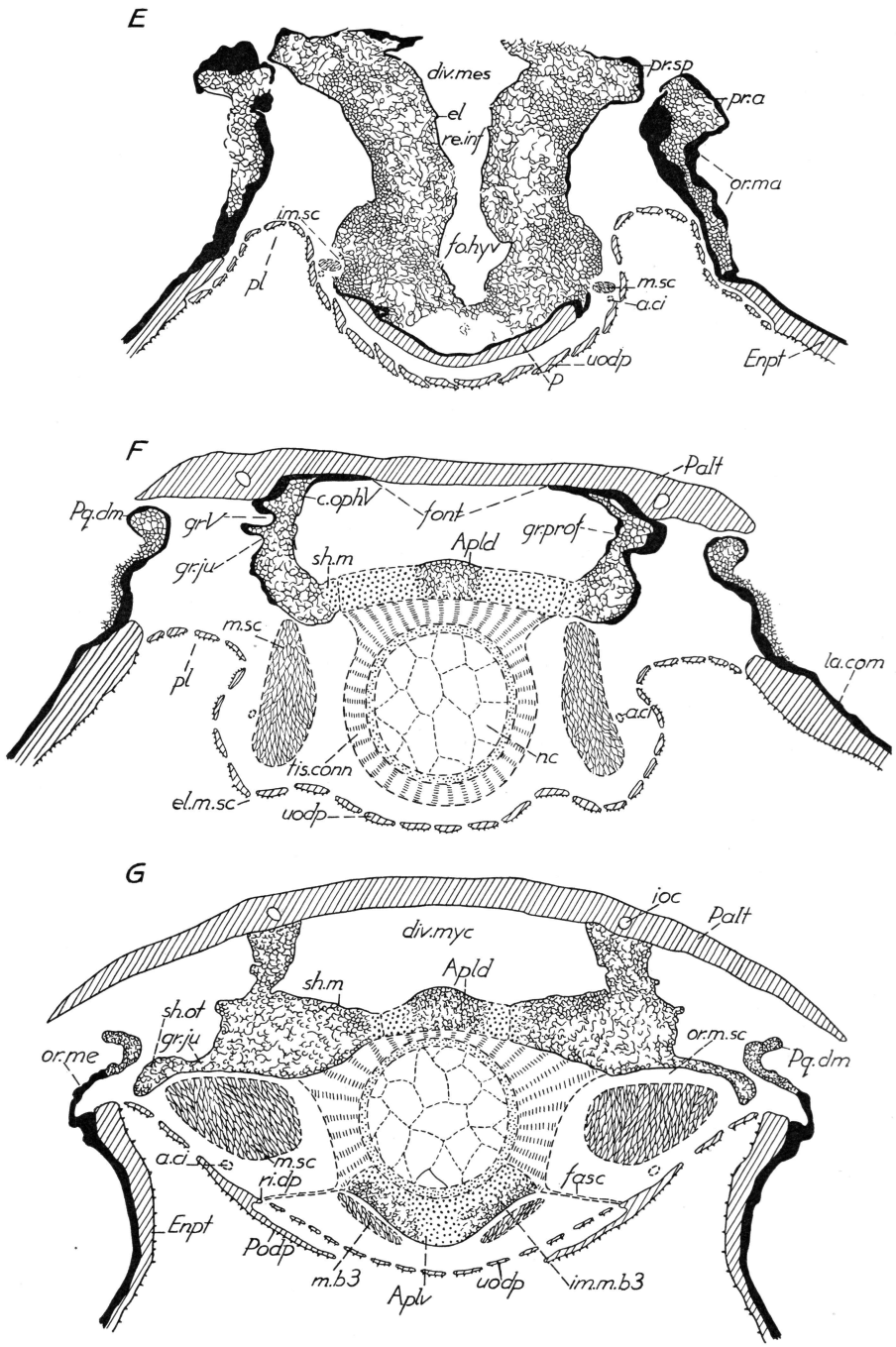


Fig. 24. Transverse sections through *A*, *B*, *E–G*, skull and, *C*, *D*, vertebral column to show position of subcranial muscle and arcual plates. *A*, *B*, *Latimeria chalumnae*. From MILLOT & ANTHONY, 1958, pls. 15, 17. *C*, *D*, *Xenopus laevis*, larvae, stages 53, 56. From SMIT, 1953, figs. 11, 12. *E–G*, *Glyptolepis groenlandica* n. sp. After sections Nos. 221, 263 and 300 of grinding series. Slightly modified. Arcual plates, upper oral dental plates, basicranial muscles and certain other soft parts restored. × 5/1 approx.

Apld, *Aplv*, suprachordal and subchordal arcual plates (pièce préoccipitale suschordale and pièce préoccipitale souschordale antérieure in *Latimeria*); *Enpt*, entopterygoid; *Fr*, frontal; *N. a*, neural arch; *Otoc*, otoccipital; *P*, parasphenoid; *PaIt*, parietointertemporal; *Podp*, paraotic dental plate; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate (epimandibular).

a. ci, a. carotis interna; *bl. sup*, blastema of suprachordal cartilage; *cart. sub*, *cart. sup*, subchordal and suprachordal cartilages in vertebral column (serially homo-



logous with subchordal and suprachordal arcual plates in basis cranii); *cav. cr*, cranial cavity; *c. ophV*, canal for r. ophthalmicus superficialis trigemini; *c. v. pit*, canal for pituitary vein; *div. mes*, *div. myc*, mesencephalic and myelencephalic divisions of cranial cavity; *el*, elevation separating infundibular recess from mesencephalic divi-

(cont. pag. 68)

imperfectly preserved being represented by fragments of endoskeletal bone found in the cranial cavity and the basicranial fenestra (see JARVIK, 1954, figs. 6B, 12, 21A, B; BJERRING, 1971) and obviously they to a considerable extent were made up of cartilage as in *Latimeria* (fig. 24B).

Disregarding the square plates (*Apv*, fig. 92A, pl. 24:2) in *Holoptychius* arcual plates in porolepiforms have been found with certainty only in *Glyptolepis groenlandica*. In the grinding series two such plates can be identified, one suprachordal and one subchordal. The suprachordal plate (*Apld*, figs. 22, 24F, G) is a long piece of bone (sections 280–350) situated in the basicranial fenestra. Its dorsal face has a periostal lining whereas such a lining is lacking laterally and ventrally. The preserved piece of bone is fairly thick and most probably it represents only the median part of the plate whereas the lateral parts were formed by cartilage, that is as in *Latimeria* (fig. 24B). When in its natural position the plate probably reached the margins of the basicranial fenestra which as we have seen lack periostal lining and formed the main part of the floor of the myelencephalic division of the cranial cavity. Whether the plate extended forwards and articulated with the processus connectens of the ethmosphenoid is impossible to decide on the basis of the available material. We can only say that the dorsal face of the processus connectens in several specimens that have been prepared is covered with a distinct periostal lining and that this face accordingly cannot have been capped with cartilage. The same is true of *Eusthenopteron*, too, (see JARVIK, 1942, pl. 3, 1954, fig. 12A) but in this form and probably also in *Glyptolepis* the posterior tip of the processus connectens lacks periostal lining, which indicates that it in some way was joined to the suprachordal plate as maintained by BJERRING (1967).

The subchordal arcual plate in *Glyptolepis* (*Aplv*, figs. 22, 24G, 31, 92A, pl. 22:1) which seems to correspond to the anterior subchordal plate

(Fig. 24 cont.)
sion of cranial cavity; *el. m. sc*, ridge-like elevation in roof of mouth cavity caused by subcranial muscle; *fasc*, hypothetical fascia; *fo. hy*, fossa hypophyseos; *fo. hyv*, posterior vertical portion of fossa hypophyseos; *font*, fontanel in roof of otoccipital; *gr. ju*, groove for jugular vein; *gr. prof*, groove probably for n. ophthalmicus profundus; *grIV*, *grV*, grooves for n. trochlearis and n. trigeminus; *im. m. b3*, impression probably for basicranial muscle 3; *i. m. sc*, area of insertion of subcranial muscle; *ioc*, infraorbital sensory canal; *la. com*, commissural lamina of palatoquadrate; *m. b3*, basicranial muscle 3; *m. sc*, subcranial muscle, probably representing basicranial muscle 2; *mu*, muscle; *nc*, notochord; *or. ma*, *or. me*, areas of origin of mm. levator mandibulae anterior and externus; *or. m. sc*, area of origin of subcranial muscle; *pl*, fold in roof of mouth cavity; *pr. a*, processus ascendens of palatoquadrate; *pr. sp*, suprapterygoid crest of ethmosphenoid; *re. inf*, recess for infundibular portion of diencephalon; *ri. dp*, ridge on inner side of paraotic dental plate; *sh. m.* medial shelf; *sh. ot*, otical shelf; *spc*, spinal cord; *tis. conn*, perichordal connective tisssue (perichordal tube, SMIT); *uodp*, upper oral dental plates.

in *Latimeria* is a fairly large element (sections 269–335) situated ventrally to the suprachordal plate. It increases in breadth posteriorly, but the left side (to the right in the sections) is incomplete in the posterior part. The ventral side only shows a periostal lining which, however, is interrupted for some distance (sections 292–302) in the median part and it appears as if the median parts of the plate were to a considerable extent made up of cartilage (fig. 24G; cf. *Latimeria* fig. 24B). A remarkable fact is that the ventral side of the plate has about the same configuration as has the ventral side of the ventral wall of the notochordal canal in *Eusthenopteron* (fig. 93D; JARVIK, 1954, figs. 1C, 7, 21B, C) showing a broad median ridge and on each side of that a shallow depression (*im.m. b3*). Of interest in this connection is specimen No. P. 342 (Pal. Sect., Stockh.) of *Eusthenopteron* in which as discussed in 1954 (p. 18, fig. 7) the ventral wall of the notochordal canal extends much farther forwards than in other specimens, ending on level with the palatine canal (*c. pal*, fig. 93E). It is now easy to see that this variation is due to the fact that a subchordal arcual plate corresponding to that which BJERRING (1967, fig. 8, *Zypv*) has restored on the basis of the serial sections in *Eusthenopteron* (*V. a2 + 3*, fig. 99) and probably also to the subchordal plate in *Glyptolepis* and the anterior subchordal plate in *Latimeria*, has been incorporated in the otoccipital. However, if we examine the ventral side of the ventral wall of the notochordal canal in specimen P. 342 closer it appears as if the depression laterally to the median ridge consists of two portions, anterior and posterior. The posterior portion (*im.m. b4*, fig. 93E) which is present also in other specimens and well shown in particular in No. P. 2564 (see fig. 93D and BJERRING, 1967, pl. 3B) is bounded posteriorly by a ridge whereas anteriorly it curves slightly laterally and merges gradually on the bridge separating the basicranial fenestra from the fenestra ovalis (*fe. ov*). The anterior portion (*im.m.b3*), shown only in No. P. 342, in its posterior part lies medially to the laterally curving part of the posterior portion and extends forwards along the median ridge to or almost to its anterior end. This portion is thus situated mainly on that part of the otoccipital that includes the subchordal plate and most likely it is the equivalent of this portion (*im.m.b3*, figs. 22, 24G) that is found on the subchordal plate in *Glyptolepis*. The possible importance of these impressions will be discussed below (p. 256).

Visceral endoskeleton

Palatoquadrate, meckelian bone and hyomandibula

The palatoquadrate (*Porolepis*, pl. 3; *Glyptolepis*, figs. 8D, 16, 19, 22, 24E–G, 25, 27, 31, 32A1–4, 33E, 71A, 92A, pl. 18:2, pl. 19:2; *Holo-*

ptychius, fig. 33C) as to its general shape is suggestive of that in *Eusthenopteron* (figs. 26A, 86A; JARVIK, 1954) and as in that form and other osteolepiforms (26D) it is a single ossification consisting of two principal parts, the pars autopalatina (*Pq. aup*, epipremandibular, JARVIK, 1954) and the postero-dorsal marginal portion (*Pq. dm*, epimandibular) with the processus ascendens (*pr. a*, suprapharyngomandibular). As in *Eusthenopteron* these two parts are connected with each other by a thin lamina, the commissural lamina (*la. com*), which extends from the area in front of the basal process (*pr. b*) to the area between the pars autopalatina and the pars quadrata (*Pq. qu*). This thin part of the palatoquadrate covers the main part of the dorsal side of the entopterygoid (*Enpt*) but behind the pars autopalatina it does not extend as far ventrally as that bone (see p. 93 and *ar. exp*, fig. 25A).

The main posterior part of the pars autopalatina situated dorsally to the dermopalatine (*Dpl*) and the ectopterygoid (*Ecpt*) forms a thin lamina which medially merges into the likewise thin commissural lamina. The pars autopalatina is therefore less distinct than in *Eusthenopteron* in which its posterior part is thickened (fig. 32B3; JARVIK, 1954, fig. 12). Anteriorly and antero-medially where its ventral side is largely exposed in front of the dermopalatine and entopterygoid the pars autopalatina forms two articular processes, the ethmoidal articular process and the antero-medial articular lamina. These two processes which are well shown only in *Glyptolepis groenlandica* are separated by a broad and shallow notch which when the palatoquadrate is in its natural position is occupied by the pronounced posterior corner (*co*, fig. 9A, B) of the postnasal wall.

The ethmoidal articular process (*pr. e*) is somewhat suggestive of the processus apicalis of the pars autopalatina in *Eusthenopteron* and if, as now seems most likely, it corresponds to that process the connection between this process and area *art. e* of the postnasal wall corresponds to the antero-medial ethmoidal connection (or articulation) in osteolepiforms and not to the postero-lateral one as I have maintained in previous papers (1942, 1954). As already mentioned the ethmoidal process has on both sides of the sectioned specimen fused with the postnasal wall postero-medially to the fenestra endochoanalis. Together with the posterior groove of the orbito-rostral passage it forms a short canal which is continued backwards by a groove on the postero-medial side of the process. This groove (*gr. buca*) which runs in a postero-lateral direction towards the inner side of the lachrymal and no doubt was caused by the anterior medial branch of the r. buccalis is well shown in particular in specimen No. P. 1490 of *G. groenlandica* (pl. 19:2). In this specimen and probably in most other porolepiforms the ethmoidal process is independent of the postnasal wall and presents an area without periostal

lining. This area which is directed dorso-medially abuts against area *art. e* of the postnasal wall but if it was a synchondrosis at this place, as seems likely in view of the conditions in the sectioned specimen, or not, is impossible to decide.

The antero-medial articular lamina (*la. am*) is somewhat different on the left and right sides of the sectioned specimen (figs. 16, 71 A). On the right side a rather broad part marginal part of the lamina is thickened and the ventral side of this thickened part has fused with the dorsal side of the ventral wall of the fossa autopalatina in two areas, anterior and posterior (*art 1*, *art 2*, fig. 25 B; *art. am 1*, *art. am 2*, fig. 20). On the left side, on the other hand, there is only one area of fusion, the anterior, and behind that the lamina forms a thin plate.

The postero-dorsal marginal portion of the palatoquadrate (*Pq. dm*, epimandibular) anteriorly forms a medially directed basal process. This process (*pr. b*) is imperfectly exposed but as is seen in some specimens of *G. groenlandica* it has a posteriorly directed area devoid of periostal lining. This area abuts against the correspondingly developed area on the anterior face of the posterior vertical portion of the basipterygoid process but again it is impossible to decide if it was an articulation or a synchondrotic connection. In the sectioned specimen (fig. 19) the basal process on both sides is imperfectly ossified and because the palatoquadrate in this area is damaged by crushing the conditions are obscure. However, as is clearly seen the medial margin of the palatoquadrate in front of the basal process is thickened and has fused to the neural endocranium in the way described above (p. 57). This thickened part (*Pq. aup*, fig. 19) which may be regarded as an anterior prolongation of the basal process is on the right side continued anteriorly by the thickened marginal part and on the left side by the thin part of the antero-medial articular lamina.

Dorsal to the basal process the postero-dorsal marginal portion of the palatoquadrate is provided with a strong processus ascendens (suprapharyngomandibular). This process (*pr. a*) in *G. groenlandica* (pl. 19:2) has a slight prominence on its inner side, but there is no articular area without periostal lining and it is clear that in this species and probably in most other porolepiforms (as regards *Holoptychius* see p. 59) there was only a ligamentous connection between the ascending and supraptery-goid processes. On the external side of the processus ascendens there is a distinct depression with some irregular ridges running in a postero-ventral direction (towards the adductor fossa of the lower jaw). This depression (*or. ma*, fig. 25 A; see also pl. 18:2) which extends somewhat behind the processus ascendens and accordingly is rather large probably is the area of origin of a muscle corresponding to the m. levator mandibulae anterior (Edgeworth, 1935; Fox, 1959, p. 171, figs. 2, 7, 24) in urodeles. Posteriorly the processus ascendens tapers in height and

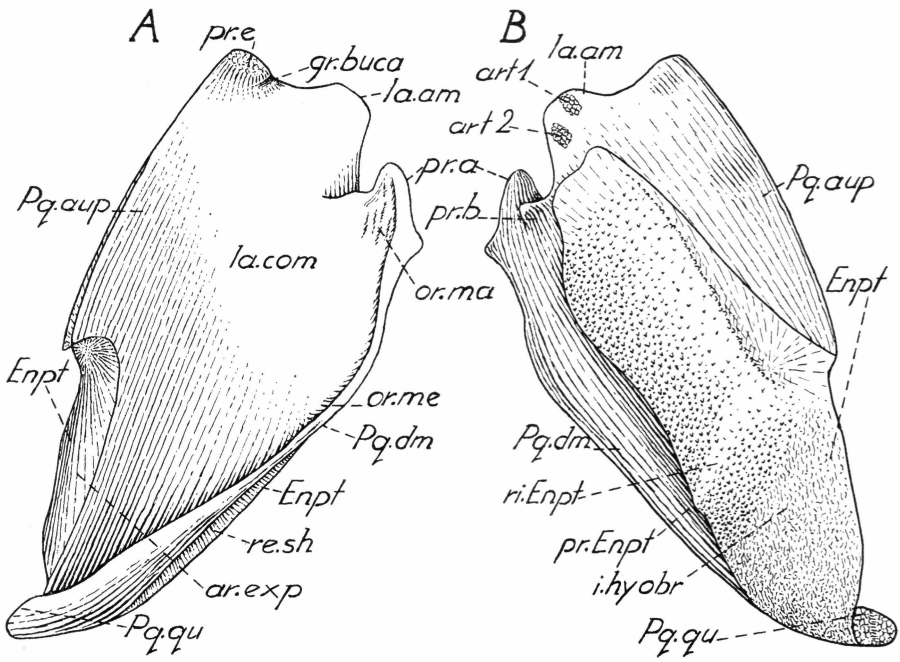


Fig. 25. *Glyptolepis groenlandica* n. sp. Palatoquadrate bone with entopterygoid in, *A*, dorsal and, *B*, ventral aspects. Restorations mainly after grinding series. × 2/1.

Enpt, entopterygoid; *Pq. aup*, pars autopalatina (epipremandibular); *Pq. dm*, postero-dorsal marginal portion (epimandibular); *Pq. qu*, pars quadrata.

ar. exp, exposed smooth area of external side of entopterygoid; *art1*, *art2*, anterior and posterior areas of articulation (or fusion) of antero-medial articular lamina; *gr. buca*, groove for anterior medial branch of r. buccalis lateralis; *i. hyobr*, depression for lateral side of hyobranchial apparatus; *la. am*, antero-medial articular lamina; *la. com*, commissural lamina; *or. ma*, *or. me*, areas of origin for mm.levator mandibulae anterior and externus; *pr. a*, processus ascendens; *pr. b*, processus basalis; *pr. e*, ethmoidal articular process; *pr. Enpt*, process of entopterygoid; *re. sh*, spiraculo-hyomandibular recess; *ri. Enpt*, oblique ridge of entopterygoid.

thickness and its dorsal margin merges gradually into the dorsal margin of the postero-dorsal portion. In contrast to *Eusthenopteron* and other osteolepiforms there is thus no notch for the rr. maxillaris and mandibularis V (*i. V*, fig. 26D; see also WATSON, 1926, fig. 33). Nor are there any traces of a paratemporal process (*pr. pt*) and there is no paratemporal articulation. Behind area *or. ma*, between that area and the pars quadrata, the postero-dorsal marginal portion is bent in such a way that it is S-shaped as seen in transverse sections (figs. 22, 24G). The external face of this part is partly rough (*or. me*) and possibly we are here concerned with the area of origin of the m. levator mandibulae externus. On the inner side of this part of the palatoquadrate there is a distinct spiraculo-hyomandibular recess (*re. sh*) bounded ventrally and

medially by the entopterygoid. The pars quadrata (*Pq. qu*) is imperfectly preserved but on the whole it seems to be somewhat as in *Eusthenopteron* and as in that form the articular area is divided by a depression into lateral and medial articular knobs. On the posterior face, dorsally to these knobs, there is a distinct pit (*p. Sym*, figs. 27 C, 33 E,pl. 3, pl. 17: 3, pl. 19:2) probably for the articulation with the symplectic.

On the external side of the palatoquadrate bone there are some shallow branching grooves (*grd, grv*, fig. 33 C, E). Similar grooves are found also in *Eusthenopteron* and are well shown especially in one specimen possessing a more completely ossified palatoquadrate than the sectioned specimen of that form. Since this specimen shows some interesting features not previously recorded with regard to the vascular supply of the endoskeletal bony tissue of the palatoquadrate a brief description may be included here.

In this specimen of *Eusthenopteron* (fig. 26 A–C) there are two groups of grooves on the outside of the palatoquadrate bone, one dorsal in which the grooves (*grd*) run from the postero-dorsal portion in a ventral direction and one ventral with grooves (*grv*) running from the posterior part of the pars autopalatina in a dorsal direction. Five almost parallel dorsal grooves are distinctly shown. Judging from their position and course it seems likely that they gave passage to branches of a vessel (artery?) running along the postero-dorsal portion of the palatoquadrate. The vascular branches in the grooves of the ventral group, on the other hand, evidently belong to a vessel related to the pars autopalatina. These conditions are in agreement with and support the view (Jarvik, 1954) that the postero-dorsal portion is the epimandibular whereas the pars autopalatina represents the epipremandibular.

All these grooves, both those running in a ventral direction and those directed dorsally, branch frequently and form a net-work on the outside of the palatoquadrate bone. This can only mean that there was a vascular plexus adhered to the palatoquadrate surface. A remarkable fact is that in the bottom of these grooves and in the faint impressions which form the meshes of the net there are numerous diminutive foramina (*f. cap*). As is clearly seen if the palatoquadrate is submerged in xylol or oil of aniseed these small foramina are the openings of very fine canals (*c. cap*), less than 30 microns in diameter, which form an intricate net-work within the bony tissue of the palatoquadrate. However, besides these very narrow canals which presumably transmitted vessels (capillaries?) there are wider canals (*c. vasc*) which also form a net-work within the endoskeletal bony tissue. These canals which also open on the external side of the palatoquadrate are well shown in particular in the posterior thick part of the pars autopalatina. Because of our still im-

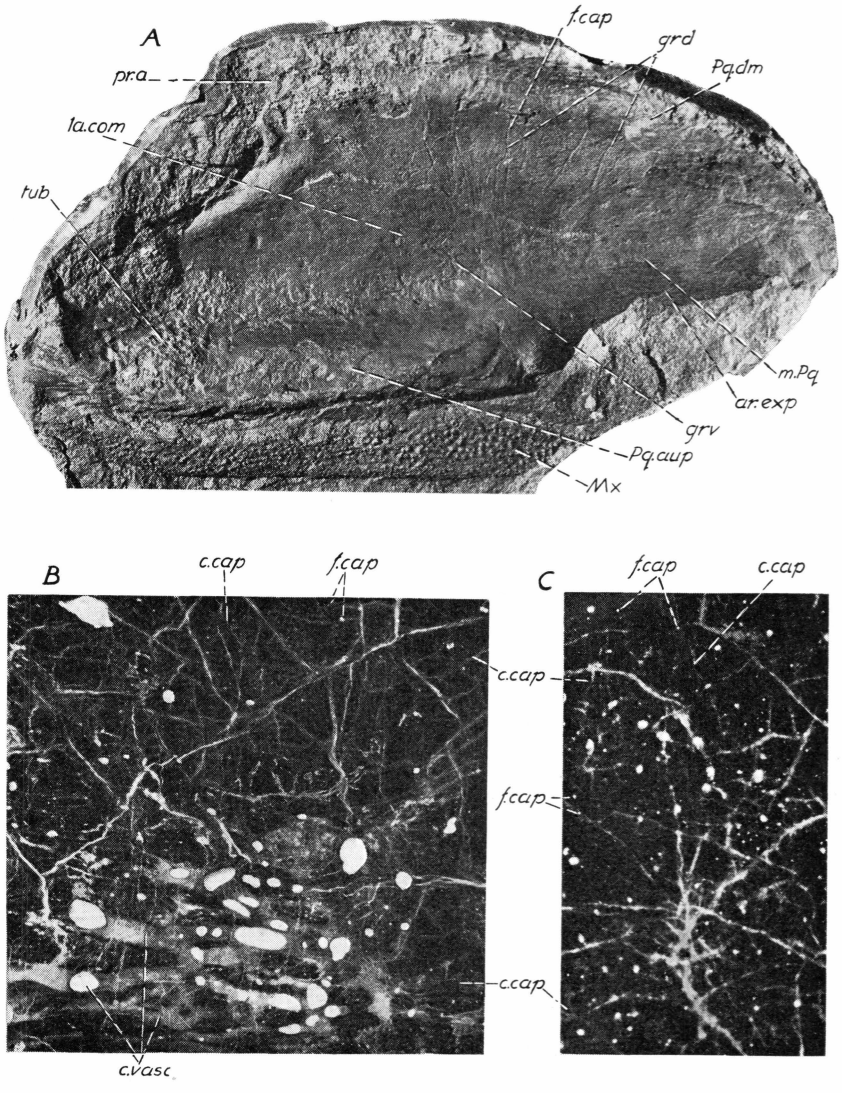
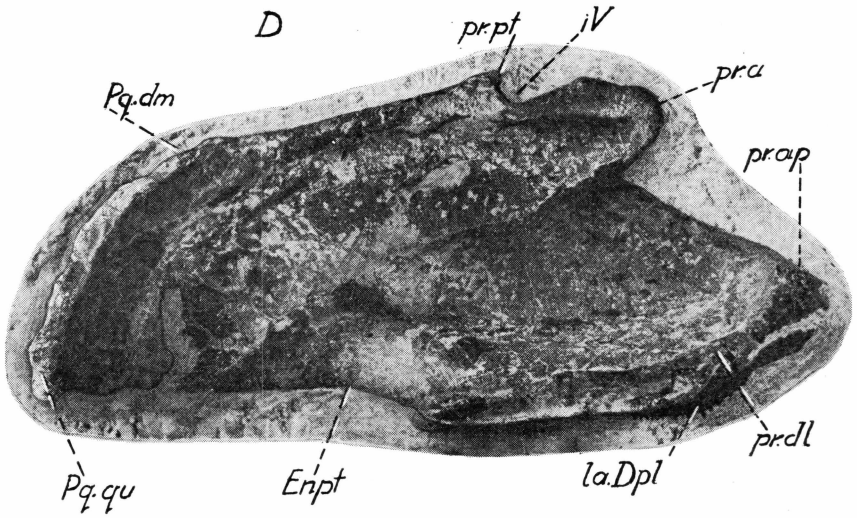


Fig. 26. *A–C*, *Eusthenopteron foordi*. Palatoquadrate and maxillary in lateral aspect to show superficial grooves for vessels on external side and (*B*, *C*) net-works of vascular canals of different calibers within bony tissue of palatoquadrate bone. *A*, photograph of latex cast. Nat. size. *B*, *C*, photographed in xylol. *B* × 6/1, C × 12/1. Sedgwick Geological Museum, Cambridge. Lowermost Upper Devonian, Escuminac Bay, Canada.

D. Undetermined osteolepid from about contemporaneous layers, Bergisch Gladbach, Germany. Palatoquadrate complex in lateral aspect. Retouched photograph placed at my disposal by H. JESSEN. Specimen No. P. 5199, Pal. Sect., Stockh. × 3/1.

Enpt, entopterygoid; *Mx*, maxillary; *Pq. aup*, pars autopalatina; *Pq. dm*, postero-dorsal marginal portion; *Pq. qu*, pars quadrata.

ar. exp, smooth, exposed area of external side of entopterygoid; *c. cap*, net-work



of very narrow canals within bony tissue; *c. vasc*, net-work of wider vascular canals; *f. cap*, openings of narrow canals on external side of palatoquadrate bone; *grd*, *grv*, dorsal and ventral grooves for vessels on external side of palatoquadrate bone; *iV*, notch for rr. mandibularis and maxillaris trigemini; *la. com*, commissural lamina; *la. Dpl*, tooth-bearing lamina of dermopalatine; *m. Pq*, margin of commissural lamina of palatoquadrate; *pr. a*, processus ascendens; *pr. ap*, processus apicalis; *pr. dl*, dorso-lateral process of pars autopalatina; *pr. pt*, paratemporal process; *tub*, area with tubercles and foramina, probably for insertion of principal portion of m.levator bulbi.

perfect knowledge of the distribution of the fine branches of the vessels in this part of the head in recent amphibians no safe interpretation can be given of these numerous canals within the bony tissue or of the grooves on the outside and they have been recorded here mainly because they exemplify how richly vascularised the endoskeletal bony tissues really were in early fishes.

The meckelian bone (*Mb*) or ceratomandibular (*Cm*, figs. 8, 16, 22, 47, 103 B, pl. 4:2, pl. 19:2; see also Gross, 1941) extends throughout the lower jaw from the articular area (*Mb. art*) to the symphysis where its anterior end (*Mb. sy*) generally is exposed in the bottom of the symphysial pit (*fo. sy*). In these respects and with regard to its general shape and the development of grooves and canals it seems to agree well with that in osteolepiforms (Jarvik, 1937, 1963a; Gross, 1941; Nilsson, 1944) and if there are any distinct differences between porolepiforms and osteolepiforms in these regards is at present difficult to say. In the porolepiform material at my disposal the bone is shown in several specimens of various forms but disregarding the sectioned specimen of *Glyptolepis* it is generally less well exposed. I have therefore found it better to postpone the

description and the comparative analysis until the grinding series has been completed.

The hyomandibula (*Hy*, figs. 27, 87A, 92A) is shown mainly in two specimens of *Porolepis* (No. P.6963, pls. 2, 3 and No. A.34004) and two specimens of *Glyptolepis* (No. P.1518, pl. 18:2, No. P.1490, pl. 19:2) but is too imperfectly preserved to be safely restored. It is of about the same relative size as in *Eusthenopteron* (fig. 86; JARVIK, 1954) and as in that form it has two proximal articular heads, dorsal (*ahd*) and ventral (*ahv*), an articular area for the ceratohyal (*art. Ch*) or—if present—the stylohyal at the distal end and is pierced by a wide canal (*c. hy*) continued distally on the lateral side of the bone by a groove which soon divides into grooves (*gr. me*, *gr. mi*) for rr. mandibularis externus and internus VII. However, there are also certain differences. In *Eusthenopteron* the proximal articular heads are similar and the dorsal head is situated straight above the ventral one. In porolepiforms (*Porolepis*), on the other hand, the dorsal head is a high and rather thin plate whereas the ventral one is a rounded knob situated a little behind and distally to the dorsal head. Another difference refers to the position in relation to the palatoquadrate. In *Eusthenopteron* the antero-ventral margin of the hyomandibula is gently concave and the bone lies close to the palatoquadrate not only in the spiraculo-hyomandibular recess but also ventrally to that recess. In porolepiforms, on the other hand, the antero-ventral margin is convex and ventrally to the spiraculo-hyomandibular recess the bone curves backwards. In consequence of this configuration the distal end of the hyomandibula lies rather far behind the pars quadrata. The triangular space thus formed between the palatoquadrate in front and the ventral part of the hyomandibula behind and which is covered externally by the submandibulopreopercular (*PSbm*) is occupied by a small bone, the symplectic (*Sym*; "interhyal", cf. p. 213), well shown in two *Glyptolepis* specimens (pl. 18:1, pl. 19:2). This bone which has no equivalent in osteolepiforms is situated between the pit (*p. Sym*) on the posterior side of the pars quadrata and the distal end of the hyomandibula but in the fossil state of preservation it has no contact with either of these structures. However, both the anterior and the posterior ends of the symplectic lack periostal lining indicating that it was capped by cartilage at both ends and very likely the bone articulated with the pars quadrata anteriorly and with the hyomandibula posteriorly, more precisely with a small but distinct articular area (*art. Sym*) which (in *Porolepis*, pl. 2) is found at the postero-ventral corner of the hyomandibula, close antero-ventrally to the articular area for the ceratohyal. With regard to the hyomandibula it may be added that it in its distal part expands postero-dorsally into a fairly large and thin lamina. This lamina which is shown only in the *Porolepis* specimens lies close to the anterior part of the inner

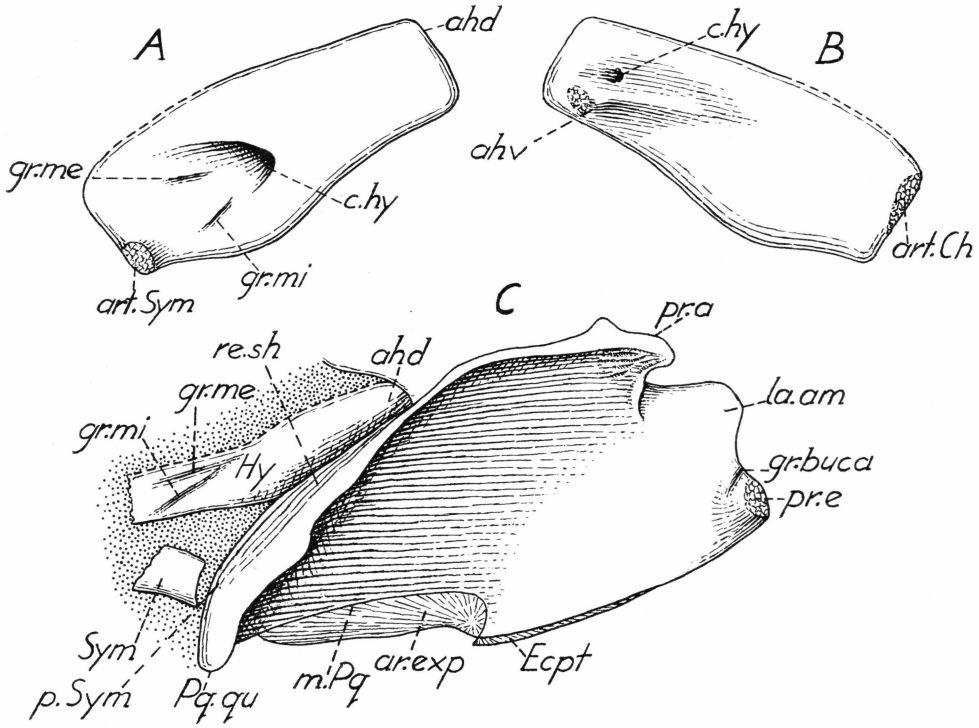


Fig. 27. *A*, *B*, *Porolepis brevis*. Sketch of hyomandibula of right side in, *A*, antero-lateral and, *B*, postero-medial views. Mainly after specimen No. P. 6963, Pal. Sect., Stockh., shown in pls. 2, 3. × 2/3 approx.

C, *Glyptolepis groenlandica* n. sp. Sketch of palatoquadrate complex with hyomandibula and symplectic of right side. Mainly after specimen No. P. 1490, Min. Mus., Copenh., shown in pl. 19:2. × 3/2.

Ecpt, ectopterygoid; *Hy*, hyomandibula; *Pq. qu*, pars quadrata; *Sym*, symplectic.

ahd, *ahv*, dorsal and ventral articular heads of hyomandibula; *ar. exp*, smooth, exposed area of external side of entopterygoid; *art. Ch*, articular area for ceratohyal or stylohyal; *art. Sym*, articular area for symplectic; *c. hy*, hyomandibular canal; *gr. buca*, groove for anterior medial branch of r. buccalis lateralis; *gr. me*, *gr. mi*, grooves for rr. mandibularis externus and internus; *la. am*, antero-medial articular lamina; *m. Pq*, margin of commissural lamina of palatoquadrate; *pr. a*, processus ascendens; *pr. e*, ethmoidal articular process; *p. Sym*, articular area for symplectic; *re. sh*, spiraculo-hyomandibular recess.

side of the opercular but if it is equivalent to the opercular process in other fishes is at present difficult to say.

In this connection may be mentioned that the epibranchials (*Eb*) of the three first branchial arches and certain other dorsal branchial elements are shown in one specimen of *Glyptolepis groenlandica* (pl. 18:2) but are too incompletely preserved to be described.

Hyobranchial skeleton

The ventral parts of the branchial skeleton that is the hyobranchial skeleton are (together with the subbranchial series) shown from the ventral side in some specimens of *G. groenlandica* (pl. 17:3, pl. 18:1, pl. 22:6) and in one specimen the basibranchial (pl. 22:2–5) and certain other elements have been almost completely freed from matrix. Moreover parts of the hyobranchial skeleton (and the urohyal) are shown in the serial sections (figs. 16, 22, 71A).

The basibranchial series in *Glyptolepis* consists of a single element (*Bb*, figs. 16, 28, 29A, B) suggestive of the single basibranchial in *Latimeria* (MILLOT & ANTHONY, 1958) and of the anterior large element (*Bb1*, fig. 29C, D) in *Eusthenopteron* (JARVIK, 1954). Like in these forms it consists of an anterior high and a posterior low portion and it has a quite smooth dorsal face which is covered with delicate dental plates. The articular areas for the hypohyals (*art. Hh*), represented by distinct pits without periostal lining, are situated on the anterior side of the bone and are dorsally separated from each other by a small median anterior process, the lingual process (*pr. ling*, JARVIK, 1963a). Three hypobranchials articulate with the bone on each side (in *Latimeria* there are four and in *Eusthenopteron* only two). The large articular area (*art. HbI*) for the hypobranchial of the first arch is situated on the lateral side of the anterior high portion and close behind it, on the lateral side of the anterior part of the posterior low portion follows the articular area (*art. HbII*) for the second hypobranchial. The small and indistinct articular area (*art. HbIII*) for the third hypobranchial is found on the posterior thin part of the bone. As in *Latimeria* and *Eusthenopteron* the lower side of the posterior low portion presents a large pit, the ventral basibranchial fossa (*fo. bb*), bounded anteriorly by the ventral part of the anterior high portion. However, there is no equivalent to the wide median canal which in *Eusthenopteron* pierces the anterior high portion and forms an anterior continuation of the pit. As in other "crossopterygians" the pit in *Glyptolepis* is covered ventrally by the broadened anterior part of the urohyal and the dorsal median crest of that element divides the space thus formed into left and right halves. It seems likely that muscles of the transversi ventralis group (mm. interarcuales ventrales) like in *Latimeria* and *Eusthenopteron* (JARVIK, 1963a, pp. 37–43, figs. 17–19) were inserted on each side of the dorsal median crest of the urohyal but whether the basibranchial fossa contained other structures e.g. the thyroid gland or parts of it as is tempting to assume remains uncertain. As is well known (see RAUTHER, 1937; VIVIEN, 1958; JARVIK, 1963a) the thyroid gland in vertebrates arises as a ventral median invagination of the pharyngeal floor close in front of the basibranchial

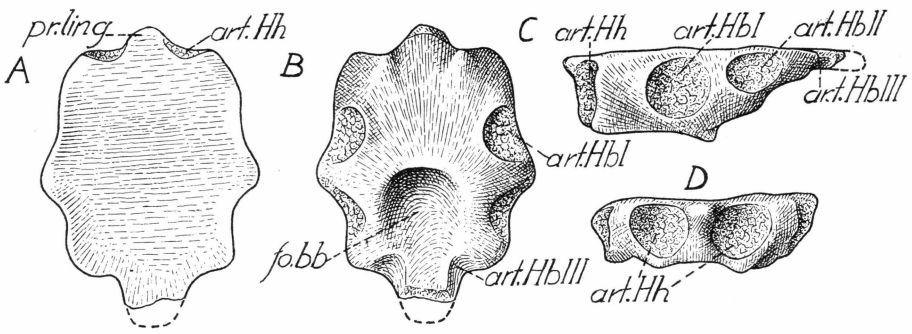


Fig. 28. *Glyptolepis groenlandica* n. sp. Basibranchial in, *A*, dorsal, *B*, ventral, *C*, lateral and, *D*, anterior views. Restorations after specimen No. P. 1515, Min. Mus., Copenh., shown in pl. 22:2–5. × 2/1.

art. HbI, *art. HbII*, *art. HbIII*, articular areas for hypobranchials I, II and III; *art. Hh*, articular area for hypohyal; *fo. bb*, ventral basibranchial fossa; *pr. ling*, lingual process.

series. In fishes it generally is found ventrally to that series in association with the truncus arteriosus. Sometimes it occupies a paired (*Polypterus*, THOMOPOULUS, 1951; cf. ALLIS, 1922, pl. 8:16, 18, 19) or median (*Chlamydoselachus*, ALLIS, 1923, p. 177, pls. 13, 14, 17) depression on the ventral side of the basibranchials and in *Polypterus* this depression lies between the areas of articulation of the first and second hypobranchials. The ventral basibranchial fossa is thus in the proper position to have lodged the thyroid gland. However, in *Latimeria* this gland is situated behind the basibranchial fossa, on the ventral side of the urohyal (MILLOT & ANTHONY, 1958), and judging also from the conditions in urodeles it seems likely that the thyroid gland in porolepiforms was situated behind the basibranchial fossa as it probably was in osteolepiforms (JARVIK, 1963a, pp. 45, 49, figs. 8B, 16C).

The ventral parts of the hyoid arch and of four branchial arches are exposed in ventral view in specimen No. P.1510 of *G. groenlandica* (pl. 17:3, pl. 18:1). No traces of a fifth arch are to be seen either in this or in other specimens. Like in *Eusthenopteron* (fig. 29C, D) the hypohyal (*Hh*, see also figs. 16, 29A, 71A) is a short stout bone which from its articular connection with the ceratohyal extends in a postero-dorso-medial direction to articulate with the anterior end of the basibranchial. The hypobranchials of the first, second and third branchial arches (*Hb I*, *Hb II*, *Hb III*) are comparatively strong bones. Antero-medially they all articulate with the basibranchial. The fourth hypobranchial (*Hb IV*), on the other hand, is short and does not by far reach the basibranchial. A remarkable fact is that hypobranchial II articulates with the middle part of hypobranchial III but as is now evident from the sections (fig. 22,

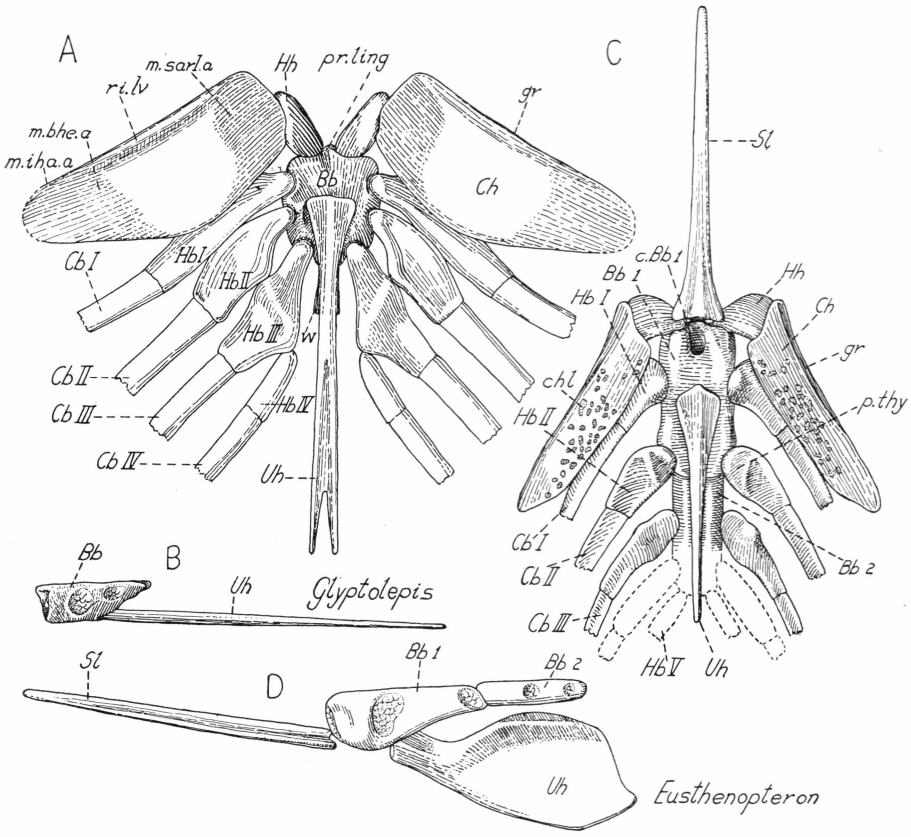


Fig. 29. Hyobranchial skeleton and subbranchial series of, *A*, *B*, porolepiform, *Glyptolepis groenlandica* n. sp. and, *C*, *D*, osteolepiform, *Eusthenopteron foordi*. *A*, *C*, hyobranchial skeleton in ventral aspect; *B*, *D*, basibranchial and subbranchial series in lateral aspect. *A*, tentative restoration, mainly after specimen No. P. 1510, Min. Mus., Copenh., shown in pl. 18:1. As revealed by grinding series (see fig. 22) mode of articulation between hypobranchials is more complex than shown in *A*. *C*, *D* after grinding series 2 of *Eusthenopteron* and wax model. From JARVIK, 1963a, fig. 16.

Bb, *Bb1*, *Bb2*, basibranchials; *CbI–CbIV*, ceratobranchials I–IV; *Ch*, ceratohyal; *HbI–HbV*, hypobranchials I–V; *Hh*, hypohyal; *Sl*, sublingual rod; *Uh*, urohyal.

c. Bb1, anterior opening of canal of basibranchial 1; *chl*, lateral ceratohyal dental plates; *gr*, lateral groove of ceratohyal; *m. bhe. a*, area of attachment of musculus branchiohyoideus externus; *m. iha. a*, area of attachment of m. interhyoideus anterior; *m. sarIa*, depressed area for attachment of m. subarcualis rectus; *pr. ling*, lingual process; *p. thy*, depression of hypobranchial II, probably for thyroid gland; *ri.lv*, ventral lateral ridge of ceratohyal; *w*, wing-like projection of urohyal.

pr. HbII, *pr. HbIII*) the mode of connection is more intricate than shown in my preliminary restoration (fig. 29A) based mainly on specimen No P. 1510. Judging from the latter specimen also hypobranchial IV articulates with hypobranchial III. As described elsewhere (JARVIK,

963a), the ceratohyal (*Ch*) in several respects differs much from that in *Eusthenopteron*. In the latter form the external (ventro-lateral) side of the ceratohyal carries dental plates (*chl*, fig. 29C) whereas in *Glyptolepis* it probably was occupied by muscles (fig. 101B). The most distinct area for the attachment of muscles is found most anteriorly on the external side. This area (*m. sar Ia*) which is shown in several specimens (pl. 17:3, pl. 18:1, pl. 22:6) is distinctly depressed and it extends farther backwards medially than laterally. With regards to its position and extent this area agrees well with the area of attachment for the m. subarcualis rectus I in larvae of urodeles (*m. sar I*, fig. 101A) and almost certainly it served as the area of attachment of a corresponding muscle. Behind this area there is a ridge (*ri. lv*) along the lateral margin of the bone and as revealed by comparisons with various recent vertebrates (Jarvik, 1963a) the large ventral area of the bone medially to the ridge was probably the area of attachment (*m. bhe. a*) of a large muscle, the m. branchiohyoideus externus (*m. bhe*), which in recent forms is found only in urodele larvae. Besides, the m. interhyoideus anterior (*m. iha*) was probably attached to the ventral side of the ceratohyal (*m. iha. a*). The four rodlike ceratobranchials (*Cb I–Cb IV*) are too imperfectly preserved to show any structural details.

Subbranchial series

A special subbranchial series situated ventrally to the basibranchial series was recognised for the first time in *Eusthenopteron* (Jarvik, 1954) in which it consists of two large median endoskeletal elements, the sublingual rod (*Sl*, fig. 29C, D) and the urohyal (*Uh*). It was suggested (op. cit. p. 26) that the urohyal is homologous with the urohyal cartilage (urobranchial, basibranchial II, copula II) in urodeles and because the latter is endomesodermal and of another origin than the ectomesenchymatic visceral skeleton it was concluded that the subbranchial series as a whole is probably endomesodermal. This assumption was later confirmed and it was demonstrated (Jarvik, 1963a) that the subbranchial series has arisen to support the somatic hypobranchial muscles, a condition which in a simple way explains why it is endomesodermal in origin.

The subbranchial series in porolepiforms consists of one element only, the urohyal. This bone (*Uh*, figs. 22, 29A, B, 101B, D, pl. 17:3, pl. 18:1) which is known only in *G. groenlandica* is situated as the corresponding bone in osteolepiforms and coelacanthiforms and like in them it consists of an anterior, broadened, triangular portion and a long posterior portion. The anterior triangular portion is suggestive of that in other "crossopterygians" and is provided with a strong dorsal median crest (cf. Jarvik, 1963a, figs. 16D, 17; *cra. Uh*). The triangular portion underlies

the ventral basibranchial fossa (*fo. bb*), and its transverse anterior margin abuts against or, as in the sectioned specimen, is confluent with the posterior margin of the anterior high portion of the basibranchial. The fact that the urohyal, at any rate in the sectioned specimen, has fused with the basibranchial is of great interest because this is what has happened in urodeles. The posterior portion of the urohyal is a long rod with a pair of small lateral wings (*w*) in its anterior part. Posteriorly it increases slightly in breadth, and becomes a narrow horizontal plate the rear of which by a deep narrow median notch is divided into two shanks. A shallow groove leads forwards from the notch on the ventral side of the bone.

Exoskeleton

Dermal bones of mouth cavity

The principal dermal bones of the mouth cavity in fishes are often covered by a shagreen of small denticles. In 1937 (p. 89), in connection with studies of the prearticular in species of *Eusthenopteron* from the Baltic area, I found that these denticles belong to a separate dental plate, the prearticular dental plate (1937, figs. 9, 17, *T. pl*), intimately connected with the underlying prearticular and have later (JARVIK, 1944a, pp. 26–29) distinguished also separate entopterygoid and parasphenoid dental plates in that genus. Moreover in 1942 (pp. 416–417) comparisons with urodeles caused me to predict independent dental plates in the posterior continuation of the vomer, ventrally to the parasphenoid, in porolepiforms. These views have been confirmed by the investigations of excellently preserved specimens of *Eusthenopteron* (JARVIK, 1954) and *Glyptolepis* (figs. 8C, D, 16, 22, 30, 71A) with the aid of Sollas' grinding method. As shown in the sections there are numerous generally small dental plates which obviously were situated in the mucous membranes lining the mouth cavity and the pharynx in both these genera. However, as to the distribution and structure of these plates there are remarkable differences. In osteolepiforms (*Eusthenopteron*) small independent dental plates are lacking in the anterior, oral or buccal part of the buccopharyngeal cavity (figs. 71B, 73B), whereas they as demonstrated elsewhere (JARVIK, 1954) are well developed in its posterior or pharyngeal part and in the gill-slits. Pharyngeal dental plates are found in porolepiforms, too, but disregarding the ventral side of the otoccipital they are weakly developed. However, in sharp contrast to osteolepiforms the oral cavity in porolepiforms, as shown not only in the sectioned and other specimens of *Glyptolepis groenlandica* (see also pl. 22:6, *odp*), but also in specimens of *Holoptychius* (pl. 26:1, 2) from East Greenland, is richly furnished with dental plates and we may distinguish between upper and lower oral dental plates.

Upper oral dental plates. – The upper oral dental plates (*uodp*, figs. 8C, D, 16, 18, 19, 24E–G, 30, 71A, 72A, 73A, 76B) occupy a large field in the roof of the mouth. As predicted in 1942 they cover the part of the ventral side of the ethmosphenoid situated between the vomer and the parasphenoid and the whole ventral side of the latter bone except the tooth-bearing part (if present, see pp. 86, 88). However, the field extends laterally to the parasphenoid and the plates cover also the parts of the palatoquadrate bone and the entopterygoid situated medially to and in front of the tooth-bearing part of the latter (the entopterygoid dental plate), the postero-medial part of the vomer and, in addition, the most posterior part of the internasal ridge. Posteriorly the field extends into the roof of the pharynx, where it includes a large paired paraotic dental plate (*Podp*, see also figs. 22, 39). The other dental plates are of moderate size and were either scattered in the mucous membrane or lay close together. This is the case below the posterior part of the parasphenoid where the plates are fairly thick and overlap each other. Moreover a remarkable fact is that these plates in the fossil are separated from the overlying parasphenoid by an interspace (figs. 18, 24E, 72A) which obviously in the living animal was filled by connective tissue. Postero-laterally to this rigid part of the field the mucous membrane of the roof of the mouth cavity, judging from the position of the dental plates in the sections, formed a slight ventral bulge (*el. m. sc*, figs. 24E, F, 30) and laterally to that a deep pocket (*pl*) between the palatoquadrate and the braincase. In these respects *Glyptolepis* agrees in a most striking way with *Latimeria* (fig. 24A) and no doubt the ventral bulge was caused by the subcranial muscle (*m. sc*) which occupied the space inside the bulge medially to the a. carotis interna (*a. ci*) and laterally to the notochord (*nc*). The deep pocket which because the sectioned head is compressed dorso-ventrally certainly was narrower and more like that in *Latimeria* than appears from the figures, anteriorly extends about to the basal articulation in front of which the roof of the mouth in the area of the upper oral field is plane. Posteriorly the pocket reaches the posterior end of the paraotic plate. This implies that the spiracular gill-slit, in contrast to conditions in osteolepiforms (see JARVIK, 1954), was closed in front of the lateral commissure (*lc*) and another remarkable fact is that equivalents to the spiracular dental plates in *Eusthenopteron* are lacking. Nor is there a large subotic dental plate and the paraotic dental plate (*Podp*) is on the inner side provided with a conspicuous longitudinal ridge (*ri. dp*) with a sharp edge directed medially. The posterior part of this edge is in some of the sections continued medially by small dental plates and very likely therefore the mucous membrane formed a pocket dorsally to the postero-medial part of the paraotic plate as it probably did also in *Eusthenopteron* (JARVIK, 1954, p. 42). If this be true the sub-

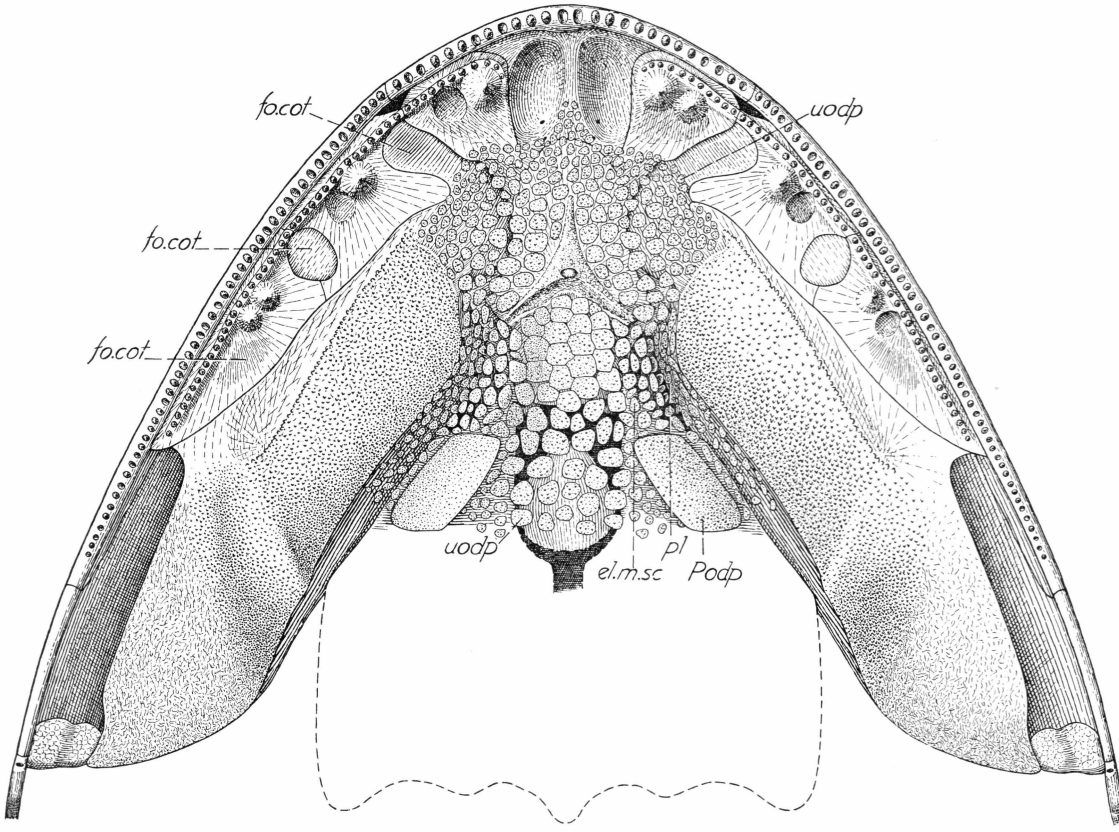


Fig. 30. *Glyptolepis groenlandica* n. sp. Palate in ventral aspect of specimen compressed dorso-ventrally. Mainly after graphical restoration from grinding series. × 2/1.

Podp, paraotic dental plate.

el. m. sc, ridge-like elevation in roof of mouth cavity caused by subcranial muscle; *fo. cot*, pits for tips of coronoid tusks of lower jaw; *pl*, fold in roof of mouth cavity laterally to subcranial muscle; *uodp*, upper oral dental plates.

For further explanations see fig. 31.

otic plate of *Eusthenopteron* is in porolepiforms represented by several separate plates (cf. BJERRING, 1967, fig. 15). However, the ridge of the paraotic plate may have served also another purpose than to form the medial boundary of the presumed pocket. For reasons discussed below it may be tentatively suggested that its edge was continued by a fascia (*fasc*, fig. 24G) separating the subcranial muscle (*m. sc*) which probably is the basicranial muscle of the second metamere from the basicranial muscle of the third metamere (*m. b3*). Behind the paraotic plates the dental plates are too much in disorder to be described (fig. 22) and if the hyomandibula and the dorsal elements of the branchial arches carry such plates is still unknown.

Lower oral dental plates. – One of the most surprising features in the porolepiforms discovered in the grinding series of *Glyptolepis* is the presence of numerous dental plates in the anterior part of the intermandibular division and on the adjoining parts of the lower jaws. These plates (figs. 8C, D, 71A, 76B, 102E, 103B), situated immediately behind the symphysis and the parasymphysial dental plates (*Psy*), were described in a previous paper (JARVIK, 1963a, pp. 31–33) and because of differences in structure it was distinguished between medial mandibular plates (*mmdp*) situated in an elongated area, the medial mandibular field (*mmf*), on the inner side of the lower jaw, and prolingual dental plates (*pldp*) which occupy a median crescent-shaped area, the prolingual field (*plf*). It was claimed that the prolingual field contained glands and is homologous with the glandular field (*glf*, figs. 102A, C, D, 103A) in larvae of urodeles and that the medial mandibular plates correspond to the larval "operculare" ("*Op*") of urodeles. The medial mandibular plates extend a little farther backwards than shown in my previous restorations and are continued medially by some dental plates hitherto not recorded. These dental plates (*dp*, figs. 16A, 71A, 102E) in the fossil lie close to the dorsal sides of the first submandibulars (*Sbm*) and the anterior ends of the principal gular plates (*G*), and—obviously because the hyobranchial apparatus as a whole in the sectioned specimen has become displaced forwards—they lie underneath the anterior parts of the hypohyals and the basibranchial. However, their teeth are directed upwards and they must have been situated in the floor of the mouth behind the prolingual field. Like in *Eusthenopteron* (JARVIK, 1954) the dorsal side of the basibranchial carries dental plates but these plates (*bbdp*, figs. 16C, 102E) are weakly developed as are also the dental plates of the hypobranchials (*dp*, fig. 22). In sharp contrast to *Eusthenopteron* ceratohyal dental plates are completely lacking (figs. 22, 29).

Principal dermal bones. – With regard to the main dermal bones of the mouth cavity porolepiforms (figs. 31, 47, 73A) in certain respects agree with, in others differ fairly much from osteolepiforms (fig. 73B, JARVIK, 1944a, 1954). On the whole the dermal bones of the palatoquadrate (dermopalatine, ectopterygoid, entopterygoid) and the corresponding bones of the lower jaw (coronoids, prearticular) resemble those in osteolepiforms whereas the dermal bones on the ventral side of the divisio cranialis anterior (vomer, parasphenoid) are different. Some of the bones (vomer, dermopalatine, ectopterygoid) are only loosely connected to adjoining structures and are therefore often missing in the fossils.

The parasphenoid (*P*, figs. 16, 18–20, 24E, 31, 39, 72A, 73A, 92A) is shown in several specimens of *Porolepis* (fig. 65B, pls. 3, 9), *Glyptolepis* (pl. 14, pl. 17:3, pl. 22:1) and *Holoptychius* (pl. 25:2, pl. 26:1). It is

clearly of the same type in these three genera and is distinguished by several common characteristics. Like the overlying ventral side of the ethmosphenoid it is always broad, its dorsal side is in the prehypophysial part plane, not guttershaped as in *Eusthenopteron* and other osteolepiforms (JARVIK, 1954, p. 37), and the bone extends forwards only to about the transition between the orbitotemporal and ethmoidal regions. Moreover the processus ascendens anterior of the bone (*pr. asc I*) which is situated mainly behind the basipterygoid process on its anterior part has a distinct and characteristic groove (*gr. psp*) for the prespiracular gill-slit. In the bottom of this groove there are sometimes small denticles or a net-work of fine ridges formed by the fusion of such denticles. A distinctive feature of the porolepiform parasphenoid is furthermore that four paired canals, three of which open into the fossa hypophyseos, pierce the bone or are partly formed by grooves on its dorsal side (see p. 51).

The parasphenoid is subject to some variations which, however, are rather inconsiderable and disregarding the dentition of no taxonomic value. In the area of the basipterygoid process the bone generally broadens and forms a thin lamina on the lower side of that process. This thin part which generally is plane and therefore most properly not included in the processus ascendens anterior (as I did in 1954) may reach the lateral margin of the basipterygoid process or end medially to that margin. However, irrespective of its lateral extent the lateral margin of the parasphenoid forms a slight process anterolaterally to the opening (*c. a. ci*) for the internal carotid artery. Close behind that opening lies the depression (*i. m. sc*) of the ethmosphenoid that has been interpreted as the area of insertion of the subcranial muscle. However, the conditions are variable and in specimens of various species the postero-medial margin of the groove for the prespiracular gill-slit forms a projecting edge which rises above the level of the part of the parasphenoid situated behind it (fig. 31, pl. 9:2). As discussed above this part of the parasphenoid was probably covered by a thick sheet of connective tissue occupying the space between the parasphenoid and the underlying upper oral dental plates and obviously extending forwards to the projecting edge. Because of these conditions it seems likely that at least some fibres or tendons of the subcranial muscle (in the posterior part together with a vessel, *a. cib*, figs. 83 A, B, 85 D) was embedded in the sheet of connective tissue and was inserted on the postero-medial side of the edge or possibly in the irregular depressions that in some specimens (fig. 65 B) are found on the ventral side of the posterior part of the parasphenoid. If this be true this would in a simple way explain why the parasphenoid and its dental plates in this part are so far apart.

As to its dentition the parasphenoid shows some interesting variations. In some specimens of *Holoptychius* (pl. 25:2) and *Glyptolepis* (pl.

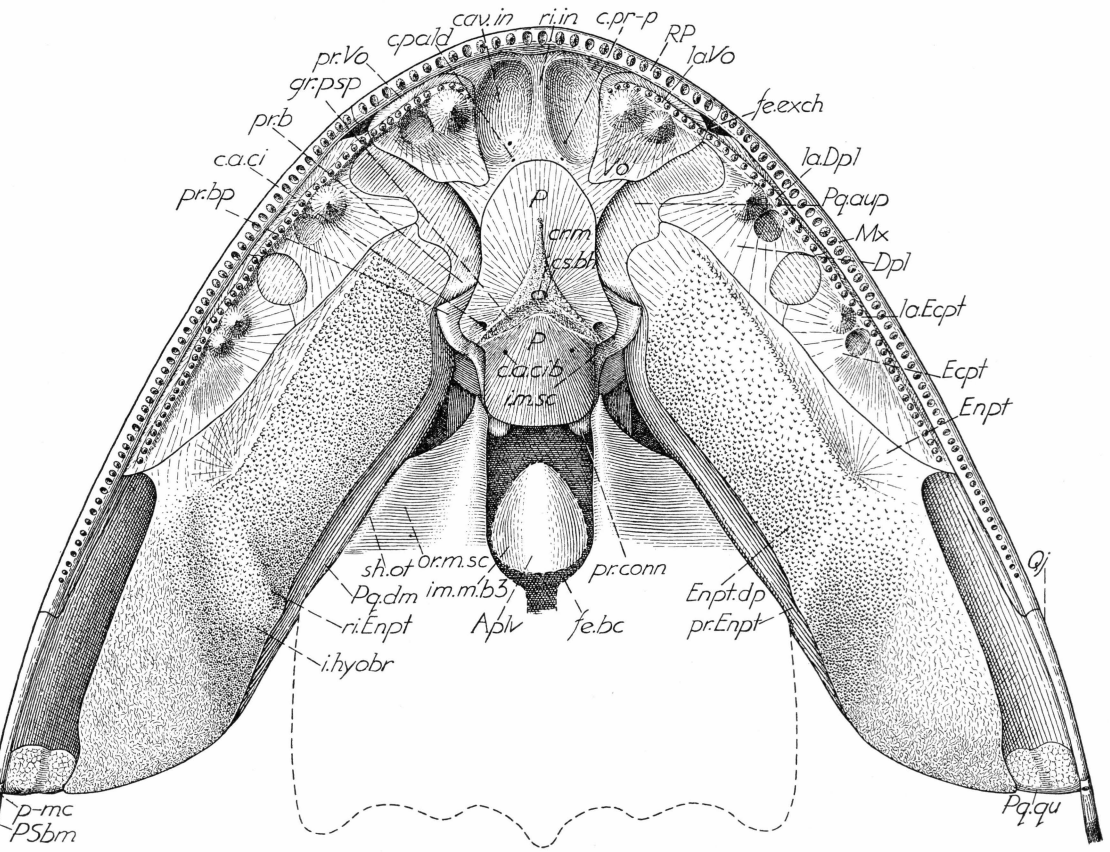


Fig. 31. *Glyptolepis groenlandica.* Palate of compressed specimen in ventral aspect. Same as in fig. 30 but without upper oral dental plates. × 2/1.

Aplv, subchordal arcual plate; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Enpt. dp*, entopterygoid dental plate; *Mx*, maxillary; *P*, parasphenoid; *Pq. aup*, *Pq. dm*, *Pq. qu*, pars autopalatina, postero-dorsal marginal portion, and pars quadrata of palatoquadrate; *PSbm*, preoperculosubmandibular; *Qj*, quadratojugal; *RP*, rostropremaxillary; *Vo*, vomer.

c. a. ci, canal for a. carotis interna; *c. a. cib*, canal for medial branch of a. carotis interna; *cav. in*, cavum internasale; *c. pald*, canal for ascending branch of r. palatinus; *c. pr-p*, canal for combined profundus-palatine nerve; *cr. m*, median hypophysial crest; *cs. bh*, left buccohypophysial canal; *fe. bc*, basicranial fenestra; *fe. exch*, fenestra exochoanalis; *gr. psp*, prespiracular groove (for vestigial prespiracular gill-slit); *i. hyobr*, depression probably for lateral side of hyobranchial apparatus; *i. m. sc*, area of insertion of subcranial muscle; *im. m. b3*, impression probably for basicranial muscle 3; *la. Dpl*, *la. Ecpt*, *la. Vo*, vertical tooth-bearing laminae of dermopalatine, ectopterygoid and vomer; *or. m. sc*, area of origin of subcranial muscle; *p-mc*, preoperculo-mandibular sensory canal; *pr. b*, processus basalis of palatoquadrate; *pr. bp*, basipterygoid process of neural endocranium; *pr. conn*, processus connectens of ethmosphenoid; *pr. Enpt*, *ri. Enpt*, process and ridge of entopterygoid; *pr. Vo*, antero-lateral process of vomer; *ri. in*, internasal ridge; *sh. ot*, otical shelf.

14:5, pl. 17:3) it lacks teeth whereas in other specimens of the same genera or of the same species there is a raised tooth-bearing area (fig. 31; JARVIK, 1954, fig. 39B, C). This can only mean that the said area is composed of dental plates which in the other specimens were independent and therefore were lost during the fossilisation, and as is now evident also the raised tooth-bearing areas of the prearticular and entopterygoid in porolepiforms and the prearticular, entopterygoid and parasphenoid dental plates distinguished in osteolepiforms (p. 82) are composed in the same way. In *Glyptolepis* and *Holoptychius* the raised tooth-bearing area broadens posteriorly and forms a winglike projection in front of the groove for the prespiracular gill-slit. Anteriorly it tapers in breadth and its anterior end may be pointed as in *Glyptolepis* or rounded as in the single specimen of *Holoptychius* (JARVIK, 1954, fig. 19B) showing this detail. In *Porolepis* the conditions are somewhat different. In the specimens of this genus available in 1942 (pl. 4, pl. 5:2) the parasphenoid is provided with a narrow median ridge (*ri. P*, fig. 65B) with a single row of fairly large teeth. However, in a specimen prepared recently (pl. 9) the tooth-bearing area is much broader occupying the main part of the ventral side of the parasphenoid in front of the opening for the buccohypophysial duct, but also in this specimen the teeth, although more numerous, are apparently fairly large.

The paired vomer (*Vo*, *Porolepis*, figs. 9A, 20A, 73A, pl. 3; JARVIK, 1942, pl. 5:2; *Glyptolepis*, figs. 8, 30, 31, 32A1, 39, 66A,C, 76B, 78A,C, pl. 17:3, pl. 18:2, pl. 22:1; JARVIK, 1962, fig. 2, 1966, fig. 1; *Holoptychius*, fig. 20B, pl. 25, pl. 26:1, 2; JARVIK, 1942, fig. 44, 1954, fig. 19B) as in osteolepiforms (figs. 65A, 66B,D, 73B; JARVIK, 1966, figs. 16C,D, 17, 18; VOROBYEVA, 1962, pl. 9:2, pl. 11) consists of a horizontal plate situated on that part (the vomeral area, *ar. Vo*) of the ventral side of the solum nasi which presumably represents the infrapharyngopremandibular (see pp. 219–220), and a vertical tooth-bearing lamina (*la. Vo*). It also carries two tusks or, more often, there is one tusk (*vot*) and a pit for the replacement tusk. However, because of the presence of the internasal cavity the two vomers diverge strongly forwards and the tooth-bearing laminae which are rather short are far apart. Consequently there are no equivalents to the intervomerine pit and the intervomerine canal of osteolepiforms. Postero-medially the bone is most often separated from the parasphenoid by an area in which the ventral side of the ethmosphenoid is exposed and there is no posterior process such as has been found in all osteolepiforms in which the vomer is well known (*Gyroptychius*, *Megalichthys*, *Eusthenopteron*, *Eusthenodon*, *Platycephalichthys*, JARVIK, 1937, 1942, 1944a, 1952, 1966; VOROBYEVA, 1962). In the sectioned specimen of *Glyptolepis* the exposed area of the ethmosphenoid and the adjoining thin part of the vomer are covered with dental plates (*uodp*). Antero-

laterally to this thin part there is often a depression bounded by distinct ridges. Antero-medially the horizontal plate in *Porolepis* (pl. 3), *Glyptolepis* (fig. 31) and more distinctly in *Holoptychius* is bent upwards (*Vod*) and covers the wall of the internasal cavity (fig. 77 A). This almost vertical part of the horizontal plate is in *Holoptychius* intimately connected with the neural endocranium which is the reason why the vomer in *Holoptychius* is more often preserved than in the other two genera. Antero-laterally the horizontal plate extends a little beyond the tooth-bearing lamina. This part of the vomer (*pr. Vo*) is situated somewhat as the antero-lateral process of the vomer in osteolepiforms and like that it forms part of the boundary of the fenestra exochoanalis. However, it is not thickened and ridgelike and is not in sutural connection with the palatal lamina of the premaxillary, but overlaps the dorsal side of that lamina slightly.

The dermopalatine (*Dpl*) and ectopterygoid (*Ecpt*), well shown only in *Glyptolepis groenlandica* (figs. 8 D, 16, 27 C, 30, 31, 32 A1–A4, 71 A, pl. 16:2, pl. 22:1; *Holoptychius*, fig. 33 C, pl. 26:1), are situated on the ventral side of the pars autopalatina (epipremandibular) and form together with the vomer a row of bones corresponding to the three coronoids on the dorsal side of the meckelian bone (ceratomandibular) in the lower jaw. Like the vomer each bone consists of a horizontal plate and a vertical tooth-bearing lamina (*la. Dpl*, *la. Ecpt*) inside which there on each bone is one pair of tusks or one tusk and a pit for a replacement tusk. Laterally the horizontal plate of both bones rests on the palatal lamina (*Mxp*) of the maxillary. Medially it slightly overlaps the dorsal side of the adjoining part of the entopterygoid (cf. *Eusthenopteron*, fig. 32 B2–3). In front of the horizontal plate of the dermopalatine, between it and the vomer, there is a fenestra in the exoskeleton and a shallow pit (*fo. cot*, fig. 30) on the lower side of the overlying part of the pars autopalatina to receive the tip of the tusk of coronoid 1. A similar fenestra and pit for the tusk of coronoid 2 are found at the boundary between the dermopalatine and ectopterygoid, but the small tusk of coronoid 3 has only caused a slight excavation on the ventral side of the ectopterygoid.

The entopterygoid (*Enpt*, *Porolepis*, fig. 73 A, pl. 3; *Glyptolepis* figs. 16, 19, 22, 24 E–G, 25, 27 C, 30, 31, 32 A4, 33 D, E, pl. 18:2; *Holoptychius*, fig. 33 A–C; Jessen, 1967, pl. 4 F) is a large bone in most respects suggestive of that in *Eusthenopteron* (figs. 26 A, 32 B2,3, 71 B, 73 B; Jarvik, 1944a, 1954). As in that form there is a raised tooth-bearing area (*Enpt. dp*) which although not found separate no doubt is composed of originally independent plates which have fused with each other forming an entopterygoid dental plate and with the overlying dermal bone. Posteriorly the denticles of this raised part gradually turn into a net-work of faint ridges. Medially to the dermopalatine and ectopterygoid the lateral

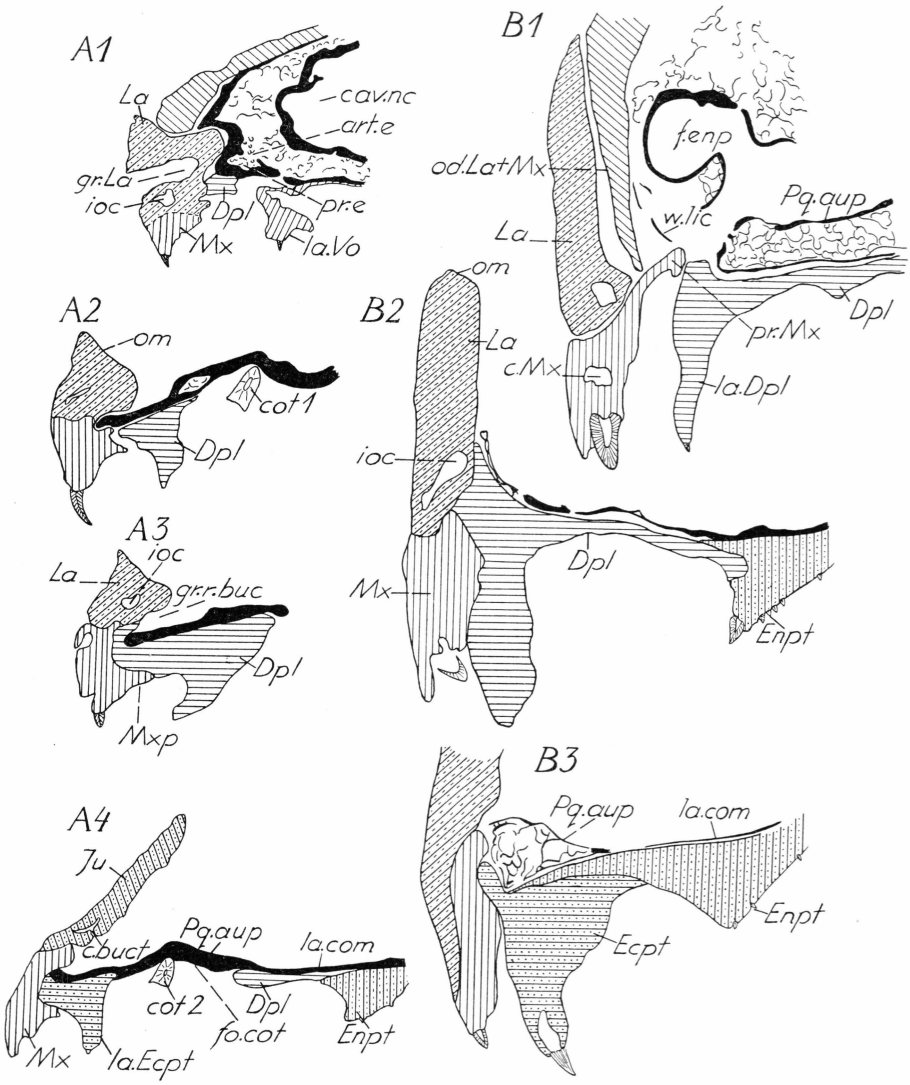


Fig. 32. Parts of sections of grinding series of, *A1–A4*, *Glyptolepis groenlandica* n.sp. and, *B1–B3*, *Eusthenopteron foordi* to show development and mutual relations of dermal bones of lateral part of palatoquadrate and adjoining dermal bones of external cheek-plate, and differences in these regards between porolepiforms and osteolepiforms. *A1–A4* sections Nos. 67, 85, 100 and 163 of grinding series of *Glyptolepis* and *B1–B3* sections Nos. 57, 93 and 201 of grinding series 2 of *Eusthenopteron*.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Mxp*, palatal lamina of maxillary; *Pq. aup*, pars autopalatina.

art. e, area of postnasal wall fused to ethmoidal articular process of pars autopalatina; *cav. nc*, cavity of nasal capsule; *c. buct*, canal for twig of r. buccalis lateralis to neuromast of infraorbital sensory canal; *c. Mx*, canal in maxillary for nerve supplying maxillary teeth; *cot1*, *cot2*, tips of coronoid tusks; *f. enp*, foramen in postnasal

margin of the raised part, also very much as in *Eusthenopteron*, forms a sharp edge set with rather large teeth. This edge is the medial boundary of a characteristic longitudinal depression formed jointly by the three dermal bones of the palatoquadrate. In *Glyptolepis* (figs. 30, 31) the part of the bottom of this depression formed by the entopterygoid exactly as in *Eusthenopteron* increases in breadth posteriorly (*Porolepis* and *Holoptychius*, *ar. expa*, fig. 33A, appear to be different in this respect). However, in contrast to *Eusthenopteron* the tooth-bearing part anteriorly is rounded and in front of that part the ventral side of the entopterygoid (*ar. uodp*) is covered by dental plates (*uodp*). Another difference is that the tooth-bearing part dorso-medially, on the inner side of the postero-dorsal marginal portion (*Pq. dm*) of the palatoquadrate, extends to the very margin of the entopterygoid. This part of the margin of the entopterygoid which is fairly thick forming a shelf on the inner side of the palatoquadrate bone (fig. 24F,G), is slightly concave as seen in lateral aspects and ends posteriorly in a more or less pronounced process (*pr. Enpt*). This process is situated at the dorsal end of the characteristic oblique ridge (*ri. Enpt*) on the inner tooth-bearing side of the entopterygoid found not only in porolepiforms and osteolepiforms but also in struniiforms (JESSEN, 1967, p. 176, pl. 4:D,F). JESSEN suggested that this ridge has to do with the spiracular gill-slit and as is evident from the wax model of *Eusthenopteron* the ridge runs upwards and backwards towards the posterior margin of the inner opening of the spiracular tube (see JARVIK, 1954, fig. 26). In front of the dorsal part of the ridge and, more distinctly, behind that ridge there are depressions. In the posterior depression (*i. hyobr*) which is fairly large the denticles of the tooth-bearing area of the entopterygoid are replaced by very faint ridges and judging also from its position (see fig. 22) it seems likely that this depression has given space for the movements of the hyobranchial apparatus. It is possible that, when the mouth was closed and the dorsal side of the hyobranchial apparatus was close to the roof of the mouth, the lateral side of that apparatus formed mainly by the ceratohyal abutted against the postero-ventral side of the ridge. If so, the floor of the mouth together with the ridge (*ri. Enpt*) and the depression in front of it may have

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wall for posterior nasal tube and certain nerves and vessels (fenestra endonarina posterior); *fo. cot*, pit for coronoid tusk; *gr. La*, groove in lachrymal for posterior external nasal tube; *gr. r. buc*, groove for r. buccalis lateralis; *ioc*, infraorbital sensory canal; *la. com*, commissural lamina; *la. Dpl*, *la. Ecpt*, *la. Vo*, vertical tooth-bearing laminae of dermopalatine, ectopterygoid and vomer; *od. La + Mx*, area of fronto-ethmoidal shield overlapped by lachrymal and maxillary; *om*, margin of orbital fenestra; *pr. e*, ethmoidal articular process of pars autopalatina; *pr. Mx*, antero-dorsal, medially curved process of maxillary; *w. lic*, ventral, medially curved part of lateral nasal wall.

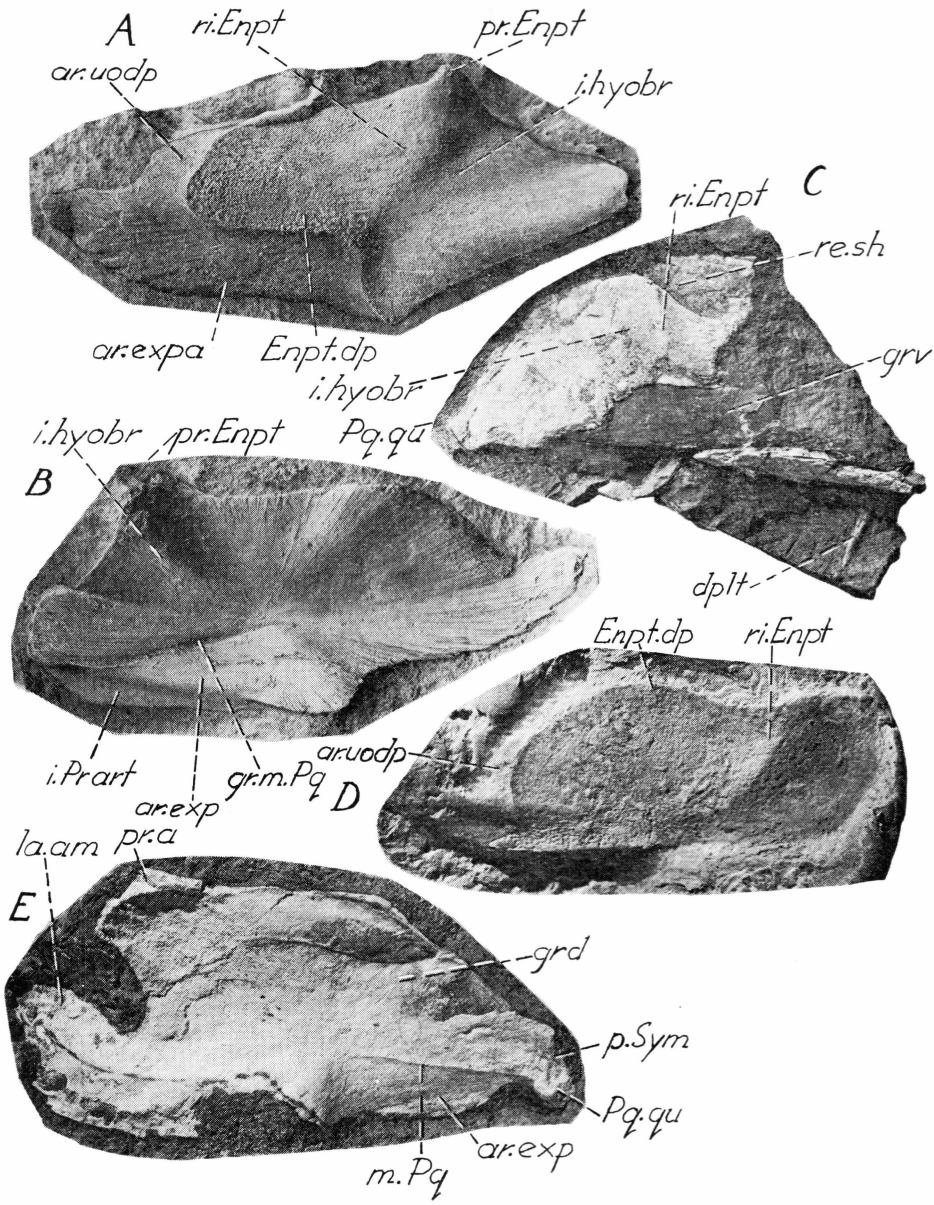


Fig. 33. *A*, *B*. *Holoptychius* sp. Entopterygoid in ventro-medial and dorso-lateral views. Photographs of latex casts. Same specimen as figured by JESSEN, 1967, pl. 4:F. Specimen No. P. 1532, Min. Mus., Copenh. Coll. 1932. N. side of Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 3/4. *C*, *Holoptychius* sp. Imperfect palatoquadrate complex in medial view. Specimen No. P. 1593, Min. Mus., Copenh. Coll. 1947. S. side of Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 3/4. *D*, *E*, *Glyptolepis groenlandica* n. sp. *D*, entopterygoid in ventro-medial view. Photograph of latex cast. Specimen No. P. 1521, Min. Mus., Copenh. *E*, palatoquadrate complex in lateral view.

formed a passage for the water which from the mouth cavity went out through the spiracular gill-slit. Ventral to the large depression (*i. hyobr*) behind the ridge the postero-ventral part of the entopterygoid (*ar. exp*), which is bent slightly ventrally, projects beyond the ventral margin of the palatoquadrate bone ending ventrally with a free and generally somewhat convex margin. As is best seen in *Eusthenopteron*, (fig. 26 A), which also in these respects agrees with porolepiforms, the external side of the entopterygoid that is exposed ventrally to the palatoquadrate bone is smooth and shiny. This smooth area (*ar. exp*) was obviously situated inside the adductor muscles passing from the palatoquadrate to the adductor fossa of the lower jaw and when the mouth was closed the most ventral part of the exposed area which may be slightly depressed (*i. Prart*, fig. 33 B; see also pl. 19:2) was situated close inside the postero-dorsal part of the prearticular of the lower jaw.

The three coronoids (*Co1*, *Co2*, *Co3*) of the lower jaw which besides in *Porolepis*, *Glyptolepis* and *Holoptychius* (figs. 8C, D, 16, 47, 71 A, 76 B, 102 E, pl. 12:2, 3, pl. 18:2, pl. 26:1, pl. 32:1, 2, 5; Gross, 1941) are known also in *Laccognathus* (Gross, 1941) are developed fundamentally as the opposing bones (vomer, dermopalatine, ectopterygoid) of the upper jaw. Like them they consist of a lateral tooth-bearing lamina (*la. Co*) and a horizontal plate which in each bone carries one pair of tusks or one tusk (*cot*) and a replacement pit. The coronoids are also suggestive of the corresponding bones in *Eusthenopteron* with the difference that coronoid 3 in the latter (like the ectopterygoid) is provided with two pairs of tusks. The prearticular (*Prart*), too, is suggestive of the corresponding bone in *Eusthenopteron* and like in that form the prearticular dental plate (*Prart.dp*) may be partly independent. However, in porolepiforms the most anterior part of the prearticular carries independent plates (the medial mandibular dental plates) which cover also the medial margin of the meckelian bone exposed between the prearticular and the infradentaries.

Specimen No. P. 1510, Min. Mus., Copenh. Both specimens from same block as holotype. Coll. 1956, Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*). × 3/4.

Enpt. dp, entopterygoid dental plate; *Pq. qu*, pars quadrata.

ar. exp, smooth exposed area of external side of entopterygoid inside adductor muscles; *ar. expa*, area of entopterygoid forming part of bottom of longitudinal depression; *ar. uodp*, area covered by upper oral dental plates; *dplt*, dermopalatine tusk; *grd*, dorsal grooves for vessels; *gr. m. Pq*, groove for ventral margin of commissural lamina of palatoquadrate; *grv*, ventral grooves for vessels; *i. hyobr*, depression for lateral margin of hyobranchial apparatus; *i. Prart*, impression for margin of prearticular of lower jaw; *la. am*, antero-medial articular lamina; *m. Pq*, ventral margin of commissural lamina of palatoquadrate; *pr. a*, processus ascendens; *pr. Enpt*, process of entopterygoid; *p. Sym*, articular area for symplectic; *re. sh*, spiraculo-hyomandibular recess; *ri. Enpt*, ridge of entopterygoid.

External dermal bones

As regards the number and disposition of the external dermal bones of the head porolepiforms (*Porolepis*, figs. 1, 2, 7, 20, 34, 43, 56, 57, pls. 1–13, pl. 33:3; JARVIK, 1950a, figs. 27A, 30, 31A, 1964, fig. 21C; *Laccognathus* GROSS, 1936, figs. 4–6, 1941; JARVIK, 1950a, fig. 31B; *Glyptolepis* figs. 3, 7, 8, 16, 18, 19, 22, 30–32, 38–42, 44, 55, 57, 66, 71, 72, 76, 104, pls. 14–23; JAEKEL, 1911, fig. 77, 1927, fig. 86; GROSS, 1941; JARVIK, 1949, figs. 7D, 10B; 1950a, figs. 27B, 31C; 1963a, figs. 13, 14; 1964, fig. 21D; 1966, fig. 10; BJERRING, 1967, figs. 14B, C, 15, 16; *Holoptychius* figs. 4–7, 20, 35–37, 45–48, 57, 58, 59, 107, pls. 24–33; HUXLEY, 1861, figs. 4, 5; WOODWARD, 1891a, fig. 49; TRAQUAIR, 1895, pl. 2:4; HOLMGREN & STENSIÖ, 1936, figs. 274, 276; WESTOLL, 1937a, fig. 1C, 1937b, fig. 9C; JARVIK, 1942, fig. 33, 1948a, figs. 33, 34, 1950a, fig. 31D, 1959a, figs. 12C, 17C, pl. 2:1, 5, 1963a, figs. 4B, C, 5B, 10, 11, 15A, B, 1964, fig. 21E) in many respects agree well with osteolepiforms (figs. 32, 61–64, 66, 71, 72, 79, 86, 90, 104, 105; SÄVE-SÖDERBERGH, 1933; WESTOLL, 1936, 1937c, 1940; JARVIK, 1937, 1942, 1944a, 1948a, 1949, 1950a, 1952, 1954, 1959a, 1963a, 1966; VOROBYEVA, 1962, 1969; JESSEN, 1966b, BJERRING, 1967, 1972b). However, as may be gathered from the subsequent description there are also many differences (see also pp. 143–158).

Dermal cranial roof. – In porolepiforms the posterior transverse margin of the fronto-ethmoidal shield (*Fr-et. sh*) meets the correspondingly developed anterior margin of the parietal shield (*Pa.sh*) but the shields are always quite separate from each other and in contrast to osteolepiforms (JARVIK, 1937, pp. 112–117, 1944a, pp. 22, 32, 1948a, pp. 64–66) there are no tendences to a fusion between these shields; and as mentioned above (p. 25) no independent bones between them have been encountered. However, in *Glyptolepis groenlandica* and at any rate in some specimens of *Holoptychius* (but not in *Porolepis*) there is a paired pocket (*i. li*) in the posterior margin of the fronto-ethmoidal shield and a corresponding pocket in the anterior margin of the parietal shield. As suggested by BJERRING (1967, p. 244, fig. 14B, C) these pockets were possibly developed for ligaments connecting the two cranial divisions. With regard to the relative length of the shields there are considerable differences. In all the specimens of *Porolepis brevis* in which both shields are preserved the fronto-ethmoidal shield is rather long, about 1.5 times longer than the parietal shield, and possibly it is still longer, proportionately, in *P. elongata* which is distinguished by a long and narrow fronto-ethmoidal shield. In *Glyptolepis?* cf. *paucidens* the two shields are about equal in length but in the other holoptychiids the fronto-ethmoidal shield is remarkably short, shorter than the parietal shield, its length being in *Holoptychius* about 0.80–0.85 and in *Glyptolepis groenlandica*

only about 0.70 of the length of that shield. A remarkable fact is that the fronto-ethmoidal shield extends farther back in relation to the ethmosphenoid in *Porolepis* (fig. 20A) and osteolepiforms (*Eusthenopteron*, fig. 105A) than it does in *Glyptolepis* and *Holoptychius*. In the latter (fig. 105B) a considerable portion of the ethmosphenoid is situated behind the posterior limit of the fronto-ethmoidal shield which ends posteriorly about dorsally to the external openings of the trochlearis and oculomotor canals and in front of the suprapterygoid process (cf. p. 264).

The fronto-ethmoidal shield (*Fr-et. sh*) is composed of numerous dermal bones, well shown in particular in the specimens of *Holoptychius* from the Upper Devonian of East Greenland in which the shield is presented in ventral aspect (figs. 35, 36, pls. 27, 28, pl. 29:4, pl. 31:1). Sutures on the external face of the shield are sometimes discernible both in *Holoptychius* (fig. 37, pl. 29:1–3) and in *Glyptolepis* (figs. 41, 42, pl. 14:3, pl. 17:2). In *Porolepis* the dermal bones have most often fused completely in their superficial parts and sutures are generally not discernible. However, in some specimens (figs. 34A, 56, pl. 8:1) the centra of radiation of the individual bones are fairly distinct and as evidenced by these specimens the disposition of the dermal bones of the fronto-ethmoidal shield in porolepids is in all essentials as in holoptychiids.

The premaxillary or more correctly the rostropremaxillary (*RP*) is a strong bone, as in the osteolepiforms consisting of three portions, pars dentalis (*Pmxd*), pars palatina (*Pmxp*) and pars facialis (*Pmxf*). In *Porolepis spitsbergensis* (JARVIK, 1942, fig. 36A, pl. 2:3) the medial parts of the partes palatinae form a median process with one or two enlarged teeth (see also *Glyptolepis groenlandica*, figs. 18, 31). In osteolepiforms the premaxillary has usually fused with medial rostral elements forming a rostropremaxillary whereas the lateral rostral (*Rl*, figs. 62A, 66B, 79A) which is provided with a strong processus dermintermedius, is always independent. In porolepiforms the conditions are reverse (see also pp. 132–135, 150). In all the specimens of *Porolepis* and *Holoptychius* showing these details there is a small independent unpaired median rostral (*Rm*) which as evidenced also by the sections of *Glyptolepis* (fig. 18) is pierced by the ethmoidal commissural canal (*et. com*) connecting the two infraorbital canals anteriorly, whereas the lateral rostral which is devoid of a processus dermintermedius has fused with the premaxillary (my description of *Holoptychius* in 1942, pp. 346–349, fig. 33 is in these regards erroneous). The compound rostropremaxillary of porolepiforms formed in this way is thus not strictly homologous with the rostropremaxillary of osteolepiforms which besides generally includes a nasal and is a nasorostropremaxillary (*NRP*).

Dorsally to the postero-lateral part of the rostropremaxillary which as we have seen includes the lateral rostral there is in *Holoptychius* a

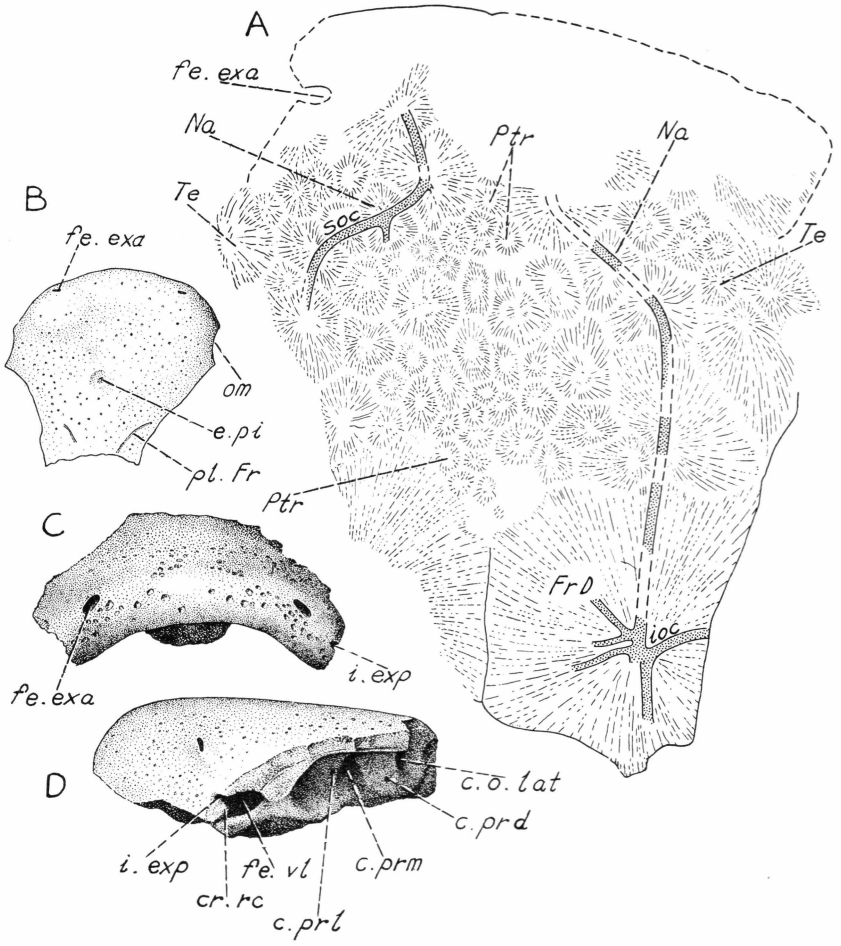


Fig. 34. *A–C*, *Porolepis brevis*. Fronto-ethmoidal shields in, *A*, ventral, *B*, dorsal and, *C*, anterior aspects. *A*, specimen No. P. 6980, Pal. Sect., Stockh. Same specimen as in pl. 8:1. × 3/2. *B*, specimen No. P. 52686, Brit. Mus., Lond. Same specimen as in pl. 11:4. × 6/5. *C*, specimen No. A. 33989, Pal. Mus., Oslo. Same specimen as in pl. 8:2–4. × 6/5. *D*, *Porolepis spitsbergensis*. Holotype. Specimen Nos. A. 34034/35, Pal. Mus., Oslo. Same specimen as in pl. 11:2,5. × 6/5.

FrD, frontodermosphenotic; *Na*, nasals; *Ptr*, postrostrals; *Te*, tectals.

c. o. lat, canal for r. ophthalmicus lateralis; *c. prd*, canal for dorsal branch of n. ophthalmicus profundus; *c. prl*, *c. prm*, lateral and medial profundus canals; *cr. rc*, crista rostro-caudalis; *e. pi*, pineal elevation; *fe. exa*, fenestra exonarina anterior; *fe. vl*, fenestra ventro-lateralis; *i. exp*, notch for posterior external nasal tube; *ioc*, infraorbital sensory canal; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line; *soc*, supraorbital sensory canal.

large opening bounded in its posterior part by a deep notch in the anterior margin of the lachrymal. As already described (p. 26) this opening, the fenestra exonarina communis (*fe. ex*), is occupied by a small

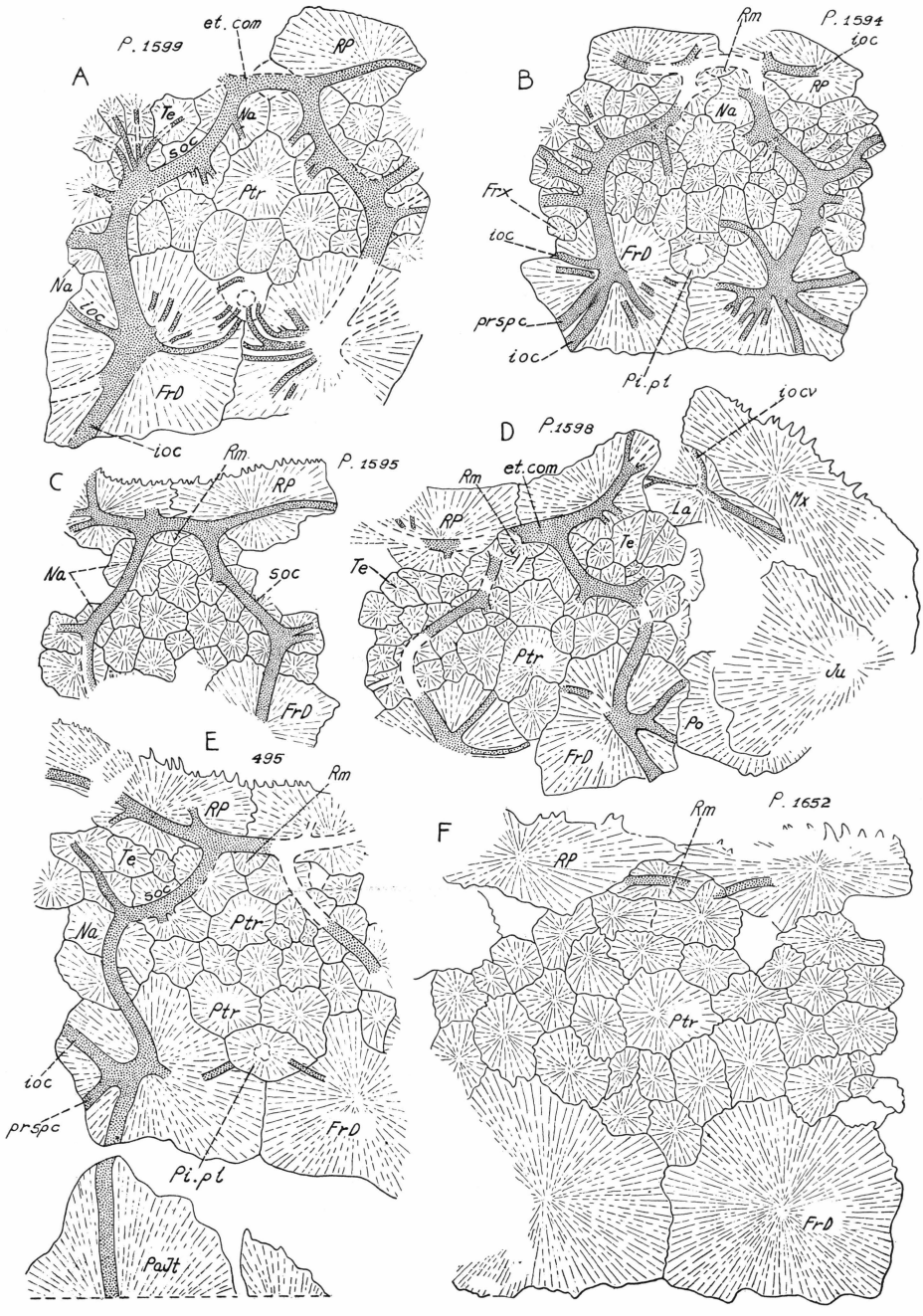


Fig. 35. *Holoptychius* sp. Diagrammatic representations of imperfect fronto-ethmoidal shields from Upper Upper Devonian (*Remigolepis* Series), East Greenland in ventral views. After specimens in pls. 28:1, 28:4, 27:3, 27:2, 28:2 and 27:4.

For explanation of index letters see fig. 36.

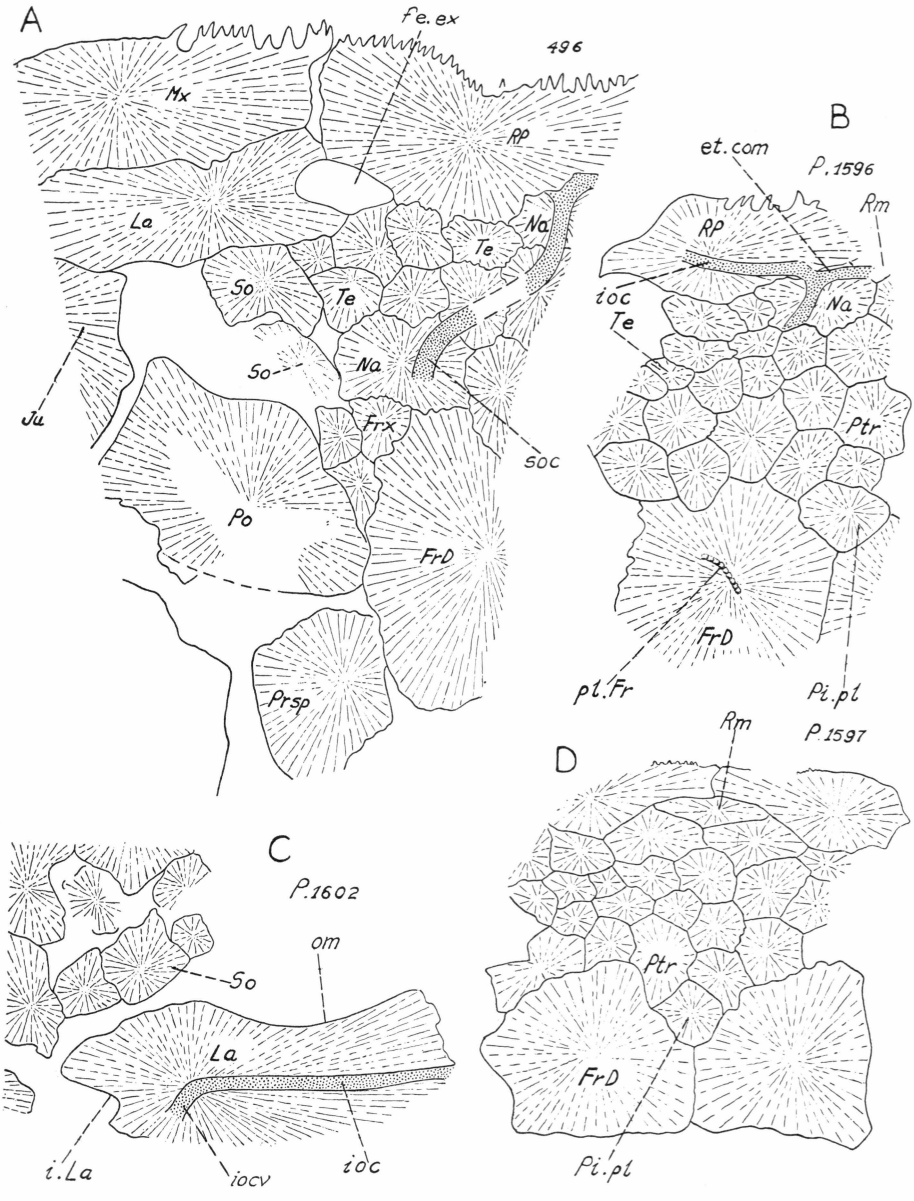


Fig. 36. *Holoptychius* sp. Diagrammatic representations of inner sides of, *A*, parts of skull-roof and external cheek-plate, *B*, *D*, imperfect fronto-ethmoidal shields and, *C*, lachrymal and part of fronto-ethmoidal shield. All from Upper Upper Devonian (*Remigolepis* Series), East Greenland. Same specimens as in pls. 24:1, 27:1, 29:5 and 28:3.

FrD, frontodermosphenotic; *Frx*, independent part of frontal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Prsp*, prespiracular plate; *Ptr*, postrostral; *Rm*, median rostral; *RP*, rostropremaxillary; *So*, supraorbital; *St*, supratemporal; *Te*, tectal.

et. com, ethmoidal commissural canal; *fe. ex*, fenestra exonarina communis; *i. La*,

elongated bone, the nariodal (*Nd*, figs. 6, 7 D, 62 C), which has a deep notch (*i. exa*) in its posterior margin and a somewhat shallower notch (*i. exp*) posteriorly and divides the fenestra exonarina communis into a fenestra exonarina anterior (*fe. exa*) for the anterior nostril and a fenestra exonarina posterior (*fe. exp*) for the posterior nostril. The nariodal hitherto has been encountered only in the excellent specimen of *Holoptychius* from Escuminac Bay but most probably it was developed also in *Holoptychius* from other localities although it has fallen out in the materials from Scotland and East Greenland. In *Porolepis* and *Glyptolepis* the fenestra exonarina anterior and posterior are situated very much as in *Holoptychius* but whether they are separated by a bone corresponding to the nariodal could not be ascertained on the basis of the available material. However, if present, which seems most likely (see figs. 8 B, 77 A, 79 C), it is firmly joined to the adjoining bones of the fronto-ethmoidal shield.

The supraorbito-tectal series in *Holoptychius* consists of a varying number of anterior tectals (*Te*, *Te. a*) one or two of which bound the fenestra exonarina communis dorsally and a series of bones in front of and dorsal to the orbital fenestra. The ventralmost of these latter bones which is situated in front of the orbital fenestra may be regarded as a posterior tectal (*Te. p*), the others which in the specimen from Escuminac Bay are three in number as supraorbitals (*So*). Between the latter laterally and the nasal series and the frontodermosphenotic medially there may be some small irregular bones (*Frx*). The nasal series consists generally of four or five elements (*Na*). The foremost nasal which meets the corresponding element of the other side in a median suture extends forwards close to the junction between the supraorbital and infraorbital canals and apparently no nasal element enters into the formation of the rostropremaxillary. The postrostrals (*Ptr*) vary as to number and size. Posteriorly they extend to the pineal plate, which they rarely do in osteolepiforms and contrary to conditions in that group there is a single pineal plate (*Pi. pl*) without pineal foramen. This plate is gently domed, its dorsal side rising slightly above the dorsal face of the surrounding part of the fronto-ethmoidal shield. On the ventral side of the bone there is a corresponding pit which as discussed above (p. 48) may be divided into lateral halves and contained the pineal and parapineal organs. The thin

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notch in lachrymal forming posterior part of fenestra exonarina posterior; *i. li*, depression probably for ligament; *ioc*, infraorbital sensory canal; *iocv*, ventrally curving part of infraorbital sensory canal; *od. Ju*, area of maxillary overlapped by jugal; *od. Po*, area overlapped by postorbital; *od. Prsp*, area overlapped by prespiracular plate; *pl. Fr*, frontal pit-line; *prspc*, prespiracular sensory canal; *soc*, supraorbital sensory canal.

roof of this pit is sometimes broken and the foramen thus formed at the tip of the plate may easily be mistaken for a pineal foramen.

In all porolepiforms known in this respect (*Porolepis*, *Glyptolepis*, *Holoptychius*, *Laccognathus*) the area of the fronto-ethmoidal shield corresponding to that which in osteolepiforms is occupied by two paired bones (frontal and dermosphenotic) shows a single paired bone, most conveniently termed frontodermosphenotic (see p. 150). Postero-laterally this bone (*FrD*) is generally produced backwards into a process, which most often is pointed. On the medial side of this process in *Glyptolepis groenlandica* BJERRING (1967, fig. 14B,C) has distinguished a small articular surface for the parieto-intertemporal, and medially to that lies the pocket (*i. li*) which probably was occupied by a ligament. A narrow depressed area overlapped by the parieto-intertemporal or occupied by connective tissue is sometimes found along the posterior margin of the frontodermosphenotic. Another broader and more distinct depressed area is found along the lateral margin of the posterior part of fronto-ethmoidal shield. This area is in its most posterior part (*od. Prspl*), on the lateral side of the posterior process of the frontodermosphenotic, generally overlapped by the prespiracular plate. Its anterior part (*od. Po*) which extends forwards to the margin (*om*) of the orbital fenestra is overlapped by the postorbital. This part of the area is generally long and narrow in particular in those forms (*Porolepis*, fig. 20A, *Glyptolepis?* cf. *paucidens*, fig. 40, pl. 14:1) in which the postorbital is long. In *Holoptychius* (figs. 20B, 37C) which has a short postorbital it is short and broad and in addition to the opening of the infraorbital sensory canal (*ioc*) it shows also the opening of the prespiracular canal (*prspc*). Antero-laterally, finally, the fronto-ethmoidal shield on each side of the notch (*i. exp*) forming the anterior part of the fenestra exonarina posterior shows more or less distinct depressed areas (*od. La*, *od. La + Mx*) overlapped by the lachrymal and maxillary.

The parietal shield (*Pa. sh*) besides in *Porolepis*, *Glyptolepis* and *Holoptychius* (figs. 3, 17A, 22, 24F,G, 37B,C, 38–45, 57, 58, 104C, 107C, pl. 2, pl. 4:1, pl. 5, pl. 6:1, 2, pl. 7:3, pl. 10:1, pl. 11:7, pls. 15, 16, pl. 17:1, pl. 19:1, pls. 20, 21, 24, pl. 29:1–3, pl. 31:1, pl. 33:6; JARVIK, 1948a, figs. 33, 34, 1950a, figs. 30, 31A,C,D, 36A) is well known also in *Laccognathus* (GROSS, 1936; JARVIK, 1950a, fig. 31B) and in an undetermined porolepiform from the Middle Devonian of East Greenland (see JARVIK, 1950a, pp. 103–108, fig. 34A, pl. 24:1). In all these forms it is on the whole similar in structure and consists of three paired bones, the parietointertemporal (*PaIt*), which probably includes equivalents to the intertemporal and the parietal of osteolepiforms (see pp. 144–150), the supratemporal (*St*) and the extratemporal (*Et*). In one specimen of *Holoptychius flemingii* the supratemporal is divided into two bones, anterior

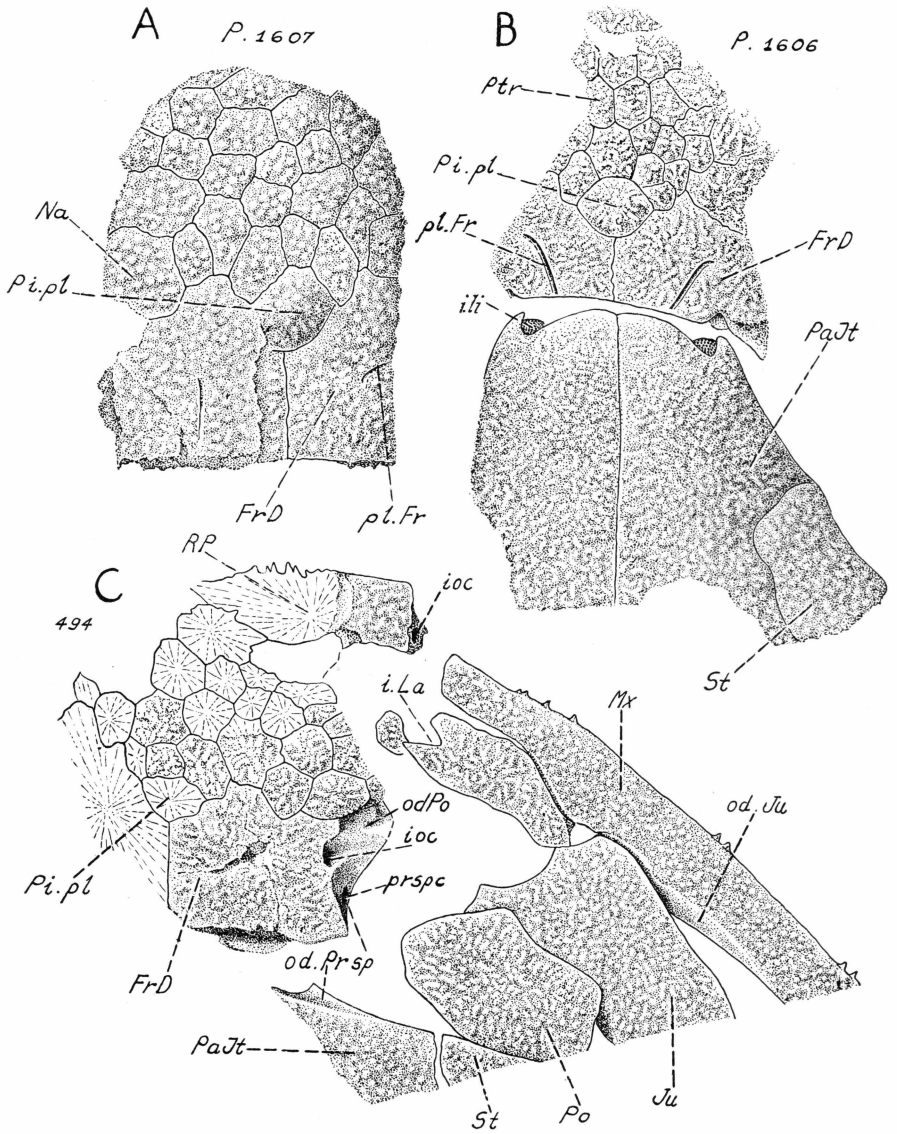


Fig. 37. *Holoptychius* sp. *A*, imperfect fronto-ethmoidal shield, *B*, imperfect fronto-ethmoidal and parietal shields and, *C*, imperfect fronto-ethmoidal shield with part of parietal shield and external cheek-plate in external views. All from Upper Upper Devonian (*Remigolepis* Series), East Greenland. Same specimens as in pl. 29:1–3. For explanation of index letters see fig. 36.

and posterior (fig. 107C; JARVIK, 1948a, figs. 33B, 34). In the anterior margin of the shield there is sometimes a paired depression (*i. li*) which presumably contained the posterior part of the ligament between the parietal and fronto-ethmoidal shields. The lateral margin of the parietal shield presents two notches, the prespiracular notch occupied by the

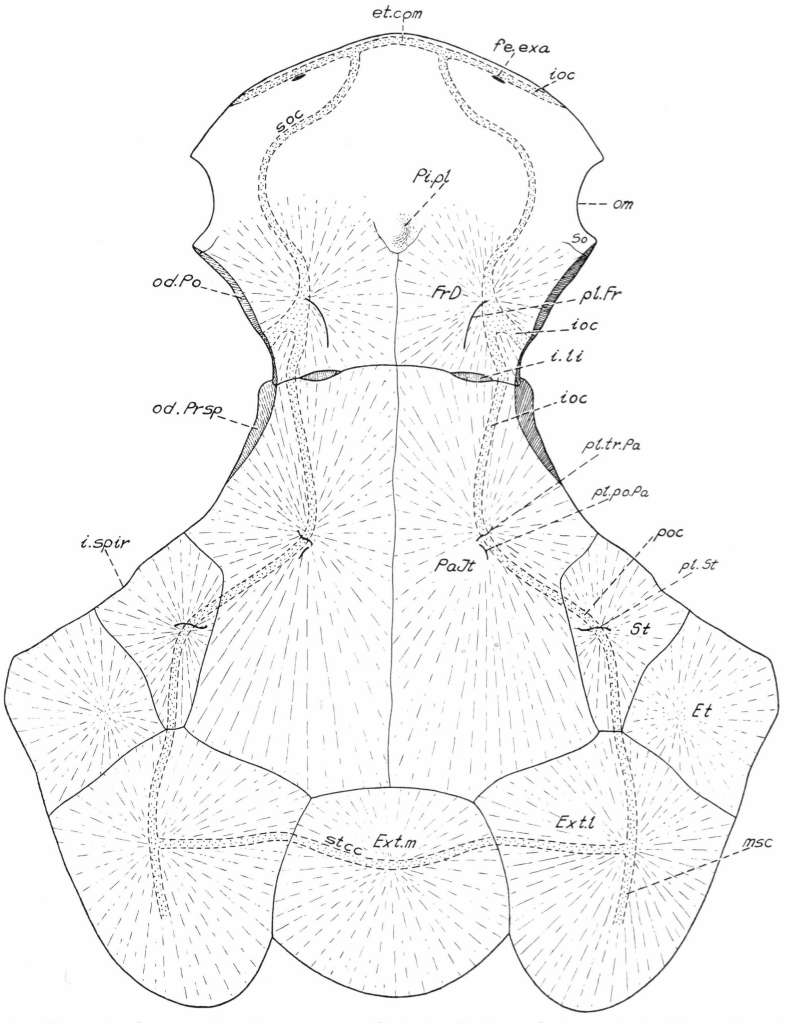


Fig. 38. *Glyptolepis groenlandica*, n. sp. Slightly flattened dermal skull-roof in dorsal aspect. Ornamentation omitted to show radiation and sensory canals. After grinding series and other specimens from the same block as sectioned specimen. × 2/1.

For explanation of index letters see fig. 39.

prespiracular plate, and the spiracular notch. The prespiracular notch along which there is a well developed overlapped area (*od. Prsp*) is large in *Porolepis* which has a large prespiracular plate and is in this genus bounded posteriorly by the supratemporal and sometimes even by the extratemporal (see JARVIK, 1950a, figs. 30, 31A). A very similar prespiracular notch is found also in the undetermined porolepiform from the Middle Devonian of East Greenland. The spiracular notch (*i. spir*) is generally represented by a shallow emargination in the lateral margin of

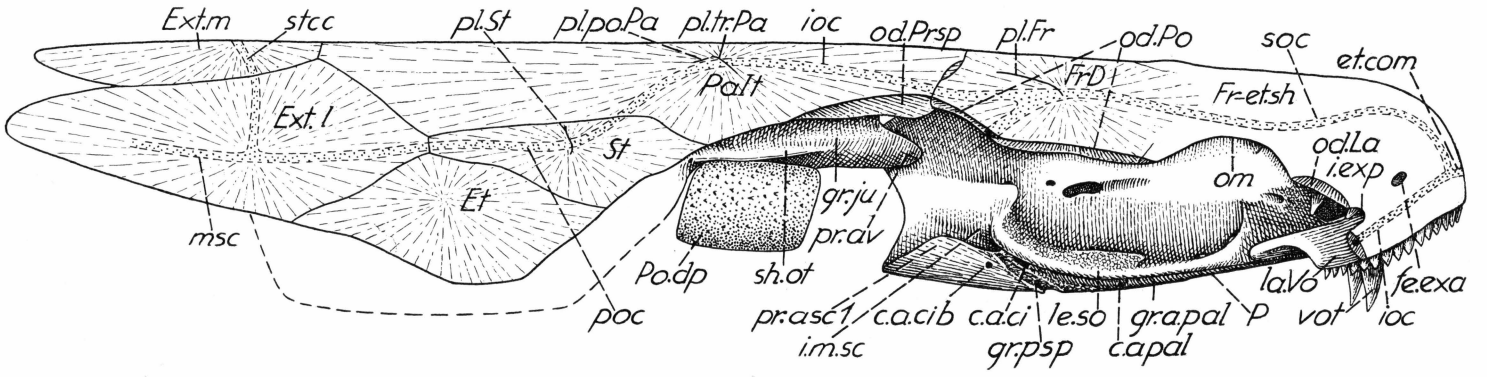


Fig. 39. *Glyptolepis groenlandica*, n. sp. Dermal skull-roof with sectioned part of neural endocranium and adjoining dermal bones of palate in lateral aspect. × 3/1.

Et, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *FrD*, frontodermosphenotic; *Fr-et. sh*, fronto-ethmoidal shield; *P*, parasphenoid; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Podp*, paraotic dental plate; *Prsp*, prespiracular plate; *So*, supraorbital; *Sq. u*, upper squamosal; *St*, supratemporal.

c. a. ci, canal for a. carotis interna; *c. a. cib*, canal for medial branch of a. carotis interna; *c. a. pal*, canal for a. palatina; *et. com*, ethmoidal commissural canal; *fe. exa*, fenestra exonarina anterior; *gr. a. pal*, groove in lateral margin of parasphenoid for a. palatina; *gr. ju*, groove for jugular vein; *gr. psp*, prespiracular groove; *i. exp*, notch in margin of fronto-ethmoidal shield for posterior external nasal tube; *i. li*, depression probably for ligament; *i. m. sc*, area of insertion of subcranial muscle; *ioc*, infraorbital sensory canal; *i. spir*, spiracular notch; *la. Vo*, vertical tooth-bearing lamina of vomer; *le. so*, suborbital ledge; *msc*, main sensory canal; *od. La*, area overlapped by lachrymal; *od. Po*, area overlapped by postorbital; *od. Prsp*, area overlapped by prespiracular plate; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. St*, supratemporal pit-line; *pl. tr. Pa*, transverse parietal pit-line; *poc*, postotic sensory canal; *pr. asc1*, processus ascendens anterior of parasphenoid; *pr. av*, antero-ventral articular process of otoccipital; *sh. ot*, otical shelf; *soc*, supraorbital sensory canal; *stcc*, supratemporal commissural canal; *vot*, vomerine tusk.

the supratemporal and the adjoining part of the extratemporal. In *Porolepis* it is sometimes found in the lateral margin of the extratemporal which in this genus may be long and narrow and extend far forwards.

The extrascapular series of bones is at first sight developed much as in osteolepiforms and consists of a paired lateral extrascapular (*Ext. l*) and a median extrascapular (*Ext. m*). As in that group the extrascapulars overlap depressed areas along the rear margin of the parietal shield but a peculiar difference is that the median extrascapular in porolepiforms which has a convex lateral margin overlaps the lateral extrascapulars (VOROBYEVA & LARSKAIA, 1968, fig. 2; see also *Laccognathus*, GROSS, 1936, fig. 4E,F), whereas in osteolepiforms it is overlapped by these bones.

External cheek-plate. – The external cheek-plate (*Porolepis* figs. 7, 43, pl. 2, pl. 4:1, pls. 5, 6, pl. 7:3, 4, pl. 11:3, pl. 33:3; JARVIK, 1950a, fig. 31A; *Glyptolepis* figs. 3, 7, 8, 16, 22, 31, 32, 40–42, 44, 55, 71, 92, pl. 15, 16, pl. 17:1, 2, pls. 19–21, pl. 22:1; JARVIK, 1950a, fig. 31C; cf. fig. 34B, pl. 24:2; *Holoptychius* figs. 4–7, 36, 37, 45, 46, 58, 107, pl. 24:1, 4, pl. 27:2, pl. 29:3, pl. 31:1, pl. 33:1, 2, 6; HOLMGREN & STENSIÖ, 1936, fig. 276B; WESTOLL, 1937a, fig. 1C; JARVIK, 1942, fig. 33, 1948a, figs. 33B, 34, 1950a, fig. 31D, 1960, fig. 17C, 1963a, figs. 4C, 10B, 11A) differs from that in osteolepiforms mainly in the structure of the lachrymal and the maxillary, the presence of a prespiracular plate and the presence of several squamosals. A remarkable fact is moreover the presence of a preoperculosubmandibular situated behind the palatoquadrate and therefore belonging to the operculogular apparatus rather than to the external cheek-plate.

The lachrymal (*La*) and the underlying anterior part of the maxillary (*Mx*) are thicker than are the corresponding bones in osteolepiforms. Judging from the serial sections of *Glyptolepis groenlandica* (figs. 8C, 32A1) the anterior end of the lachrymal rests in an endoskeletal groove formed by the lateral part of the postnasal wall and the adjoining ethmoidal articular process of the palatoquadrate which in that specimen has fused with the neural endocranium. The broad dorsal side of the lachrymal abuts against the thickened ventral margin of the frontoethmoidal shield. In front of the orbital fenestra the lachrymal slightly overlaps that shield but the overlapped area (*od. La*) is in *Glyptolepis* less distinct than in *Porolepis*. At the margin (*om*) of the orbital fenestra the lachrymal is thickened and forms a rather broad dorso-medially facing area (fig. 32A2–3) which is continued by similar areas along the anterior and dorsal margins of the orbital fenestra and which obviously supported the eyeball. Ventral to this part of the lachrymal there is a space between the lachrymal and the pars autopalatina of the palato-

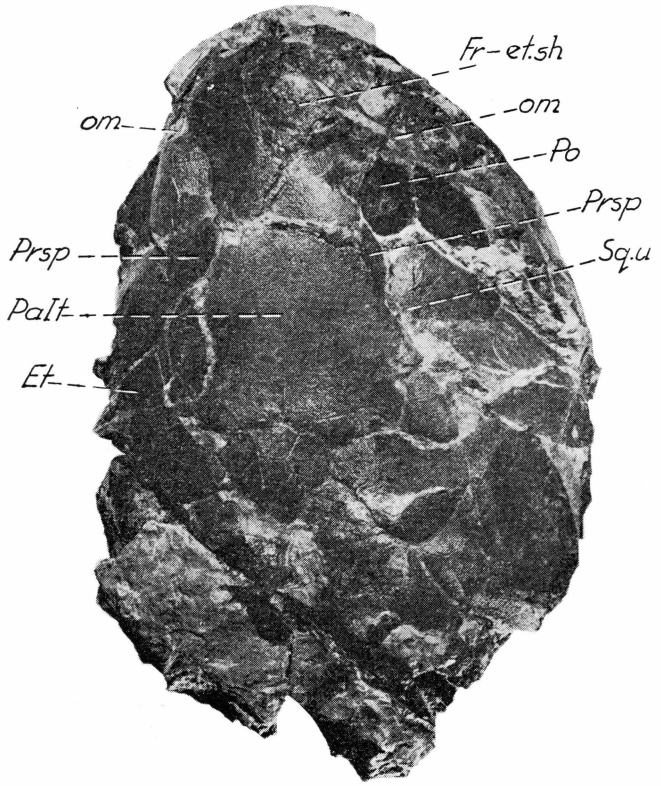


Fig. 40. *Glyptolepis?* cf. *paucidens*. Imperfect skull in dorsal view. Specimen No. RSM, Edinb. No. 1964.18. From THOMSON, 1966, pl. 1. For explanation of index letters see fig. 39.

quadrate. Because there are indications of narrow canals (*c. buct*, fig. 32A4) running from this space or from a groove (*gr. r. buc*) in some sections shown on the ventro-medial side of the lachrymal to the parts of the infraorbital canal enclosed in the lachrymal and the jugal it is likely that the r. buccalis lateralis passed forwards through the space giving off twigs to the infraorbital neuromasts. An important characteristic feature of the porolepiform lachrymal is moreover the presence of a distinct notch (*i. La*) at the anterior end of the bone. This notch which forms the posterior boundary of the fenestra exonarina posterior (*fe. exp*) has no equivalent in osteolepiforms in which the posterior external nasal tube had already been transformed into a nasolachrymal duct passing directly to the orbit through an opening (*f. enp*, figs. 39B1, 68B1, 2) in the postnasal wall. In *Glyptolepis groenlandica* but obviously not in other porolepiforms known in this respect a groove (*gr. La*, fig. 7B) for the external nasal tube leads upwards and backwards on the external side of the bone towards the orbital fenestra. Because of the thickness of the

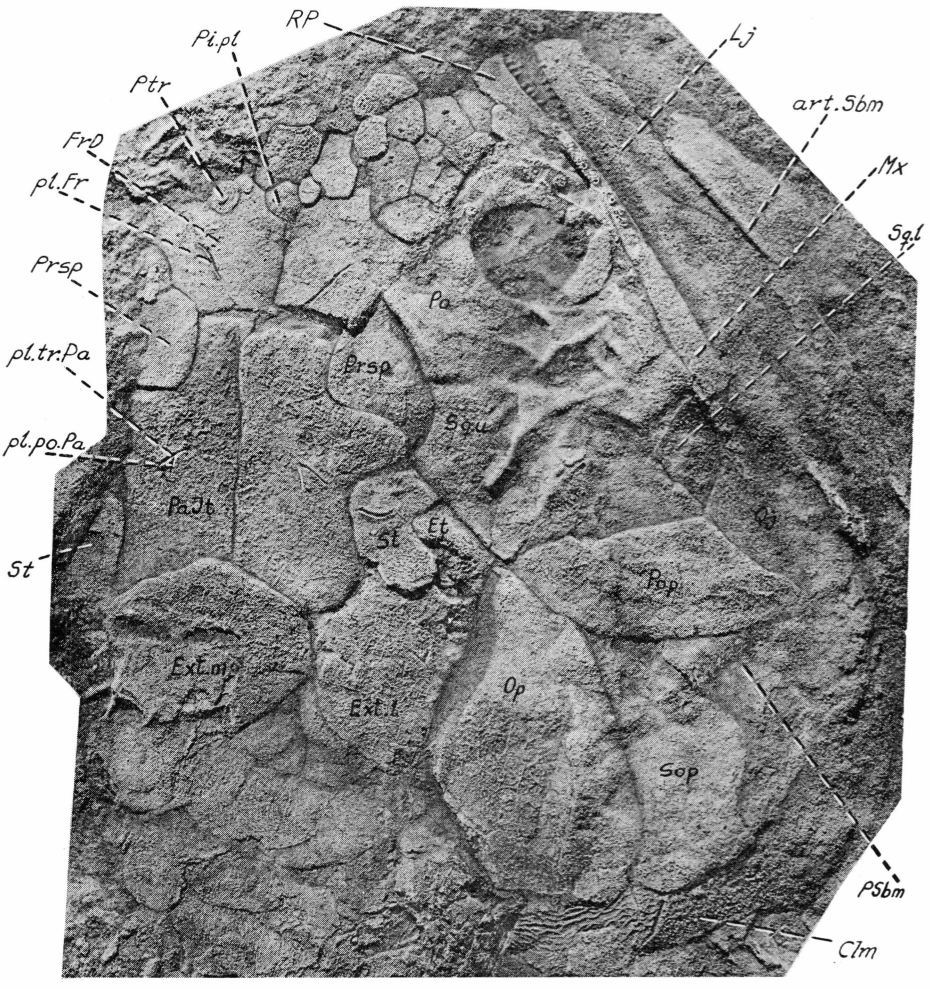


Fig. 41. *Glyptolepis leptopterus*. Flattened imperfect skull in dorsal aspect. Photograph of latex cast. Specimen No. P. 4120, Pal. Sect., Stockh. Lethen Bar, Scotland. Middle Devonian. × 2/1.

For explanation of index letters see fig. 45.

bone this groove anteriorly is deep (fig. 32A1). Ventrally the broad ventral margin of the lachrymal rests on and is intimately connected with the likewise broad dorsal side of the maxillary (*Mx*, figs. 32A1–4, 37C, pl. 33:1–3). There is thus no depressed area on the external side of the maxillary overlapped by the lachrymal and the area (*od. Ju*) overlapped by the jugal is narrow. The anterior dorsal process of the maxillary characteristic of osteolepiforms (see JARVIK, 1966, p. 77) has no equivalent in porolepiforms. But in porolepiforms there is a ridgelike palatal lamina (*Mxp*) on the inner side of the bone overlapped by the lateral parts of the horizontal plates of the dermopalatine and ectopterygoid.

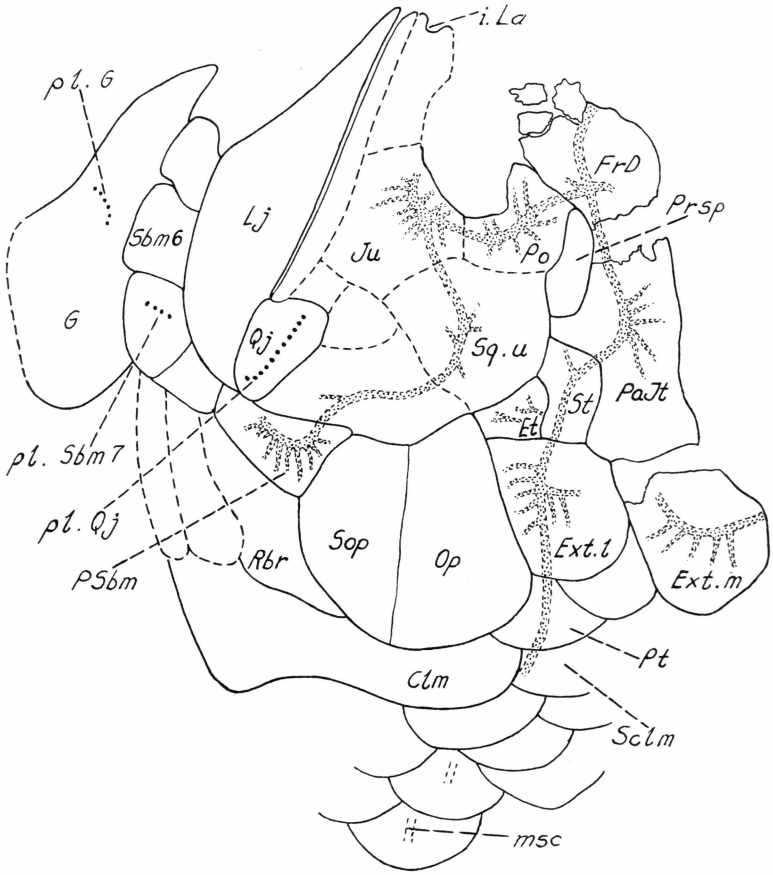


Fig. 42. *Glyptolepis leptopterus*. Sketch of flattened skull. Specimen No. 53406, Geol. Surv., Lond. Lethen Bar, Scotland. Middle Devonian. × 3/2.
For explanation of index letters see fig. 45.

Owing to the differences in proportions and in the position and size of the orbital fenestra (*fe. o*) the jugal (*Ju*) and in particular the postorbital are subject to considerable variations within the porolepiforms. In *Porolepis* the postorbital (*Po*) is large, and generally long and low, sometimes almost twice as long as high. In *Glyptolepis?* cf. *paucidens* and —judging from the length of the area (*od. Po*) of the fronto-ethmoidal shield overlapped by the bone—in one of the specimens of *G.* sp. from Scotland (pl. 14:3, 4), the bone is also rather long, whereas in *G. groenlandica* and *G. leptopterus* it is somewhat shorter and higher. A short and high postorbital is characteristic of *Holoptychius* in which the bone generally is higher than long. The prespiracular plate (*Prsp*) like the other dermal bones of the external cheek-plate is situated outside the palatoquadrate and it fills a space approximately corresponding to that

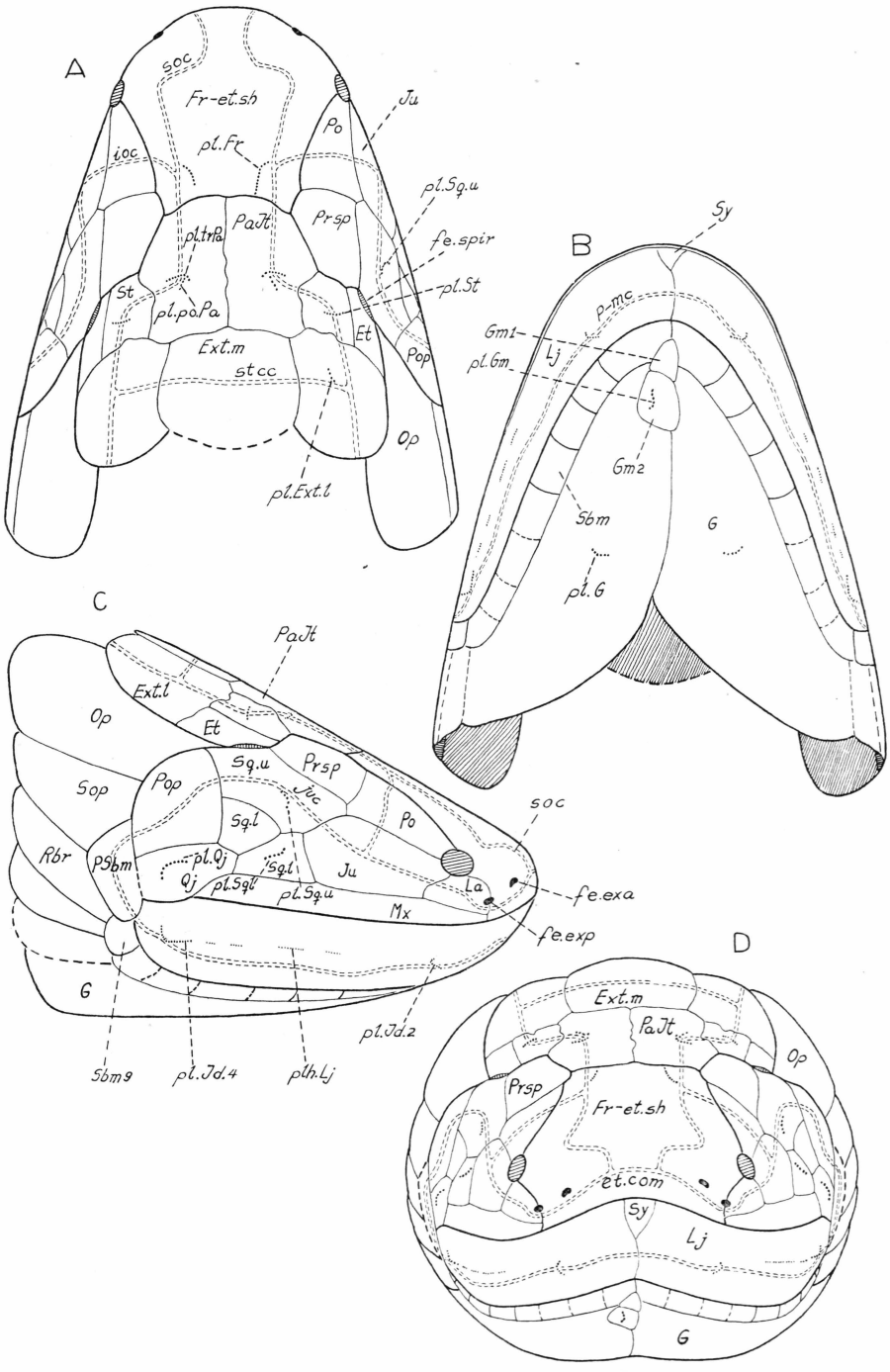


Fig. 43. *Porolepis brevis*. Restoration of skull in, *A*, dorsal, *B*, ventral, *C*, lateral and, *D*, anterior aspects.

For explanation of index letters see fig. 45.

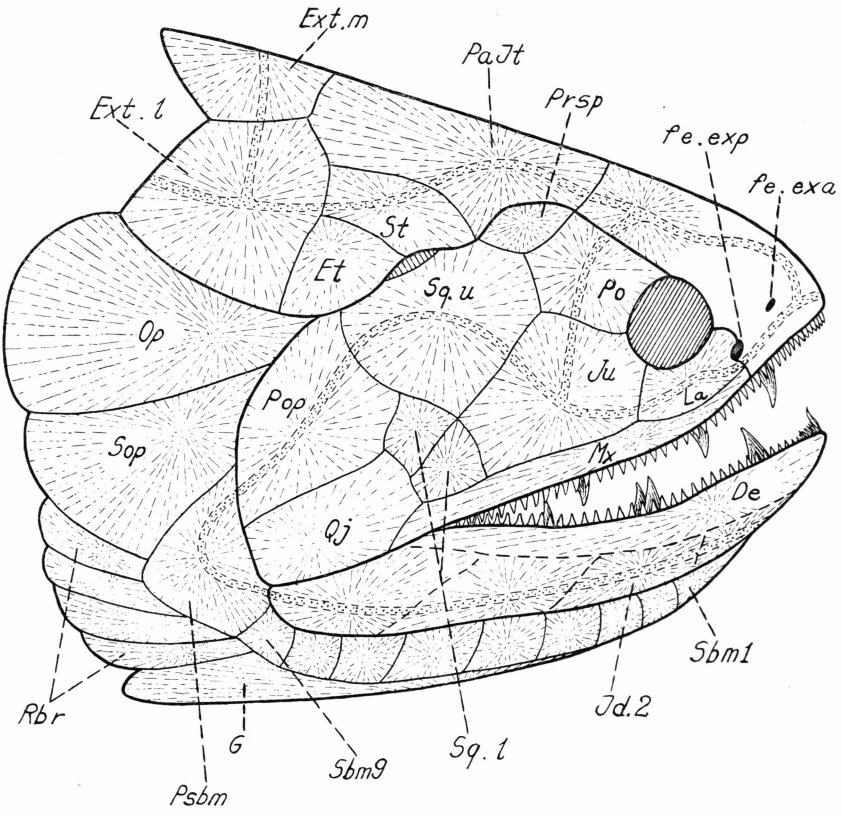


Fig. 44. *Glyptolepis groenlandica.* Restoration of skull in lateral aspect. Mainly after specimen shown in pl. 16. × 4/3.

For explanation of index letters see fig. 45.

which in *Eusthenopteron* is occupied by the posterior part of the postorbital (cf. JARVIK, 1948a, p. 88). It varies considerably, too, and is in *Porolepis* larger proportionately than in *Glyptolepis* and *Holoptychius.* More precisely its length in *Porolepis* amounts to ca 0.80, in *Glyptolepis ?* cf. *paucidens* to ca 0.60, in *G. leptopterus* to ca 0.55, in *G. groenlandica* to ca 0.40–0.45, and in *Holoptychius* to only about 0.30 of the length of the parietal shield. The prespiracular plate overlaps the parietointertemporal and it generally extends so far forwards so as to reach and overlap also the most posterior part of the lateral margin of the frontodermosphenotic.

A constant feature in osteolepiforms is the presence of a single large squamosal extending ventrally to the maxillary. In porolepiforms, on the other hand, the corresponding area is always occupied by a fairly large upper or principal squamosal (*Sq. u*) and a varying number of lower squamosals (*Sq. l*). The latter most often appear to be two in number. However, in one specimen of *Holoptychius* (fig. 46) an interesting varia-

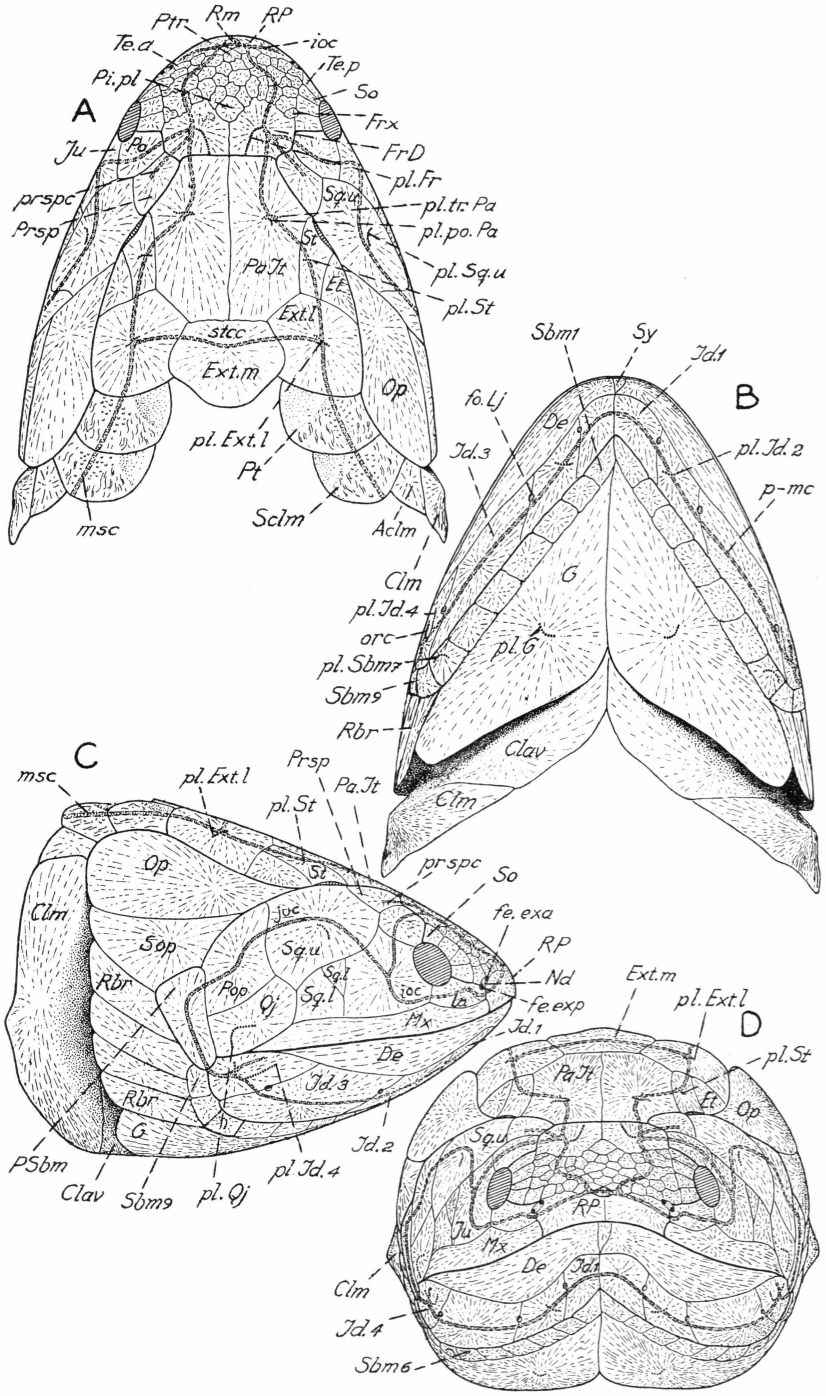


Fig. 45. *Holoptychius* sp. Restoration of skull in, *A*, dorsal, *B*, ventral, *C*, lateral and, *D*, anterior aspects.

Aclm, anocleithrum; *Clav*, clavicle; *Clm*, cleithrum; *De*, dentary; *Et*, extra-

tion is found. In this specimen there is a fairly large lower squamosal between the ventral parts of the upper squamosal and the preopercular and below that element there is a row of four square-shaped bones (*Sq. l 1*, *Sq. l 4*), each carrying a portion of the squamosal pit-line.

Behind the upper squamosal follows a large bone also pierced by the sensory canal of the cheek. This bone (*Pop*) has hitherto generally been regarded as a squamosal element (JARVIK, 1948a, figs. 33, 34, 1950a, fig. 31, 1963a, fig. 4C, *Sq2*) but as pointed out previously (1963a, p. 13) it is situated much as the preopercular in osteolepiforms and although not strictly homologous with that there is no reason why it should not be termed preopercular. Like the osteolepiform preopercular it ventrally overlaps the quadratojugal (*Qj*) but whereas the preopercular canal (*p-mc*) in osteolepiforms passed to the lower jaw in the soft tissues inside the posterior part of the quadratojugal or close behind that bone it in porolepiforms pierces a separate bone situated behind the quadratojugal and the lower jaw and because of its relations to the preoperculomandibular sensory canal hitherto generally regarded as the preopercular (JARVIK, 1963a, figs. 4C, 5B, *Pop*). However, this bone (*Psbm*) lies wholly behind the palatoquadrate (pl. 16:2), outside the triangular space occupied by the symplectic (*Sym*, pl. 19:2, see also fig. 92A). Moreover it forms a direct dorsal continuation of the submandibular series of bones

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temporal; *Ext.l*, *Ext.m*, lateral and median extrascapulars; *FrD*, frontodermosphenotic; *Fr-et.sh*, fronto-ethmoidal shield; *Frx*, additional frontal; *G*, principal gular plate; *Gm1*, *Gm2*, anterior and posterior median gular plates; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentaries 1, 2, 3, and 4; *Ju*, jugal; *La*, lachrymal; *Lj*, lower jaw; *Mx*, maxillary; *Nd*, nariodal; *Op*, opercular; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Pt*, posttemporal; *Ptr*, postrostral; *Qj*, quadratojugal; *Rbr*, branchiostegal ray; *Rm*, median rostral; *RP*, rostropremaxillary; *Sbm*, *Sbm1*, *Sbm6*, *Sbm9*, submandibulars; *Sclm*, supracleithrum; *So*, supraorbital; *Sop*, subopercular; *Sq. l*, *Sq. l1*, *Sq. l4*, lower squamosals; *Sq. u*, upper squamosal; *St*, supratemporal; *Sy*, symphysial dermal bone; *Te. a*, *Te. p*, anterior and posterior tectals.

art. Sbm, medial articular ridge of submandibular; *et. com*, ethmoidal commissural canal; *fe. exa*, fenestra exonarina anterior; *fe. exp*, fenestra exonarina posterior; *fe. spir*, spiracular fenestra; *fo. Lj*, foramen of lower jaw; *i. La*, notch in anterior margin of lachrymal forming part of fenestra exonarina posterior; *ioc*, infraorbital sensory canal; *juc*, jugal sensory canal; *msc*, main sensory canal; *od. Mx*, *od. Pop*, areas of quadratojugal overlapped by maxillary and preopercular; *orc*, oral sensory canal; *pl. Ext. l*, pit-line of lateral extrascapular; *pl. Fr*, frontal pit-line; *pl. G*, *pl. Gm*, pit-lines of principal and median gular plates; *plh. Lj*, horizontal pit-line of lower jaw; *pl. Id.2*, *pl. Id.4*, pit-lines of infradentaries 2 and 4; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. Qj*, quadratojugal pit-line; *pl. Sbm7*, pit-line of submandibular 7; *pl. Sq. l*, *pl. Sq. u*, pit-lines of lower and upper squamosals; *pl. tr. Pa*, transverse parietal pit-line; *p-mc*, preoperculo-mandibular sensory canal; *prspc*, prespiracular sensory canal; *soc*, supraorbital sensory canal; *stcc*, supratemporal commissural canal.

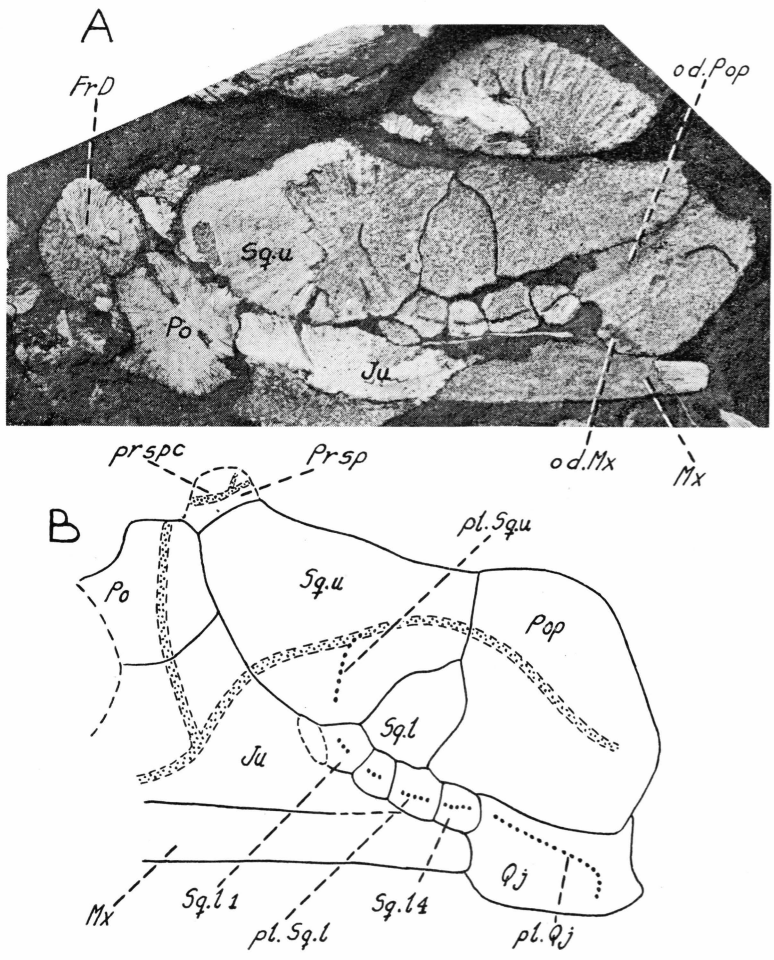


Fig. 46. *Holoptychius* sp. Photograph and restoration of main part of external cheek-plate. Specimen No. P. 1592, Min. Mus., Copenh. Coll. 1954. Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 5/4.
For explanation of index letters see fig. 45.

and because of these conditions I have suggested (1963a, p. 13) that it is a complex structure composed of submandibulars which have fused with each other and with lateral sensory components (see JARVIK, 1967b, p. 191) developed in relation to the portion of the sensory canal piercing the bone. Because these sensory canal components obviously, at least partly, belong to a portion of the preoperculo-mandibular canal the equivalent of which in osteolepiforms runs in soft tissue in the region of the posterior part of the quadratojugal these components are to be regarded as preopercular components. The bone in porolepiforms which

hitherto has been termed preopercular and which has no equivalent in osteolepiforms may therefore be termed preoperculosubmandibular (*Psbm*).

Lower jaw. – As to the external dermal bones of the lower jaw and the structure of the lower jaw as a whole porolepiforms (*Porolepis*, fig. 43, pl. 4:2, pl. 6:1, 3, pl. 7:3, 4, pl. 12:1–5; Gross, 1941; Jarvik, 1950a, fig. 27A; *Heimenia*, pl. 12:6; *Laccognathus*, Gross, 1941; *Glyptolepis*, figs. 8, 16, 22, 44, 55, 71, 76, pl. 16–18, pl. 19:2, pl. 22:1, 6, pl. 23:1, 2, pl. 32:5; Gross, 1941; Jarvik, 1949, fig. 9C, D, 1950a, fig. 27B, 1962, fig. 2, 1963a, figs. 13, 14, 1965a, fig. 5B; *Holoptychius*, figs. 45, 47, 102, 107, pl. 30:1–3, pl. 31, pl. 32:1–4; Westoll, 1937a; Gross, 1941; Jarvik, 1948a, figs. 33B, 34, 1963a, figs. 4C, D, 11A, B, 1967a, fig. 8A, D) agree well with osteolepiforms. As described above the meckelian bone, the coronoids and the prearticular are similar in the two groups and in both the external side is covered by a strong dentary (*De*) and below that a row of four infradentaries (*Id.1*, *Id.2*, *Id.3*, *Id.4*) pierced by the preoperculo-mandibular sensory canal (*p-mc*). The sutures have, when discernible, a similar course and between the two jaws there are one or more small symphysial bones (*Sy*). The outside of the lower jaw in *Laccognathus* shows three large pits of unknown importance. As pointed out above (p. 19) such pits (*fo. Lj*) are present also in *Holoptychius* but have hitherto been observed only in material from East Greenland. In this genus, too, they are three in number but they are usually much smaller than in *Laccognathus* and are situated one in each of the sutures between the infradentaries and well below the suture between these bones and the dentary. In one large specimen (No. P.1653, Min. Mus., Copenh.) which comes from the *Phyllolepis* series they are somewhat larger approaching the size in *Laccognathus*. No such pits have been found in *Porolepis*, *Heimenia* and *Glyptolepis* and in osteolepiforms they are unknown.

Parasymphysial dental plates. – As recently has been established another common feature of porolepiforms and osteolepiforms is the presence of independent paired tooth-bearing elements in the area of the symphysis, a feature which, however, is shared with other groups, e.g. with struniiforms and brachiopterygians. These elements, although specialised in different ways in the various groups, will be referred to under the common name parasymphysial dental plates. The reason why they are treated here is that they generally are carried by the anterior part of the dentary which has become more or less modified for this purpose.

The peculiar parasymphysial dental plates of struniiforms which for a long time puzzled scientists and were confused first with the tooth-whorls of acanthodians (see Gross, 1956, 1957; Ørvig, 1957, p. 397) and later with the parasymphysial dental plates of porolepiforms (Jarvik,

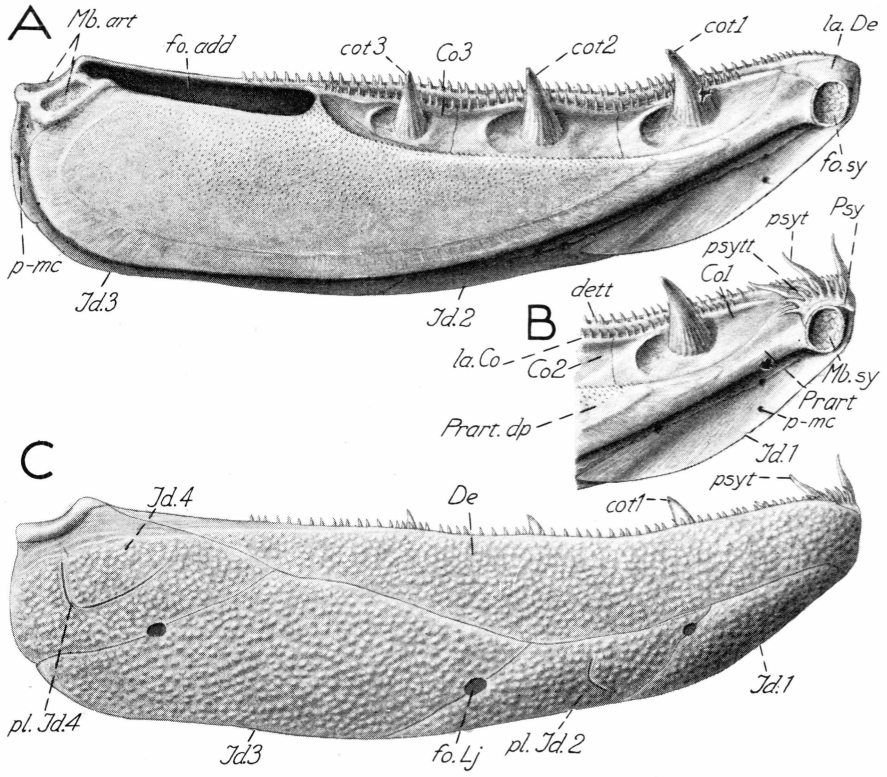


Fig. 47. *Holoptychius* sp. Restorations of lower jaw in, *A*, medial, *C*, lateral and *D*, dorsal aspects. *B*, *E*, anterior part with parasymphysial plate in medial and dorsal aspects. After specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland (see pls. 26, 30–32).

Co1, *Co2*, *Co3*, coronoids 1, 2 and 3; *De*, dentary; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentaries 1–4; *Mb. art*, articular area of meckelian bone; *Mb. sy*, anterior part of meckelian bone exposed in symphysial pit; *Prart*, prearticular; *Prart. dp*, prearticular dental plate; *Psy*, parasymphysial dental plate.

cot1, *cot2*, *cot3*, coronoid tusks; *de. tl*, toothless anterior part of dorsal margin of dentary; *dett*, teeth of dentary; *fo. add*, adductor fossa; *fo. Lj*, foramina in sutures between infradentaries; *fo. sy*, symphysial pit; *la. Co*, tooth-bearing lamina of coronoid; *la. De*, antero-medial lamina of dentary carrying parasymphysial dental plate; *pl. Id.2*, *pl. Id.4*, pit-lines of infradentaries 2 and 4; *p-mc*, preoperculo-mandibular sensory canal; *psyt*, tusks of parasymphysial dental plates; *psytt*, rows of small parasymphysial teeth.

1961, p. 202; the tooth-plate from East Greenland described by STENSIÖ as *Onychodus* certainly belongs to that genus and not to *Holoptychius* as I claimed in 1961) have been described in detail by JESSEN (1966a, 1966b, 1967), who also considered the peculiar modifications of the anterior part of the lower jaw in that group. The parasymphysial dental plates of brachiopterygians are the small toothed plates at the anterior end of the

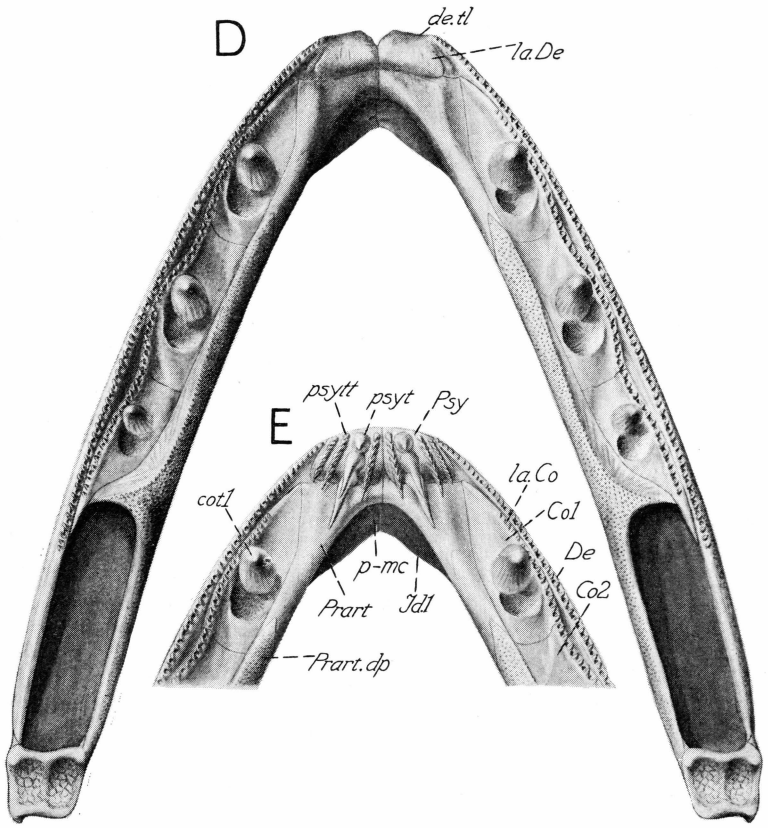


Fig. 47 D–E.

lower jaw in *Polypterus* previously regarded as coronoids (Holmgren & Stensiö, 1936, p. 327; de Beer, 1937, p. 87; Jarvik, 1947, fig. 5F).

In osteolepiforms (figs. 49, 50A, B) the paired parasymphysial dental plates are represented by the "predentary" of Vorobyeva (1962) and the adsymphysial dental plates described more recently by Jessen (1966b). In this group the tooth-bearing margin of the dentary which anteriorly bends medially to meet the corresponding margin of the other side is equipped with teeth also in this anterior almost transverse part (*dets*) and usually some of the teeth of this part are somewhat enlarged. Behind and postero-medially to this tooth-bearing part the dentary is provided with a thin lamina, the antero-medial lamina (*la. De*), which extends medially to the symphysis and forms the roof of the symphysial pit. At the postero-medial corner of that lamina, which in certain forms (*Panderichthys*, *Eusthenodon*; see also Jarvik, 1966, p. 57) carries one or two tusks (*det*) sometimes together with smaller teeth, Vorobyeva (1962) discovered a small dental plate termed "predentary". This plate, the parasymphysial dental plate (*Psyv*, fig. 49E), was found in several rhizo-

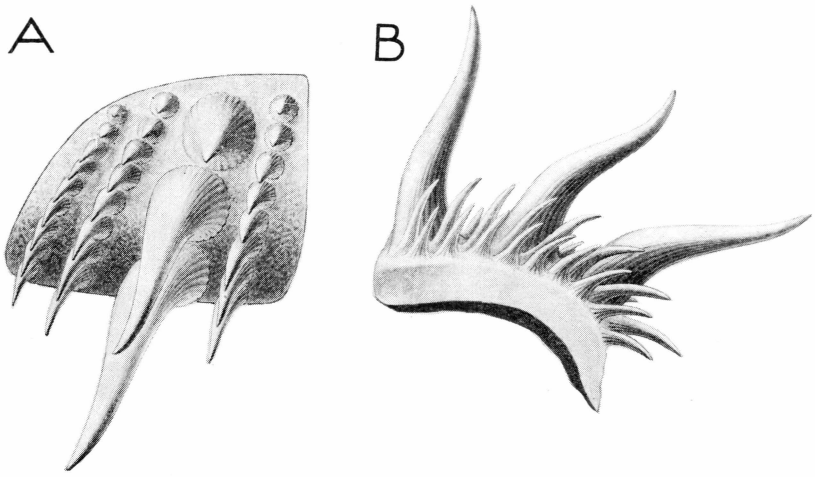


Fig. 48. *Holoptychius* sp. Parasymphysial dental plate in, *A*, dorsal and, *B*, medial aspects. Mainly after specimens shown in pl. 26.

dontids from the Sovjet Union (*Eusthenopteron saevesoederberghi*, *Eusthenopteron wenjukowi*, *Platycephalichthys bischoffi*, *Panderichthys rhombolepis*, VOROBYEVA, 1962, figs. 19, 30, pl. 1:3, pl. 5:1, pl. 6:1, pl. 9:1) but has hitherto not been observed in rhizodontids from other areas. In *Eusthenopteron wenjukowi* (fig. 49D) the parasymphysial plate was most likely carried by the small shelf of the dentary described in 1937 (p. 111, fig. 17C, *sh*) and the adjoining parts of the meckelian bone (*Mb*) and the prearticular (see 1937, fig. 17B, *ar*). However, in *E. foordi* (fig. 49B, C) from Escuminac Bay there is a distinct but small depressed area (*od. Psyo*) which extends from the postero-medial corner of the antero-medial lamina of the dentary over the meckelian bone, which usually is exposed in a narrow area between the antero-medial lamina and the prearticular, to the anterior end of the latter bone. This area no doubt is the area of attachment of the parasymphysial dental plate and because a similar area appears to be present also in *Eusthenodon* (fig. 49A) from East Greenland it seems likely that parasymphysial dental plates similar to those described by VOROBYEVA are present in Devonian rhizodontids in general (*Psyo*, fig. 50B).

In osteolepids the parasymphysial dental plate (*Psyo*) is obviously represented by the adsymphysial plate recently recorded by JESSEN (1966b, pp. 331–334, 382–383) in a number of forms (*Litoptychus bryanti*, *Gyroptychius milleri*, *Latvius grewingki*, *Megalichthys nitidus*) and described in detail in an undetermined osteolepid from Belgium (fig. 50A). Of great interest is that the plate in this form postero-laterally is continuous with coronoid 1 and as suggested by JESSEN it almost certainly is an anterior derivative of the coronoid series. That this is so is sup-

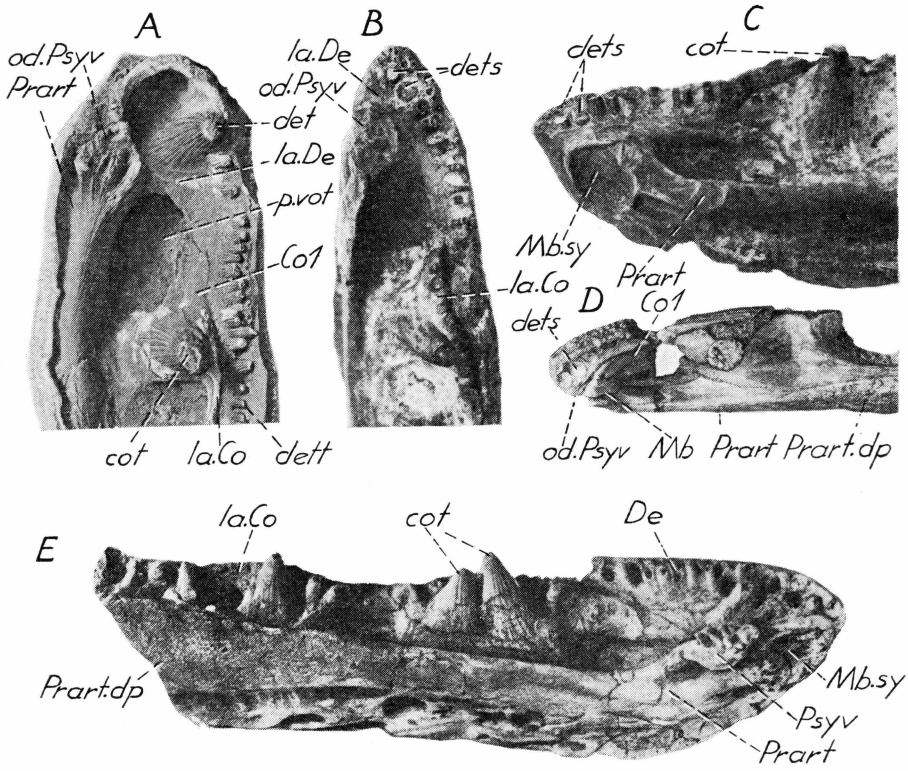


Fig. 49. Anterior part of lower jaw in rhizodontid osteolepiforms to show parasymphysial dental plate and its area of attachment. *A*, *Eusthenodon waengsjoei*. Dorsal aspect. Photograph of latex cast. Specimen No. P. 1649, Min. Mus., Copenh. Coll. 1949. 1174 m Sederholms Bjerg, Gauss Halvø, East Greenland, Upper Upper Devonian (*Remigolepis* Series). × 1/1. *B*, *C*, *Eusthenopteron foordi*. Dorsal and medial aspects. Specimen No. P. 35, Pal. Sect., Stockh. Escuminac Bay, Canada, Lowermost Upper Devonian. × 8/3. *D*, *Eusthenopteron wenjukowi*. Dorsal aspect. From JARVIK, 1937, fig. 17 C. × 4/3. *E*, *Panderichthys rhombolepis*. Medial aspect. From VOROBYEVA, 1962, pl. 18:3.

For explanation of index letters see fig. 50.

ported by the fact, also mentioned by JESSEN, that the coronoid series in paleoniscids (NIELSEN, 1942, figs. 38–40; LEHMAN, 1952, fig. 37) is formed by dental plates with a shagreen of small denticles which in a similar way extend to the symphysis, and by the conditions in coelacanthiforms and brachiopterygians. Another important fact is that the antero-medial part of the parasymphysial plate in the undetermined osteolepid is much broader than its postero-lateral part. As is readily seen this broad antero-medial part is situated as and no doubt corresponds to the parasymphysial plate in the rhizodontids. The main difference between rhizodontids and osteolepids with respect to the para-

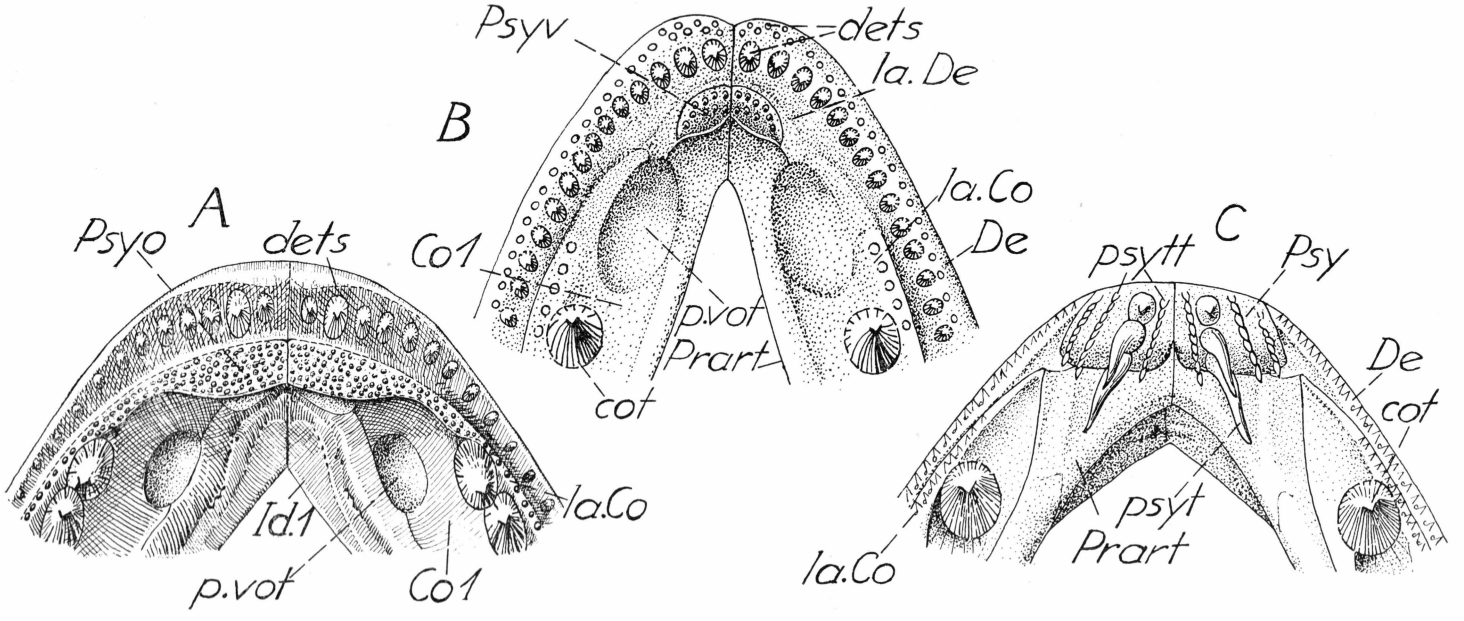


Fig. 50. Restorations of anterior parts of lower jaws with parasymphysial dental plates in osteolepiforms and porolepiforms. *A*, undetermined osteolepid. From JESSEN, 1966b, fig. 5B. *B*, rhizodontid, *Eusthenopteron foordi*. Parasymphysial dental plate after *Panderichthys* (fig. 49E). *C*, porolepiform, *Holoptychius* sp. (cf. fig. 47).

Co1, coronoid 1; *De*, dentary; *Id.1*, infradentary 1; *Mb*, meckelian bone; *Mb. sy*, anterior end of meckelian bone exposed in symphysial pit; *Prart*, prearticular; *Prart. dp*, prearticular dental plate; *Psy*, parasymphysial dental plate of porolepiforms; *Psyo*, parasymphysial dental plate of osteolepids (adsymphysial dental plate, JESSEN, 1966b); *Psyv*, vestigial parasymphysial dental plate of rhizodontids ("predentary", VOROBYEVA, 1962).

cot, coronoid tusk; *det*, tusk of anterior part of dentary; *dets*, parasymphysial teeth of dentary; *dett*, teeth of dentary; *la. Co*, vertical tooth-bearing lamina of coronoid; *la. De*, antero-medial lamina of dentary; *od. Psyv*, area for attachment of vestigial parasymphysial dental plate in rhizodontids; *psyt*, tusks of parasymphysial dental plate; *psytt*, rows of smaller teeth of parasymphysial dental plate; *p. vot*, pit receiving tip of tusk of vomer.

symphysial plate is accordingly only that the antero-medial part of the original plate of the osteolepids has been retained in the rhizodontids, whereas the narrow postero-lateral part which is continuous with coronoid 1 has been reduced.

In porolepiforms, too, the dentary anteriorly has an antero-medial lamina (*la. De*) which extends to the symphysis and forms the roof of the symphysial pit. But in them (figs. 47, 50C, pl. 12:1–4, pl. 32) the transverse part of the dorsal margin of the dentary lacks teeth (*de. tl*), it is slightly depressed and usually in level with the antero-medial lamina which is also devoid of teeth. It is this tooth-less almost square area of the dentary, the parasymphysial area, that carries the parasymphysial dental plate. The antero-medial lamina which forms the main part of this area is modified for its special purpose. It is strongly arched and as seen in medial view it has a concave ventral face and a correspondingly convex dorsal face. On the latter face, which anteriorly is directed upwards and posteriorly almost straight backwards, there are some irregular but on the whole longitudinal grooves and ridges for the attachment of the dental plate. Behind the more or less transverse posterior margin there is a slight depression on the dorsal face of the expanded anterior part of the prearticular. This depression is situated below the hindmost parasymphysial tusk and is probably developed to receive the tip of that tusk.

This description of the parasymphysial area is based mainly on material of *Holoptychius* from East Greenland and of *Glyptolepis* from the Baltic area and although there is some variation (cf. Gross, 1941, figs. 2, 6) the conditions in other holoptychiids appear to be much the same (as regards *Laccognathus* see Gross, 1941, p. 25, figs. 7–9). A similar parasymphysial area is found also in *Porolepis* (pl. 7:3, pl. 12:1–4; Gross, 1941, fig. 23A). However, in that genus the more or less depressed tooth-less anterior part (*de. tl*) of the dorsal margin of the dentary rises a little above the level of the antero-medial lamina which is rather long and narrow extending backwards behind the symphysial pit. Along the medial margin of the postero-medial lamina there is in one specimen (pl. 12:3, 3) an arched bone-fragment (*Psy*) which probably is a broken part of the parasymphysial plate.

The parasymphysial dental plate (*Psy*) is well shown in two specimens of *Holoptychius* from East Greenland (figs. 47, 48). In one of these specimens (No. 496, pl. 26:1–3) both plates are found almost in their natural position whereas in the other specimen (No. P.1605, pl. 26:4, 5), a detached plate is found among other cranial remains. The plate is a foursided, almost square, thick, arched bone with anterior, posterior, lateral and medial margins and a ventral concave and a dorsal convex face. The ventral face shows grooves and ridges corresponding to those

on the dorsal face of the parasymphysial area. When the plate is in its natural position the anterior slightly convex margin runs along the anterior margin of the parasymphysial area and is apparently situated but slightly inside the ornamented external face of the most anterior part of the dentary. The anterior margin of the plate accordingly forms a continuation of the tooth-bearing part of the dorsal margin of the dentary. The lateral margin has a nearly longitudinal position and it diverges posteriorly from the tooth-bearing margin of the dentary. If the plate medially meets the corresponding plate of the other side as shown in the restoration remains uncertain.

The teeth of the parasymphysial plate in specimen No. 496 are arranged in four longitudinal rows, one row of tusks (*psyt*) approaching the vomer tusks in size, and one medial and two lateral rows of smaller teeth (*psytt*) in size comparable to the teeth of the dentary. The small teeth are rather slender, about 3–4 mm long, and bent slightly backwards and there are about eight such teeth in each row. The tusks, well shown also in No. P.1605, are in both specimens three in number, faintly striated, slender and slightly sigmoid in shape. In No. 496 they measure about 10–11 mm in length and are shorter and more slender than the anterior coronoid tusk (*cot 1*) and the vomer tusk (*vot*) which in the same specimen (pl. 26:1–3; see also pl. 31:1) measure 18 and 14 mm respectively.

The parasymphysial dental plates in the sectioned and other specimens of *Glyptolepis groenlandica* (figs. 8A–C, 76B, 78A) appear to be similar to those in *Holoptychius* described above and it may be mentioned that parasymphysial tusks are discernible at the anterior end of the jaw in some of the casts of *Glyptolepis leptopterus*. Detached parasymphysial dental plates from the Baltic area have been described by BYSTROW (1939, fig. 9, "*Hamodus*") and GROSS (1957, pl. 6:1, 2; see also JESSEN, 1966b, fig. 14C, D). These plates which are incomplete show the bases of three tusks and one or two medial and three lateral rows of smaller teeth. A still greater number of rows of small teeth is found in a detached parasymphysial dental plate from the Lower Devonian of Spitsbergen. This plate (pl. 26:6; JESSEN, 1967, pl. 3D) which may be referred to *Porolepis* shows two medial and no less than five lateral rows of small teeth together with a row of tusks.

Submandibular and operculogular series. – As explained in a previous paper (1963a) the gill-cover or operculogular membrane in fishes is composed of two originally separate gill-covers, the mandibular and the hyoidean (fig. 5). Both these gill-covers can be traced in tetrapods and remarkable is that the musculature of the mandibular gill-cover has been retained with surprisingly small changes up to man. In fishes each of these gill-covers is supported by a special series of raylike dermal bones:

the submandibular series in the mandibular, and the operculogular series in the hyoidean gill-cover. The latter series, composed of branchiostegal rays which have retained their independence or have fused into opercular and gular bones, is generally well developed, whereas the submandibular series often is more or less vestigial. In elasmobranchiomorphs the conditions are obscure but elements which possibly belong to the submandibular series have been described by STENSIÖ in *Bothriolepis* (see JARVIK, 1963a, p. 13, fig. 12B; see also STENSIÖ, 1969, p. 417, figs. 135A, 165, *Sb*) and as recently suggested by JESSEN (1968b) the gular plates in certain actinopterygians (*Amia*, *Elops*) and perhaps also the anterior part of the principal gular plate in brachiopterygians may include submandibular elements. A submandibular series has also been recognised in early dipnoans (JARVIK, 1967a, fig. 5, 1968a, pp. 228–229) but it is in osteolepiforms and in particular in porolepiforms that this series is best developed and the most primitive conditions are retained.

The submandibular series (*Sbm*) in porolepiforms (*Porolepis*, fig. 43, pl. 6:1, 3; JARVIK, 1950a, fig. 27A; *Glyptolepis*, figs. 16, 22, 42, 44, 55, 71A, pl. 16, pl. 23:1, 2; JAEKEL, 1927, fig. 86; JARVIK, 1950a, fig. 27B, 1963a, fig. 14B, 1966, fig. 1; *Holoptychius*, figs. 5, 45, 58, 107C, pl. 30:1; HUSSAKOF & BRYANT, 1918, fig. 58; BRYANT, 1919, pl. 11:2; JARVIK, 1948a, figs. 33, 34, 1963a, p. 13, figs. 4C,D, 5B, 11A,B, 14B) includes 8–9 submandibulars (up to 1963 called "branchiostegal rays") situated along the ventro-medial and posterior margins of the lower jaw. These plates which may fuse with each other in various ways are continued postero-dorsally by the preoperculosubmandibular (*PSbm*) which probably includes some further submandibulars (see JARVIK, 1963a, fig. 4D *Sbmh*), situated behind the palatoquadrate. If so this means that a dorsal part of the mandibular gill-cover, originally associated with the distal part of the epimandibular is retained in porolepiforms which in this respect would be more primitive than osteolepiforms. Another interesting feature is that the lateral marginal parts of the submandibulars, which are situated along the ventro-medial margin of the lower jaw, are thickened and rounded, forming an articular area (*art. Sbm*, fig. 41) which fits well into a corresponding articular groove made up by the infradentaries and to some extent by the meckelian bone (ceratomandibular). The fact that the submandibulars articulate with the ceratomandibular is also to be regarded as primitive and primitive, too, is probably the retention of a skin-flap of the mandibular gill-cover. This skin-flap (*fl. mgc*) has been restored (fig. 5; JARVIK, 1963a, p. 25, figs. 10A, 11A,B) on the basis of a well preserved principal gular plate of *Holoptychius*. Medially to the depressed area (*od. Sbm*) without ornamentation overlapped by the submandibulars this plate shows a large somewhat depressed, but ornamented area which no doubt was caused by

the soft distal part of the mandibular gill-cover. This area (*i. mgc*) is also discernible in other specimens of *Holoptychius* (pl. 30:1, 4) and is more or less well shown in the sectioned and other specimens of *Glyptolepis* and in *Porolepis*. A similar area has recently been described by JESSEN (1966b, p. 360, *od. sbmm*, fig. 9E, pl. 13:4) in *Strunius* but has hitherto not been found in osteolepiforms.

The presence of a moveable mandibular gill-cover along the lower jaw suggests that the ventral part of the spiracular gill-slit, represented in gnathostomes in general by the plica hyomandibularis (JARVIK, 1963a, pp. 17–21), in porolepiforms was still open. However, considering the posterior extent of the intermandibular musculature and for other reasons given in 1963 (pp. 25–27) it seems likely that its external openings was rather short (*spir. po*, fig. 5) and if present at all situated in the area of submandibular 7. In two specimens of *Glyptolepis groenlandica* showing the inner side of submandibular 7 this side is slightly depressed; and that there really was an opening is further supported by the fact that the excellent gular plate of *Holoptychius* (JARVIK, 1963a, fig. 10A) referred to above, exactly at the place where such an opening is to be expected, shows a depressed area without ornamentation which may have been caused by the soft tissues forming the dorso-medial wall of the presumed opening.

The operculogular series (*Porolepis*, fig. 43, pl. 4:1, pls. 5, 6, pl. 13: 1, 2; GROSS 1936, pl. 7:8; JARVIK, 1950a, fig. 27A; *Laccognathus*, GROSS, 1936, fig. 6A; *Glyptolepis*, figs. 16, 22, 41, 42, 44, 55, pls. 15, 16, pl. 19:1, pl. 20:1, pl. 21:2, pl. 23:1, 2; JAEKEL, 1927, fig. 86; JARVIK, 1949, fig. 10, 1950a, fig. 31C; *Holoptychius*, figs. 5, 6, 45, 58, 107, pl. 23:3, pl. 24:4, pl. 30:1, 4–6, pl. 33:4, 5; HUSSAKOF & BRYANT, 1918, fig. 58; BRYANT, 1919, pl. 11:2; JARVIK, 1948a, figs. 33, 34, 1950a, fig. 31D, 1963a, figs. 4C, D, 5B, D, 10, 11A, B) includes opercular, subopercular, three or possibly sometimes four independent branchiostegal rays, principal gular plate and, in *Porolepis* only, one or two median gular plates.

The opercular (*Op*) has a characteristic shape. In contrast to osteolepiforms (see fig. 86; JARVIK, 1944a, 1948a, 1950a, 1951c, 1952; JESSEN, 1966b) the anterior margin is short and the bone increases in height backwards. The antero-dorsal part which forms a pointed corner extends far forwards along the extratemporal which always together with the lateral extrascapular overlaps the dorsal margin of the bone. The inner side of the bone shows a depression (*p. pr. Op*, pl. 23:3) similar to that in osteolepiforms and other groups of fishes and like that probably receiving the opercular process of the hyomandibula. The subopercular (*Sop*) which dorsally is overlapped by the opercular is in contrast to that bone high anteriorly where it meets and is overlapped by the preopercular and the preoperculosubmandibular, and decreases in height

posteriorly. The branchiostegal rays (*Rbr*) which are well shown in *Glyptolepis leptopterus* (fig. 55) are three or sometimes probably four in number. The principal gular plate (*G*) is generally about 2–3 times longer than broad but there are considerable variations and in some detached plates from Spitsbergen it is strikingly short and broad (pl. 13:1). Posterolaterally the plate usually extends higher up on the side of the head than it does in osteolepiforms and another characteristic feature is that one of the plates, in most specimens that of the left side, is overlapped (*od. G*) by the plate of the other side. This can only mean that the right opercular membrane, in contrast to conditions in recent fish (see JARVIK, 1963a, p. 25, fig. 1) usually overlaps the left one. In this connection may be mentioned that it has been possible with the aid in the first hand of the excellent specimen of *Holoptychius* from Escuminac Bay (fig. 6) and the principal gular plate referred to above (JARVIK, 1963a, fig. 10A) to restore this membrane (*fl. hgc*) in almost its whole extent (fig. 5; JARVIK, 1963a, pp. 23–25). In front of the area overlapped by, or overlapping, the principal gular of the other side there is in *Porolepis* an area (*od. Gm*) overlapped by median gular plates. Two such plates (*Gm1*, *Gm2*) are present in the figured specimens (pl. 6:3; JARVIK, 1950a, fig. 27A) whereas in another specimen (No. A.34037, Pal. Mus., Oslo) there is only one. In *Glyptolepis* and *Holoptychius* median gular plates are lacking.

Exoskeletal shoulder-girdle. – The exoskeletal shoulder-girdle in porolepiforms (*Porolepis*, figs. 51G,H, 53D, pl. 4:1, pl. 5:2, pl. 13:3–7; GROSS, 1936, figs. 1A, 3D,G, pl. 8:1–3; *Glyptolepis*, figs. 41, 42, 52D, 53C,E–G, 55, pl. 15, 16, pl. 18:2, pl. 23:4, pl. 34:5; GROSS, 1936, figs. 1B, 3C,F, 8A,B,E–H; NILSSON, 1939, fig. 5A; JARVIK, 1944b, fig. 9A,C, 1949, fig. 9A,B, 1950a, figs. 27B, 37; see also fig. 35 and 1950b, fig. 3A; ANDREWS & WESTOLL 1970b; *Laccognathus*, fig. 53A,B; GROSS, 1936, fig. 8D; *Holoptychius*, figs. 5, 6A, 45, 51A–F, 52A–C, 54, 59B, 60A–C, pl. 34:1–4, pl. 35; WATSON & DAY, 1916, fig. 1; STENSIÖ, 1931, fig. 94, pl. 34:7; JARVIK, 1944b, fig. 8E, 1948a, figs. 33, 34, 1950a, fig. 36, 1963a, figs. 4C,D, 10B) consists like in osteolepiforms (figs. 52E–H, 60D,E; see also WATSON, 1926, fig. 39; JARVIK, 1944b, 1948a, 1950a, 1950c; VOROBYEVA, 1962; JESSEN, 1966b; ANDREWS & WESTOLL, 1970a, 1970b) of five paired bones: posttemporal, supracleithrum, anocleithrum, cleithrum and clavicle. In addition there is probably a median interclavicle.

The posttemporal (*Pt*) in contrast to osteolepiforms does not meet the median extrascapular but in other respects this bone and the supracleithrum (*Sclm*) appear to be developed much as in osteolepiforms and both are overlapped by the opercular. The anocleithrum (*Aclm*), shown only in a few specimens of *Glyptolepis groenlandica* and *Holoptychius flemingii* is too incompletely preserved to be described.

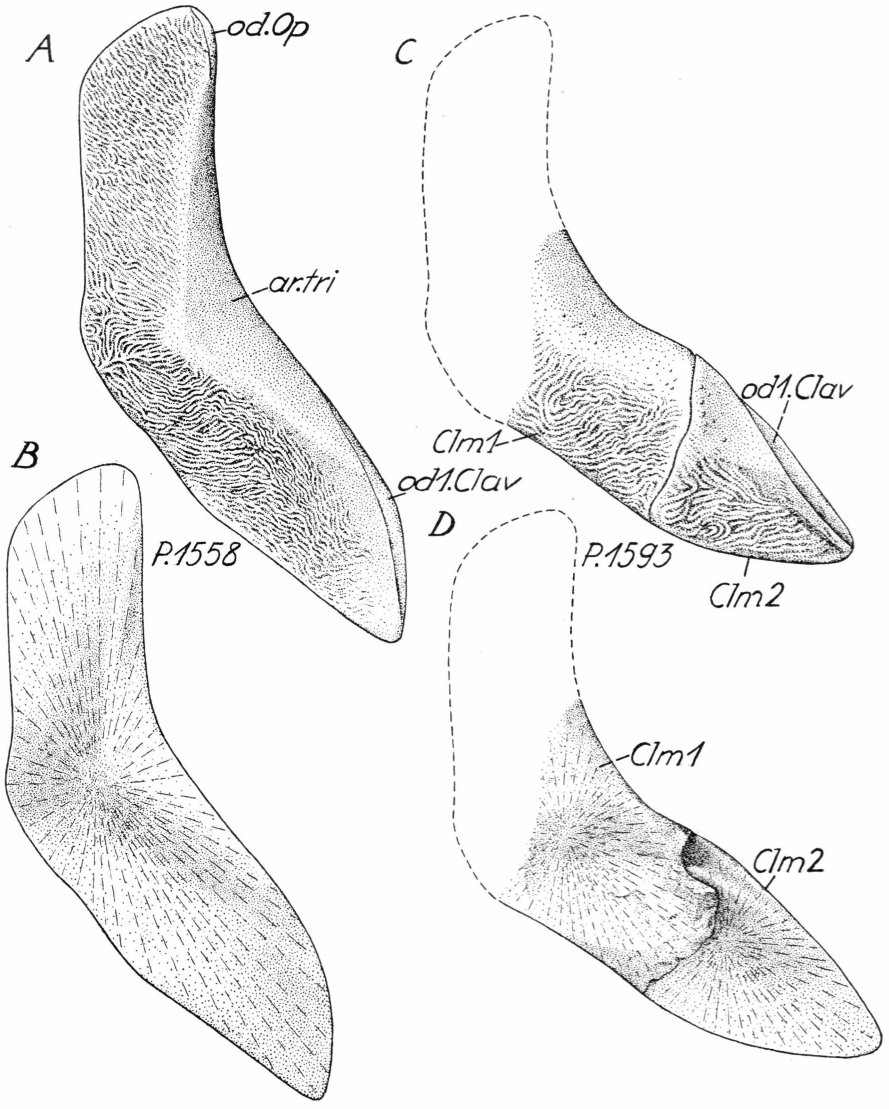


Fig. 51. Cleithrum in, *A–F*, *Holoptychius* spp. from Upper Upper Devonian (*Remigolepis* Series) of East Greenland and, *G*, *H*, *Porolepis* from Lower Devonian (Wood Bay Series) of Spitsbergen in outer and inner aspects. *A*, *B*, *E–H*, after specimens shown in plates 34:2, 34:3, 13:5 and 13:4. *C*, *D*, after specimen figured by JARVIK, 1950a, fig. 36.

For explanation of index letters see fig. 52.

The cleithrum (*Clm*) in some specimens occurs in association with head and body but is generally found detached and such isolated cleithral bones are common in particular in the material from the Upper Devonian of East Greenland. A characteristic feature of porolepiforms

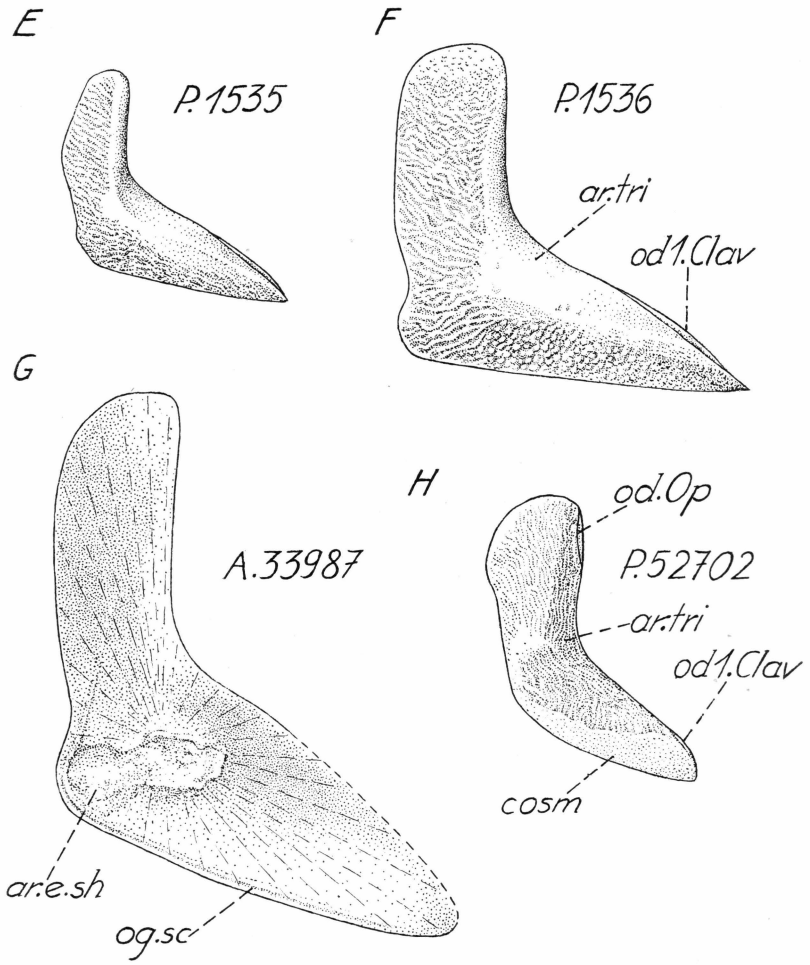


Fig. 51 E–H.

is that the pectoral fin arises higher up on the side of the fish than it does in osteolepiforms (figs. 4, 5, 6A; JARVIK, 1960, fig. 12), a condition which has influenced the shape of the cleithrum. As in osteolepiform the bone consists of a dorsal rectangular and a ventral triangular division but the ventral division is much lengthened forwards giving the impression that the bone also includes the clavicle. Anteriorly the middle part of the bone is bent inwards within a triangular area which as to its position and extent reminds of area *od. gc* in *Eusthenopteron*. This area (*ar. tri*) which in *Porolepis* bears an ornamentation of ridges but in *Laccognathus*, *Glyptolepis* and *Holoptychius* is smooth or shows a few tubercles probably took part in the formation of the posterior wall of the branchial cavity. Outside this area the branchial cavity opened outwards by a rather large opening in the skeleton. This opening which is

bounded posteriorly by the cleithrum and anteriorly by the subopercular and the branchiostegal rays was covered externally by the soft parts (*fl. hgc*) of the operculogular membrane. Dorsally to that opening, along the dorsal part of the anterior margin of the rectangular division, there is sometimes a narrow depressed area (*od. Op*) overlapped by the opercular. The anterior margin of the ventral triangular division is received by a groove in the posterior margin of the clavicle. Along this margin which often is a little convex as seen in lateral view there is generally a distinct depressed area (*od1. Clav*) on the external side of the bone overlapped by the external lamina of the clavicle. On the inner side of this part of the cleithrum there may be a slight impression caused by the inner lamina of the clavicle and the ascending clavicular process. A more distinct depressed area (*og. sc*) on the inner side of the bone, probably caused by scales, is found in *Porolepis* along the postero-medial margin of the triangular portion. The area (*ar. e. sh*) for the attachment of the endoskeletal shoulder-girdle ("scapulocoracoid") which in contrast to osteolepiforms is single is situated about at the transition between the rectangular and triangular divisions. This area which is discernible only in a few specimens is elongated rostro-caudally and is sometimes restricted in its middle part.

The cleithrum displays a considerable range of variation in that the rectangular and triangular divisions as seen in lateral views may meet at angles which may be more or less obtuse or sometimes almost straight. In the latter case the ventral margin of the bone was probably nearly horizontal in position. These variations can be studied in the large material from the Upper Devonian of East Greenland tentatively referred to *Holoptychius* and most probably the extreme types of cleithra belong to different species or perhaps to different genera. Also several other varia-

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Fig. 52. Restorations of cleithrum in outer and inner aspects and clavicle and interclavicle in outer aspects of, *A–C*, *Holoptychius* sp., *D*, *Glyptolepis* sp., and, *E–H*, *Eusthenopteron foordi*. *D*, from GROSS, 1936, fig. 8G (cf. pl. 34:5); *E–H*, from JARVIK, 1944b, figs. 3D, F, H, 4D.

Clav, clavicle; *Clm*, cleithrum; *Clm1*, *Clm2*, dorsal and ventral cleithral bones. *ar. e. sh*, areas for attachment of endoskeletal shoulder-girdle; *ar. mem*, area probably for attachment of membraneous posterior wall of branchial cavity; *ar. tri*, triangular inwardly bent area of cleithrum; *cosm*, part of cleithrum covered with cosmine; *dl. pl*, dorso-lateral, vertical plate of clavicle; *fo. l*, *fo. m*, lateral and medial fossae on inner side of clavicle; *le. Clav*, *li. Clav*, external and internal lamellae of clavicle; *od. Clm*, area of clavicle overlapped by cleithrum; *od. gc*, areas of cleithrum and clavicle covered by skin-flap of hyoidean gill-cover; *od. Op*, area of cleithrum overlapped by opercular; *od1. Clav*, *od2. Clav*, areas overlapped by clavicle; *og. sc*, area of cleithrum overlapping scales; *pr. Clav*, ascending process of clavicle; *ri. vm*, rod-like continuation of ascending clavicular process on inner side of ventro-medial plate; *vm. pl*, ventro-medial, horziontal plate of clavicle.

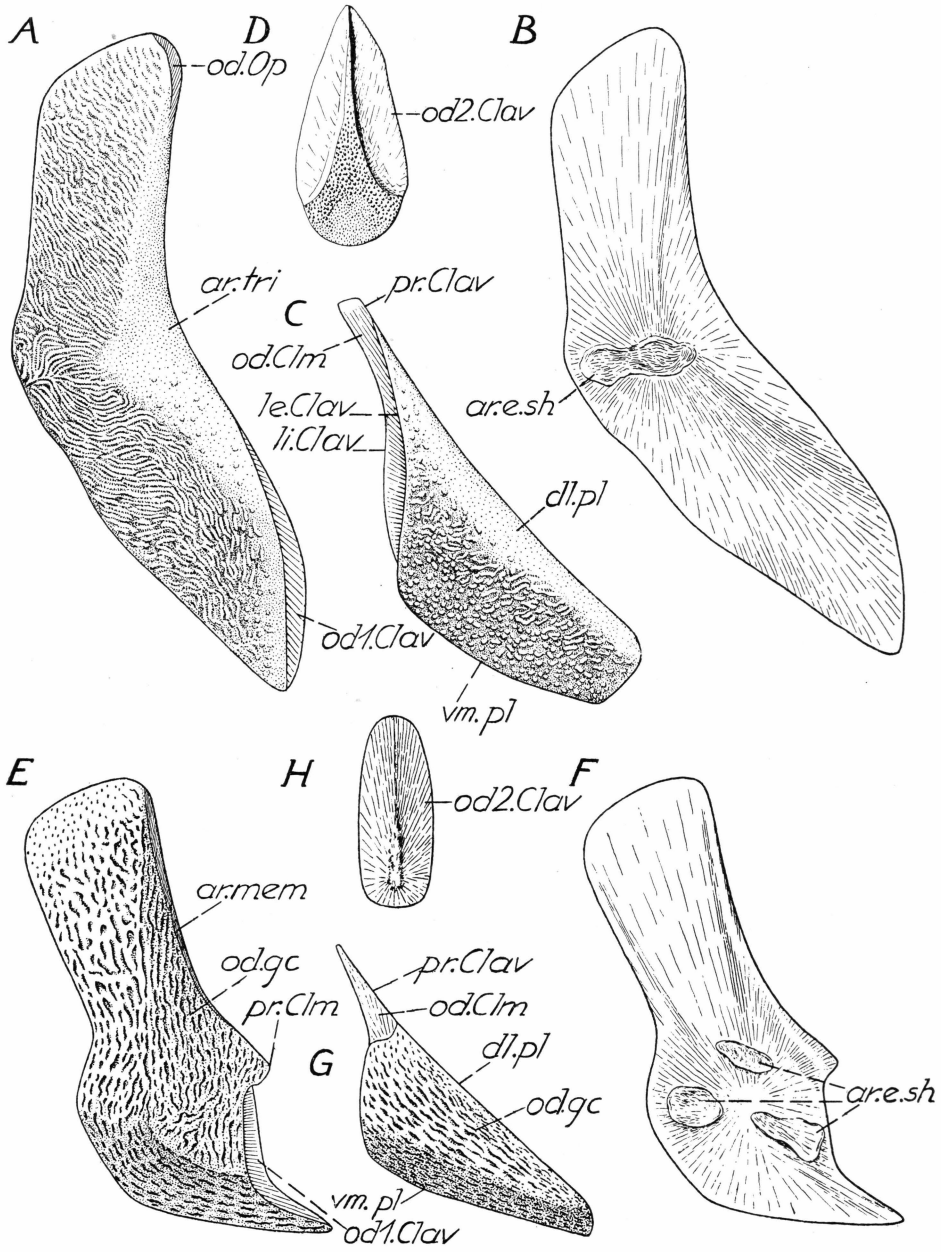

A
od.Op
ar.tri
D
od2.Clav
B
pr.Clav
C
od.Clm
le.Clav
li.Clav
ar.e.sh
dl.pl
od1.Clav
vm.pl
E
H
od2.Clav
F
ar.mem
od.gc
pr.Clm
pr.Clav
od.Clm
G
dl.pl
od.gc
ar.e.sh
vm.pl
od1.Clav

Fig. 52.

tions in the development of the cleithrum occur (see e.g. GROSS, 1936, fig. 9C, D, pl. 8:1–3; JARVIK, 1950a, fig. 35) and an interesting fact is that the bone sometimes may be subdivided into dorsal and ventral elements. As described elsewhere (1950a, pp. 116–117, fig. 36) this subdivision is well shown in a specimen of *Holoptychius* from East Greenland in which the main part of the two cleithral bones (*Clm 1*, *Clm 2*, figs. 51C, D, 60A) and the clavicle have been completely removed from the stone. The dorsal cleithral bone which occupies the rectangular and the dorsal part of the triangular portion is thickened at its ventral end where it is overlapped by the ventral element. On the inner face of the latter there is a distinct groove along the anterior margin bounded dorsally by a deep pocket in the thickened ventral end of the dorsal element. This groove and pocket received the ascending process of the clavicle. A similar subdivision has been found in a specimen of an undetermined porolepiform from the Middle Devonian of East Greenland (JARVIK, 1950a, fig. 35A, pl. 21:5) but if the cleithrum may be subdivided also in *Porolepis* and *Glyptolepis* as I claimed in 1950 (pp. 117–120) is now uncertain.

The clavicle (*Clav*), which also varies considerably, as in osteolepiforms consists of a principal part and an ascending process (*pr. Clav*), and as in that group the principal part is bent in such a way so as to be composed of an almost horizontal ventro-medial plate and an almost vertical dorso-lateral plate. When in its natural position the ornamented external side of the ventro-medial plate (*vm. pl*) forms a direct continuation of the ornamented external side of the ventral division of the cleithrum, whereas the dorso-lateral plate (*dl. pl*) lies in the continuation of the triangular anterior portion of the cleithrum. A characteristic feature of the porolepiform clavicle, shown also in *Rhizodus* (ANDREWS & WESTOLL, 1970b, fig. 10), is that the cleithrum is received in a groove in the posterior margin of the bone. This groove is bounded by two lamellae, an outer (*le. Clav*) which overlaps area *od1. Clav* of the cleithrum and an inner (*li. Clav*) which is overlapped by that bone. The clavicular process, which like in *Rhizodus* may be twisted (fig. 53A), is pointed or more or less truncate (JARVIK, 1950a, fig. 36). The external side sometimes shows a deep depression (pl. 35:5) similar to that recently figured by ANDREWS & WESTOLL (1970b, pl. 5:B) in *Rhizodus* but most often the clavicular process as seen in external view is a broad-based structure which passes over gradually into the dorso-lateral plate. As seen in inner view, on the other hand, it appears as a rodlike structure which continues downwards inside the dorso-lateral plate, separated from that by a deep fossa (*fo. l*) to merge gradually into the horizontal plate causing a broad ridge (*ri. vm*) on the dorsal side of that plate. In all these respects porolepiforms differ distinctly from osteolepiforms in which the ascending

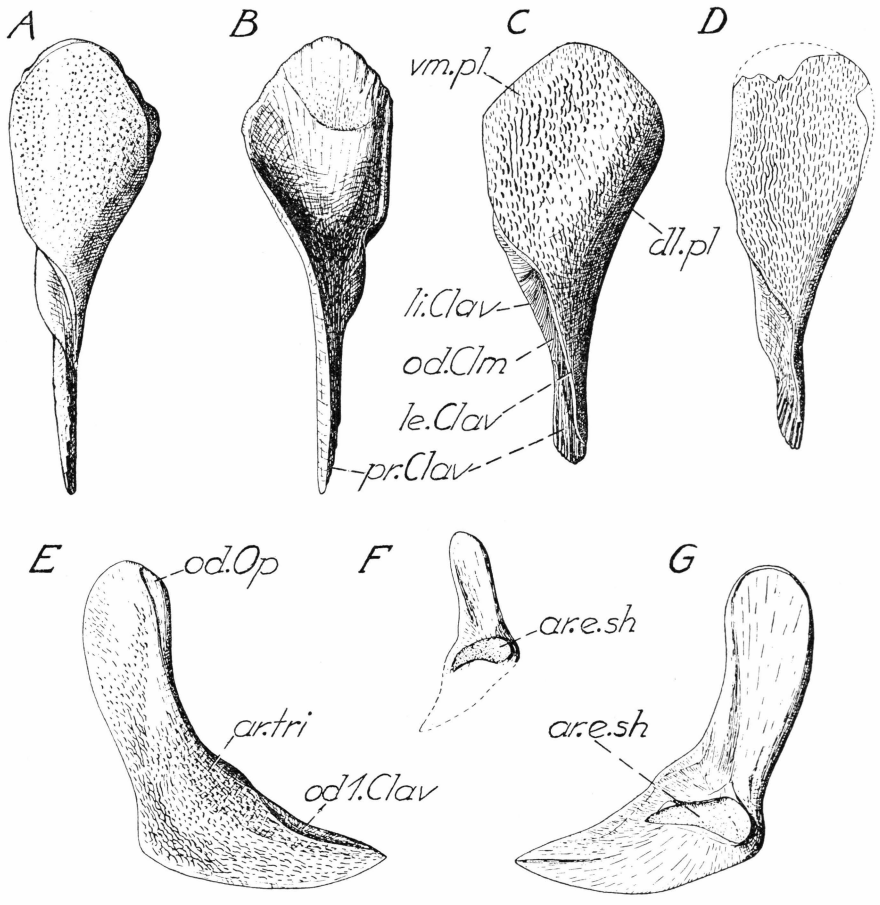


Fig. 53. *A–D*, clavicle and, *E–G*, cleithrum in outer and inner aspects of *A*, *B*, *Laccognathus panderi*, *C*, *E*, *G*, *Glyptolepis baltica*, *F*, *Glyptolepis leptopterus* and, *D*, *Porolepis siegenensis*. From Gross, 1936, figs. 3, 8.

For explanation of index letters see fig. 52.

process is a simple extension of the dorso-lateral plate wholly overlapped by the cleithrum and not rodlike on the inner side. It is because the rodlike appearance of the ascending process that I have assumed that the clavicles from the Carboniferous of Scotland referred to *Rhizodus* by Woodward (1891a, pl. 12:4, 7) belong to a porolepiform rather than to an osteolepiform (cf. p. 19). On the medial side of the ventral part of the rodlike clavicular process, about opposite the deep fossa (*fo. l*) mentioned above, there is sometimes another although less distinct fossa (*fo. m*) and in front of that, along the postero-medial margin of the bone, there may be a rather broad depressed area (*og. Icl*, pl. 35:1) possibly caused by the interclavicle and very similar to that recently shown by Andrews & Westoll (1970b, pl. 7:A, *o.a.Icl*) in *Rhizodus*.

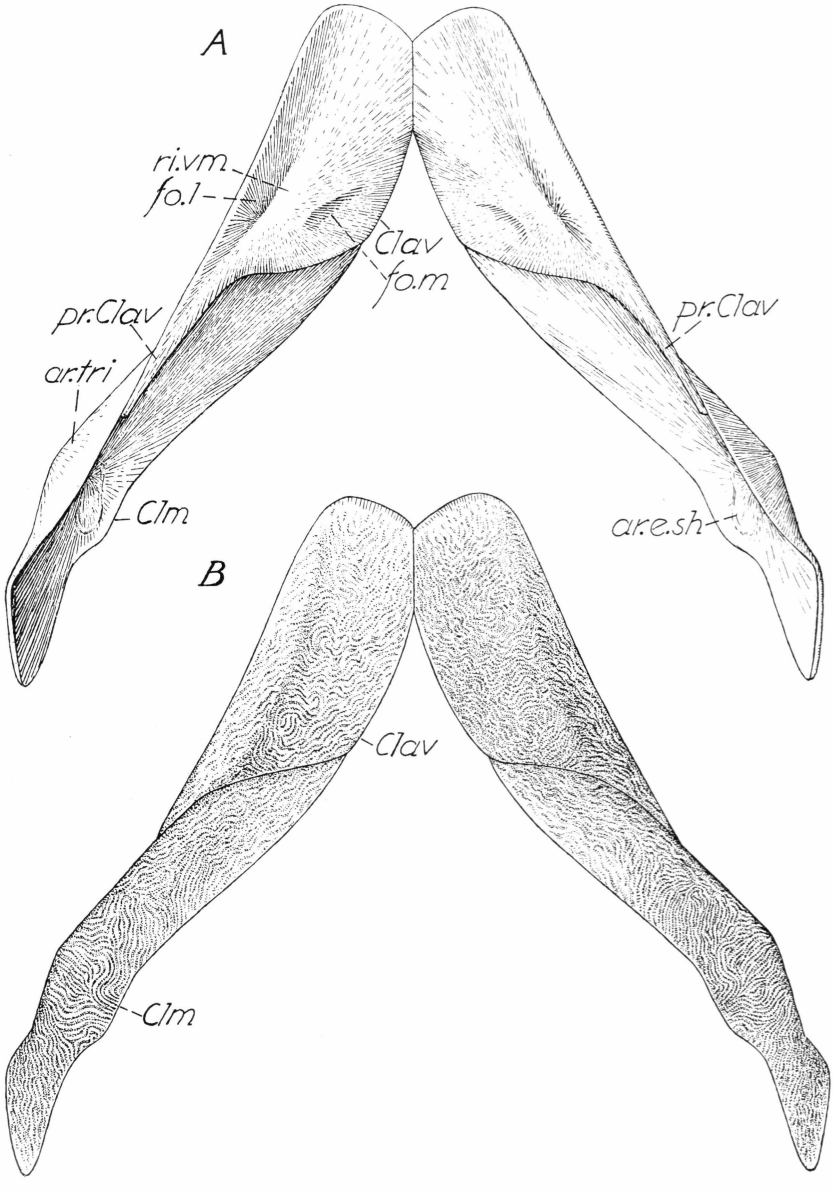


Fig. 54. *Holoptychius* sp. Restoration of ventral parts of exoskeletal shoulder-girdles in dorsal and ventral aspects.

For explanation of index letters see fig. 52.

The assumption that *Rhizodus* may be a porolepiform has recently, although unconsciously, been confirmed by ANDREWS & WESTOLL (1970b). As far as may be judged from their figures and descriptions there are no important differences as to the structure of the cleithrum and the clavicle between the Devonian porolepiforms described in this paper and the post-Devonian forms (*Rhizodus*, *Strepsodus*) for which

they, solely on the basis of alleged differences in the structure of the exoskeletal shoulder-girdle, have created a new order of the "Rhipidistia". The post-Devonian forms, and *Sauripterus* which is also included in that order, are still too incompletely known to be seriously considered and until more cogent evidence has been presented the new classification of the "Rhipidistia" proposed by ANDREWS & WESTOLL (1970b, p. 479) is to be disregarded.

Whether an interclavicle occurs in porolepiforms could not be ascertained but possibly it is represented by the detached bone from the Baltic Devonian area which GROSS described in 1936 (p. 151; cf. p. 153) and referred to *Glyptolepis*. This plate (fig. 52D, pl. 34:5) is suggestive of the median gular plate in *Eusthenopteron* (JARVIK, 1944a, fig. 9D) but because such a plate is absent in other holoptychiids and it lacks pit-line, it now seems most likely that it is an interclavicle as originally suggested by GROSS.

Sensory canals and pit-lines

The sensory canals and pit-lines of the head (*Porolepis*, figs. 1, 7A, 20A, 34, 43, 56, 57A,B, 77A, pls. 4–6, pl. 7:2, 3, pl. 8, pl. 11:1, 3, 4, 7, pl. 12:1, 5; STENSIÖ, 1922, pl. 1, 5, 1932, fig. 10; HOLMGREN & STENSIÖ, 1936, fig. 271; GROSS, 1936, pl. 7:3, 4, 7, 1941, fig. 23; JARVIK, 1942, figs. 37, 40, 41, 1950a, figs. 27A, 30, 31A; *Heimenia*, pl. 12:6; *Laccognathus*, GROSS, 1938, 1941, figs. 7, 14; *Glyptolepis*, figs. 7B, 8, 16, 18, 22, 24G, 32A, 38, 39, 41, 42, 44, 55, 57C, 71A, 76B, 104C, pl. 14:3, 4, pl. 15, pl. 19:1, pl. 20, pl. 21:2, 3, pl. 23:1, 2, pl. 32:5; GROSS, 1941, figs. 1–3; JARVIK, 1949, figs. 9–10, pl. 7:5, 1950a, figs. 27B, 31C, 34, 1963a, figs. 13, 14; *Holoptychius*, figs. 6A, 7C,D, 20B, 35–37, 45–47, 57D, 58, 107C, pl. 24:1, 3, 4, pl. 27–30, pls. 31:3, pl. 32:1, pl. 33:6; HOLMGREN & STENSIÖ, 1936, figs. 274, 276B; STENSIÖ, 1947; HOLMGREN & PEHRSON, 1949; HOLMGREN, 1953; WESTOLL, 1937a, fig. 9C, 1937b, fig. 1C; JARVIK, 1948a, figs. 33, 34, 1950a, fig. 31D, 1963a, fig. 4C,D), are well developed and strong and richly branching tubes which open by numerous pores are given off from the canals. This is true also of the Lower Devonian porolepids which is remarkable because the tubes in the early (Middle Devonian) osteolepids generally branch very little and open by few pores (SÄVE-SÖDERBERGH, 1933; JARVIK, 1948a; JESSEN, 1966b). But no groups of small pores in the cosmine layer of the kind which are frequently found in osteolepids (JARVIK, 1948a, pp. 137–139, fig. 36, *grp. so*, 1966, figs. 12, 15A, pl. 1, pl. 14:3; JESSEN, 1966b, p. 318; BJERRING, 1972b) and which usually lie close to the sensory lines have been observed in porolepids.

In *Holoptychius* there is a prespiracular sensory canal (*prspc*) but in other respects no important differences between the various porolepiform

genera and species as to the development of the sensory canals and pit-lines have been found. Characteristic for porolepiforms as compared with osteolepiforms is the distinct displacement of the sensory lines that have occurred in connection with fusion (or subdivision) of dermal bones (pp. 150–156; see also JARVIK, 1948a, 1967b, pp. 191–194, fig. 7) but they differ from osteolepiforms also in some other regards.

One remarkable but probably not very important fact is that the supraorbital sensory canal (*soc*) anteriorly, contrary to what is to be expected, does not join the infraorbital canal at the centre of radiation of the rostropremaxillary but at the place where this bone meets the foremost nasal and the median rostral. More interesting are the differences with regard to the series of bones, the rostral series (pp. 95, 150), pierced by the anterior parts of the infraorbital canal (*ioc*) and the ethmoidal commissure (*et. com*). In *Eusthenopteron* and other osteolepiforms (JARVIK, 1942, 1944a, 1948a) there is generally a small median postrostral at the tip of the snout. This bone overlaps the nasorostropremaxillaries but is not pierced by the ethmoidal commissure which passes ventrally to the tip of the neural endocranium lodged in a ridge on the dorsal side of the palatal lamina of the fronto-ethmoidal shield. In view of this fact and because the infraorbital canal farther laterally pierces an independent lateral rostral it is clear that one or more medial rostral elements have fused with the underlying premaxillary forming a rostropremaxillary. The porolepiforms, too, have a small median bone at the tip of the snout and in 1942 (fig. 33) I took it for granted that this bone which was shown in material of *Holoptychius* from East Greenland is a median postrostral homologous with that in osteolepiforms and on the basis of the material at my disposal at that time I found it reasonable to assume that there is also a separate lateral rostral and that accordingly the conditions at the tip of the snout in porolepiforms are similar to those in osteolepiforms. However, new material of *Holoptychius* collected in East Greenland after the second world war shows clearly that the lateral rostral has fused with the premaxillary and as a consequence of this fusion the centre of radiation of the compound rostropremaxillary lies strikingly far

Fig. 55. *Glyptolepis leptopterus*. Ventral parts of two flattened skulls from Lethen Bar, Scotland. Middle Devonian. Photographs of guttapercha casts. *A*, specimen No. P. 1666, Pal. Sect., Stockh. Same specimen as figured by JARVIK, 1950a, fig. 27B. × 9/8. *B*, specimen No. P. 1665, Pal. Sect., Stockh. × 9/4.

Clm, cleithrum; *De*, dentary; *Ju*, jugal; *Lj*, lower jaw; *Op*, opercular; *Pop*, preopercular; *PSbm*, preoperculosubmandibular; *Qj*, quadratojugal; *Rbr*, branchiostegal rays; *Sbm*, submandibulars; *Sop*, subopercular; *Sq. u*, upper squamosal.

juc, jugal sensory canal; *od. Ext. l*, area of opercular overlapped by lateral extrascapular; *od. G*, area of principal gular overlapped by principal gular of other side; *od. Sbm*, area of principal gular overlapped by submandibulars; *pl. G*, pit-line of principal gular; *pl. Qj*, quadratojugal pit-line.

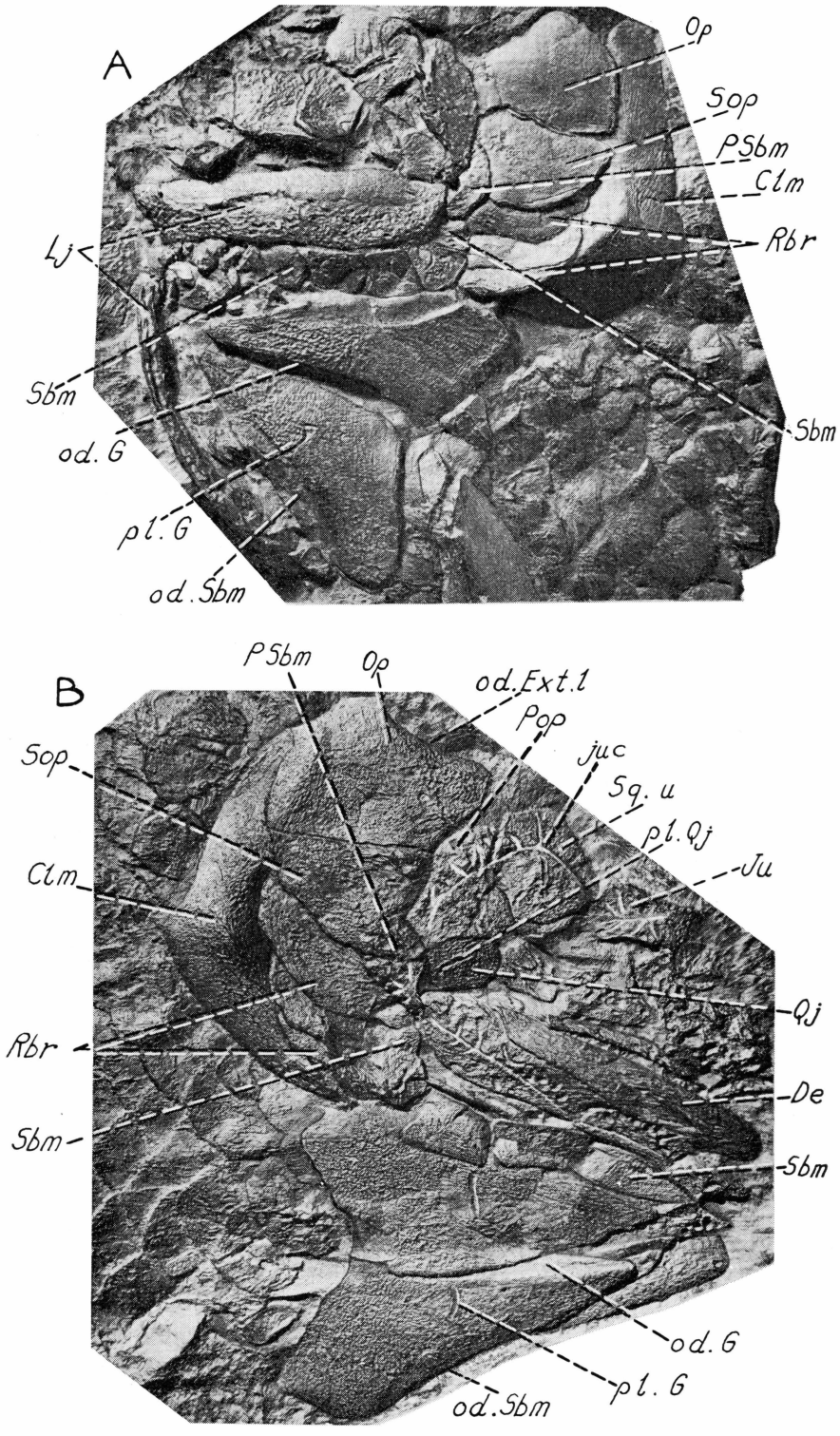

A
Op
Sop
PSbm
Ctm
Rbr
Lj
Sbm
od. G
pl. G
od. Sbm
Sbm
B
PSbm
Op
od. Ext. 1
Pop
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Fig. 55.

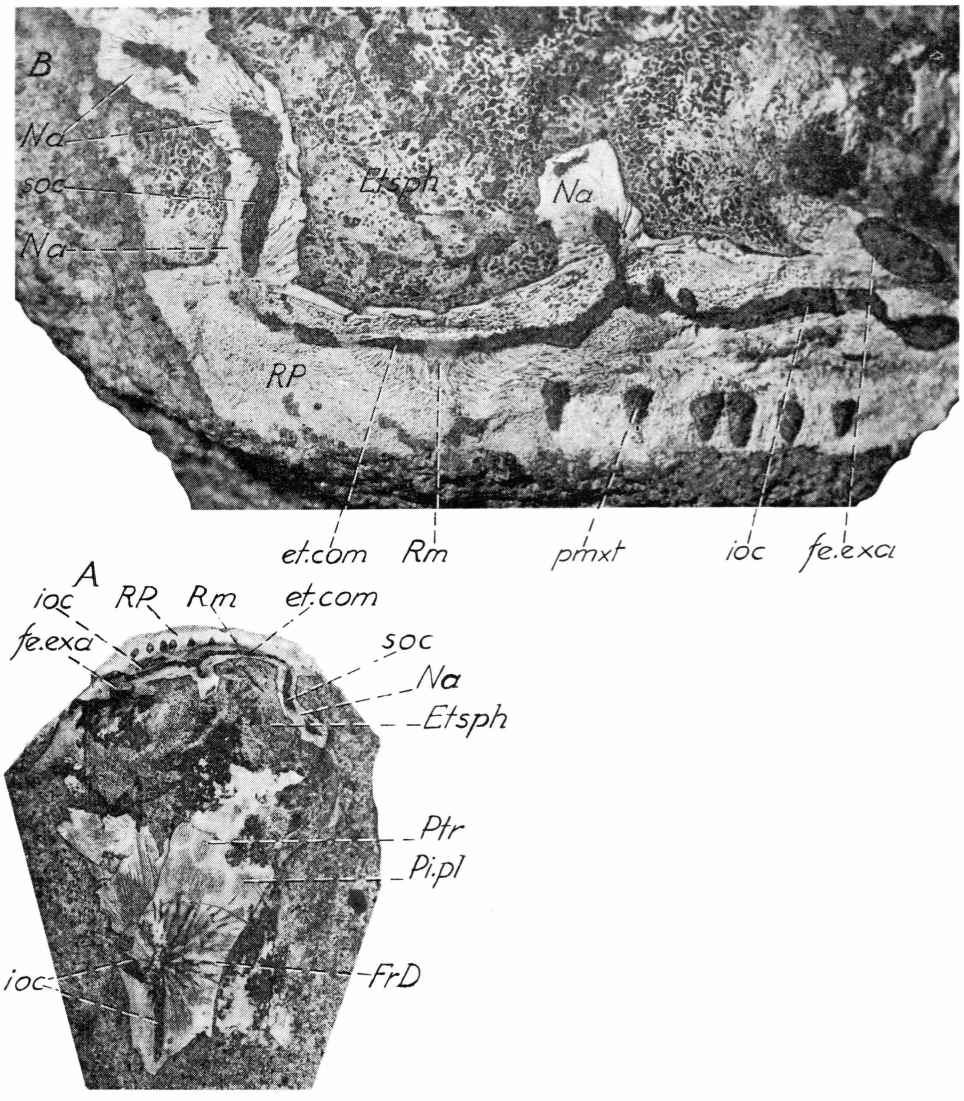


Fig. 56. *Porolepis brevis*. *A*, deficient divisio cranialis anterior in dorsal view. Photographed in alcohol. Specimen No. P. 52680, Brit. Mus., Lond. Coll. ENS. exp. 1939. Barmfjellet, Dicksondalen, Spitsbergen. Lower Devonian (Wood Bay Series). × 9/8. *B*, same specimen in anterior view to show median rostral. × 9/2.

Etsph, ethmosphenoid; *FrD*, frontodermosphenotic; *Na*, nasals; *Pi. pl*, pineal plate; *Ptr*, postrostral; *Rm*, median rostral; *RP*, rostropremaxillary.

et. com, ethmoidal commissural canal; *fe. exa*, fenestra exonarina anterior; *ioc*, infraorbital sensory canal; *pmxt*, premaxillary teeth; *soc*, supraorbital sensory canal.

laterally. Moreover, dissections of a great number of the fronto-ethmoidal shields from East Greenland now available (figs. 35, 36, pls. 27, 28) and

of a specimen of *Porolepis* (fig. 56) have revealed that the presumed median postrostral is pierced by the ethmoidal commissural canal. This bone is accordingly not a postrostral but a median rostral (*Rm*). As to the rostral series there are thus remarkable differences between porolepiforms and osteolepiforms. In the latter group the lateral rostral (*Rl*) is independent and medial rostral elements have fused with the premaxillary whereas in porolepiforms the conditions are just the other way about. In them it is the lateral rostral that has fused with the premaxillary whereas the medial rostral has fused with that of the other side forming an independent median rostral. The latter is rather thickened and as shown in the sections of *Glyptolepis* (fig. 18) the ethmoidal commissure also in porolepiforms passes ventrally to the anterior tip of the neural endocranium.

In its course backwards the infraorbital canal (*ioc*) passes ventrally to the fenestra exonarina posterior and enters the lachrymal. In the anterior part of that bone it runs in a postero-dorsal direction (*iocv*) to the centre of radiation, where it turns sharply backwards (cf. pp. 153, 195–196). Farther back the canal pierces the jugal and the postorbital, enters the fronto-ethmoidal shield and joins the supraorbital canal at the centre of radiation of the frontodermosphenotic. At this place the canal turns sharply backwards and runs in a postero-medial direction to the centre of radiation of the parietointertemporal where it turns postero-laterally and is continued by the postotic canal. Both in the frontodermosphenotic and in the parietointertemporal its course is influenced by the fusions of bones (cf. pp. 150, 156). The postotic canal (*poc*), which pierces the supratemporal, in the posterior part of that bone runs more or less close to or sometimes even in (*Laccognathus*, Gross, 1936, p. 140) the suture to the extratemporal giving off a richly branching tube to that bone. The main sensory canal (*msc*) in the head and the dorsal part of the exoskeletal shoulder-girdle runs about as in osteolepiforms and also the supratemporal commissural canal (*stcc*) is about as in that group.

The prespiracular sensory canal (*prspc*; see also Jarvik, 1948a, p. 130) is well shown in several specimens of *Holoptychius* but is absent in *Porolepis* and *Glyptolepis*. It branches off from the infraorbital canal at the centre of radiation of the frontodermosphenotic and runs in a postero-lateral direction more or less close to the infraorbital canal to the postero-lateral corner of the fronto-ethmoidal shield. There it leaves the cranial roof and enters the prespiracular plate which is a bone of the external cheek-plate situated outside the palatoquadrate and for this and other reasons not to be confused with the intertemporal. In the prespiracular plate the prespiracular canal breaks up into several tubes. As a whole the canal has the character of a large tube of the infraorbital sensory canal and because also it has no equivalent in the Lower and

Middle Devonian porolepiforms it most likely is a secondary formation (cf. HOLMGREN & PEHRSON, 1949, p. 280).

The jugal canal (*juc*) joins the infraorbital canal at the centre of radiation of the jugal forming a characteristic acute angle with that canal and from there it runs in a curve, concave ventrally, through the large upper squamosal and enters the preopercular where it is continued by the preoperculo-mandibular canal. In these regards porolepiforms differ clearly from osteolepiforms in which the jugal canal meets the infraorbital canal at a more or less straight angle and runs almost straight backwards through the squamosal. However, if we now imagine that the upper and lower squamosal elements in porolepiforms fuse into a single element, the centre of radiation of the compound bone thus formed will be situated ventrally to the original centre of the upper squamosal and in order to reach the new centre the jugal canal will run straight backwards on the cheek as it does in osteolepiforms. Evidently we are here concerned with a case of displacement of sensory lines in connection with fusion (or subdivision) of bones (cf. p. 150) and as is readily seen also the fact that the preoperculo-mandibular canal (*p-mc*) makes a characteristic loop backwards running behind the palatoquadrate enclosed in the preoperculosubmandibular is due to the fusion between preopercular and submandibular components. The mandibular canal in the lower jaw runs about as in osteolepiforms. In *Heimenia* its course is marked by a distinct groove (*gr.msc*, pl. 5:2) on the outside of the jaw (cf. *Thursius macrolepidotus*, JARVIK, 1948a, p. 123). No distinct oral canal (*orc*) is developed in porolepiforms but it may be represented by a strong tube which as seen in some specimens of *Holoptychius* (pl. 31:3) is given off from the mandibular canal at the centre of radiation of infradentary 4.

The frontal pit-line (*pl. Fr*) may be short but in most specimens it reaches to, or almost to, the posterior margin of the frontodermosphenotic. A characteristic feature of porolepiforms is that the transverse and posterior oblique parietal pit-lines (*pl.tr.Pa*, *pl.po.Pa*) are situated far forwards and generally well in front of the supratemporal pit-line (*pl.St*) which crosses the postotic canal at the centre of radiation of the supratemporal. This position of the parietal pit-lines is very likely due to the fact that the parietal has fused with the intertemporal into a compound parietointertemporal (see pp. 147–150). In connection with the fusion the parietal pit-lines have moved antero-medially to the new centre of the compound bone whereas the supratemporal pit-line has retained its original position. However, in osteolepiforms and other fishes the supratemporal and transverse parietal pit-lines generally are continuous forming the so called middle pit-line (cf. JARVIK, 1944a, p. 44, 1947, p. 66). This connection has been retained in one specimen of *Porolepis* (fig. 57B, pl. 11:7) and of great interest is that the medial end of the supratemporal

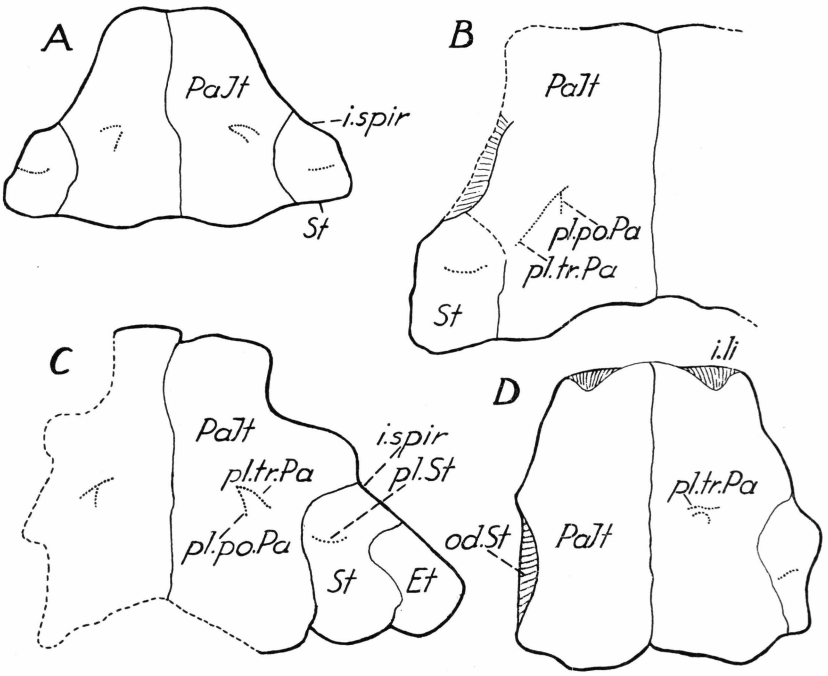


Fig. 57. Sketches of parietal shield of various porolepiforms to show variations in pit-lines. *A*, *Porolepis brevis*. Specimen SVB 2, Mus. de Pal., Paris. Same as in pl. 6:2. *B*, *Porolepis* sp. Specimen No. A. 33991, Pal. Mus., Oslo. Same as in pl. 11:7. *C*, *Glyptolepis leptopterus*. Specimen No. P. 4120, Pal. Sect., Stockh. Same as in fig. 41. *D*, *Holoptychius* sp. Specimen No. P. 1593, Min. Mus., Copenh. Same as in pl. 24:3.

Et, extratemporal; *PaIt*, parietointertemporal; *St*, supratemporal.

i. li, depression probably for ligament; *i. spir*, spiracular notch; *od. St*, area of parietointertemporal overlapped by supratemporal; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. St*, supratemporal pit-line; *pl. tr. Pa*, transverse parietal pit-line.

pit-line in this case has been dragged forwards when the parietal pit-lines as a consequence of the fusion moved to the new centre.

The pit-line of the lateral extrascapular (*pl. Ext. l*) is shown in several specimens of *Holoptychius* and has been found also in *Porolepis* (pl. 6:2) and *Laccognathus* (Gross, 1936, fig. 4E).

The squamosal pit-line (*pl. Sq*, *pl. Sql*), well shown only in a few specimens of *Porolepis* and *Holoptychius*, consists of a dorsal almost horizontal and an anterior more or less vertical shank. The dorsal shank is always short. It never extends to the preopercular and no preopercular pit-line has been found. The anterior shank is generally longer and in the specimen with a row of four lower squamosals (fig. 46) it crosses these bones and passes over into the quadratojugal pit-line. A long continuous squamoso-quadratojugal pit-line similar to that in many osteolepiforms is thus formed (Jarvik, 1948a, fig. 35). One specimen of *Holoptychius*

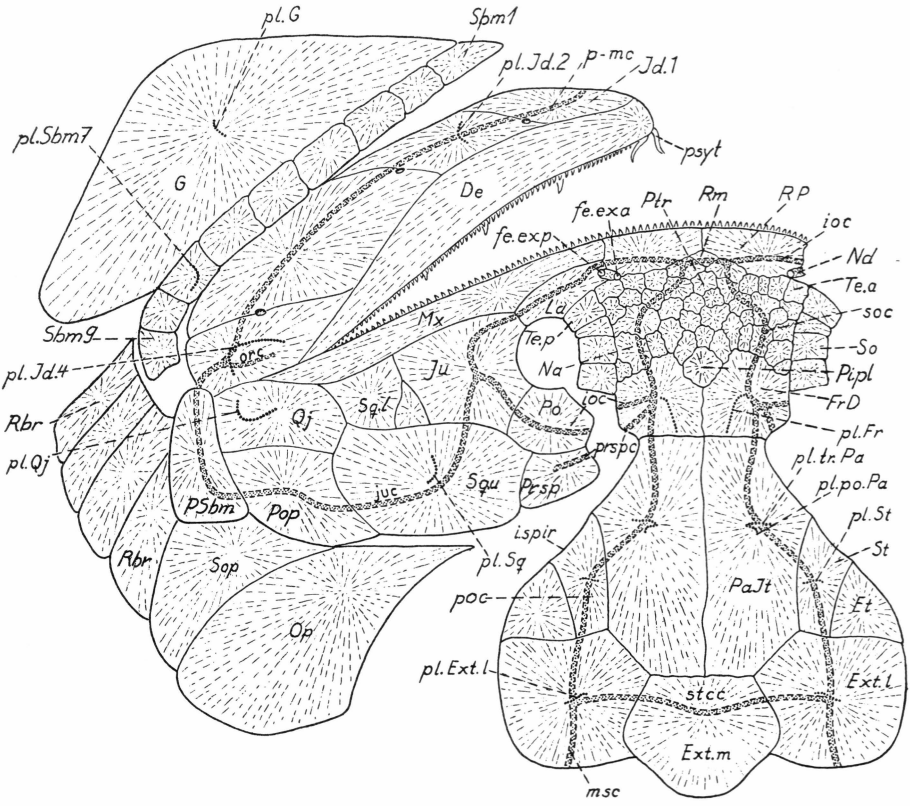


Fig. 58. *Holoptychius* sp. Dermal bones and sensory lines of head.

De, dentary; *Et*, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *FrD*, frontodermosphenotic; *G*, principal gular plate; *Id.1*, infradentary 1; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *Nd*, nariodal; *Op*, opercular; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Ptr*, postrostral; *Qj*, quadratojugal; *Rbr*, branchiostegal rays; *Rm*, median rostral; *RP*, rostropremaxillary; *Sbm1*, *Sbm9*, submandibulars 1 and 9; *So*, supraorbital; *Sop*, subopercular; *Sq. l*, lower squamosal; *Sq. u*, upper squamosal; *St*, supratemporal; *Te. a*, *Te. p*, anterior and posterior tectals.

fe. exa, *fe. exp*, fenestra exonarina anterior and posterior; *ioc*, infraorbital sensory canal; *i. spir*, spiracular notch; *juc*, *msc*, *orc*, jugal, main and oral sensory canals; *pl. Ext. l*, pit-line of lateral extrascapular; *pl. Fr*, frontal pit-line; *pl. G*, pit-line of principal gular; *pl. Id. 2*, *pl. Id. 4*, pit-lines of infradentaries 2 and 4; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. Qj*, quadratojugal pit-line; *pl. Sbm7*, *pl. Sq*, *pl. St*, pit-lines of submandibular 7, squamosal and supratemporal; *pl. tr. Pa*, transverse parietal pit-line; *p-mc*, *poc*, *prspc*, preoperculo-mandibular, postotic and prespiracular sensory canals; *psyt*, tusks of parasymphysial dental plate; *soc*, supraorbital sensory canal; *stcc*, supratemporal commissural canal.

flemingii shows an interesting variation. In that specimen (JARVIK, 1948a, figs. 33B, 34) the continuous pit-line is replaced by a distinct canal which,

giving off branching tubes, runs from the jugal canal in the upper squamosal through the single lower squamosal to the quadratojugal where it turns ventrally exactly as does the pit-line of that bone.

The pit-line of infradentary 4 (*pl. Id. 4*), like the quadratojugal pit-line (*pl. Qj*), consists of two shanks one posterior or vertical so situated that it forms a continuation of the posterior shank of the quadratojugal pit-line, and one anterior running forwards. As is best shown in *Heimenia* (pl. 12:6; see also *Porolepis*, GROSS, 1941, fig. 23C) this pit-line may be continued forwards by pit-lines corresponding to the horizontal pit-lines of infradentaries 2 and 3 in osteolepiforms. The vertical pit-line of infradentary 2 (*pl. Id. 2*) and the pit-lines of the seventh submandibular (*pl. Sbm7*), the principal (*pl. G*) and median gular plates (*pl. Gm*) are also developed much as in that group.

V. COMPARATIVE SECTION

Comparison with osteolepiforms

General remarks on porolepiforms and osteolepiforms

The studies of the exo- and endoskeleton of the head and the exoskeletal shoulder-girdle in the large collections of *Porolepis* (Lower Devonian), *Glyptolepis* (Middle Devonian) and *Holoptychius* (Upper Devonian) at my disposal have demonstrated a most remarkable uniformity in structure even as to minor and seemingly unsignificant structural features. Also the less well known genera *Heimenia* and *Laccognathus* agree well with these forms in all known respects. The differences between the various genera and species are inconsiderable and disregarding the cosmine layer it is hardly possible to distinguish clearly between the families *Porolepidae* and *Holoptychidae* on the basis of cranial characters. If we add that *Heimenia* is intermediate between porolepids and holoptychiids in scale structure (ØRVIG, 1969b) and that the tail in *Porolepis*, as evidenced by the new material collected by the French Spitsbergen expedition in 1969, is developed much as in *Glyptolepis* and *Holoptychius* it is clear that the Porolepiformes is a most distinct and homogenous group, a group which moreover is distinguished by a great number of specialisations not found in any other groups of fishes.

Our knowledge of the Osteolepiformes, too, has increased greatly during the last few decades. We have now a most detailed and safe knowledge of the external dermal bones and the sensory lines of the head and shoulder-girdle, and in many cases also of the fins and squamation, in great number of Devonian forms, both osteolepids (*Osteolepis*, *Thursius*, *Gyroptychius*, *Latvius*, *Glyptopomus*, SÄVE-SÖDERBERGH, 1933, 1941; WESTOLL, 1936; JARVIK, 1944b, 1948a, 1949, 1950a,b,c; JESSEN, 1966b, 1968a; and others) and rhizodontids (*Eusthenopteron*, *Tristichopterus*, *Eusthenodon*, *Platycephalichthys*, *Panderichthys*, SÄVE-SÖDERBERGH, 1932, 1933; JARVIK, 1937, 1942, 1944a, 1944b, 1950a,c, 1952, 1954, 1960, 1963a, 1966; WESTOLL, 1937c; GROSS, 1941; VOROBYEVA, 1962, 1969; BJERRING, 1967, 1971; and others). All these forms are in these regards very similar and disregarding the cosmine layer and the fact that there is an extratemporal in osteolepids but a postspiracular plate in rhizodon-

tids (see JARVIK, 1948a; BJERRING, 1972b) no differences between these two families have been recorded.

The braincase, the visceral endoskeleton, the subbranchial series, and the dermal bones and tooth-plates of the mouth cavity are completely known only in *Eusthenopteron foordi* (HOLMGREN & STENSIÖ, 1936; JARVIK, 1942, 1944a, 1954, 1960, 1963a, 1964, 1966; WESTOLL, 1943b; BJERRING, 1967, 1968, 1971) which has been investigated with the aid of Sollas' grinding method. But we know well the braincase and the hyomandibula in the post-Devonian osteolepid *Megalichthys* (ROMER, 1937, 1941; JARVIK, 1966) and have a more or less complete knowledge of the endoskeletal structures and the dermal bones of the mouth cavity in a number of Devonian forms, both osteolepids (*Osteolepis*, WATSON, 1925, 1926, 1954; HOLMGREN & STENSIÖ, 1936; JARVIK, 1942; *Gyroptychius*, JARVIK, 1942; *Glyptopomus*, JARVIK, 1950c, 1966; undetermined osteolepid, JESSEN, 1966b) and rhizodontids (*Eusthenopteron saevesoederberghi*, *E. wenjukowi*, JARVIK, 1937, 1944a; VOROBYEVA, 1962; *Eusthenodon*, JARVIK, 1952; *Platycephalichthys*, VOROBYEVA, 1962; *Panderichthys*, GROSS, 1941; as regards the braincase in the post-Devonian rhizodontid *Rhizodopsis*, see SÄVE-SÖDERBERGH, 1936). Also in these regards the various osteolepids and rhizodontids agree well with each other and if we add that the processus dermintermedius of the lateral rostral, which is an important structure indicating that the nasal cavity is subdivided in the same way as in *Eusthenopteron*, has been found in a great number of forms (see JARVIK, 1966, pp. 69–75; JESSEN, 1968a) it is evident that osteolepids and rhizodontids are very similar in all known regards and no doubt the Osteolepiformes as far as our present knowledge goes (cf. JARVIK, 1968b, p. 511) is a most uniform and homogenous group as well.

Common features

These two distinct groups have certain characters in common and have therefore often been classified together as Rhipidistia. However, as always when we claim that two groups are more closely related to each than to other groups (see JARVIK, 1968b, pp. 499–501) we cannot rely on characters that are, or may be suspected to be, primitive or on such characters that are shared with other groups. We have to rely on common specialisations, but if we ask which are the specialised characters that are common to porolepiforms and osteolepiforms and not found in any other groups the answer is not so easy to give.

One common feature of porolepiforms and osteolepiforms is the presence of an intracranial joint and structural features associated with that joint (short parasphenoid, paired subcranial muscle, large notochord, etc.). But an intracranial joint is found also in coelacanthiforms and

probably also in struniiforms and, moreover, it has during the last few years become increasingly clear that the presence of this joint implies a retention of primitive conditions. The intracranial joint cannot accordingly be used as an argument for a close relationship and the same applies in my opinion also to the presence of the lateral commissure, the otical shelf, the processus ascendens of the palatoquadrate, and other visceral elements incorporated into the neural endocranium or forming part of the palatoquadrate. Nor has it been possible to find common specialisations proving relationship in other parts of the neural endocranium and the visceral endoskeleton.

Another common feature is the presence of openings in the skeleton for the choana. The problem of the choana has been much discussed during the last few years (for review see PANCHEN 1967) but its origin is still wrapped in obscurity and disregarding the choana-like conditions in certain teleosts it is at present difficult to say if the choana is a primitive or a secondary formation. What is for example the importance of the nasal fontanelle in sharks (see JARVIK, 1942, pp. 251–252, 383)? However, is the choana a secondary acquisition, as most writers seem to take for granted, the question immediately arises if it is of independent or common origin in porolepiforms and osteolepiforms. In view of the differences in the development of the fenestra endochoanalis and adjoining structures and considering also the fact that a kind of choana has arisen secondarily in certain teleosts we cannot quite exclude the possibility of an independent origin and under these circumstances it is doubtful if the choana can be used as an argument for a close relationship. However, the fenestra exochoanalis is developed in a similar way in the two groups and there are other similarities in the exoskeleton which cannot be ignored.

The most striking resemblances of that kind are found in the lower jaw. The parasymphysial dental plates are specialised in different ways (fig. 50) but in other respects the agreement is very close (figs. 63, 64). There is a dentary of similar shape and extent and below that is a row of four infradentaries. The sutures between these bones and between them and the dentary run in exactly the same way and the second infradentary carries a vertical pit-line. Moreover there are symphysial dermal bones between the jaws, a symphysial pit, and the three coronoids and the prearticular are similar in structure. There are also considerable similarities in the development of the dermal bones of the palatoquadrate and in the dentition of the upper and lower jaws. A remarkable fact is also that the seventh submandibular from in front carries a pit-line and if we add that the sensory lines as a whole run in a similar way and that the dermal bones of the cheek and the cranial roof may be easily derived from a common ancestral pattern the only reasonable conclusion must

be that porolepiforms and osteolepiforms are closer related to each other than to any other group of fishes and therefore probably of a common ancestry. But this does not mean that we can accept Rhipidistia as a taxonomic unit (see p. 284 and JARVIK, 1968b).

Main differences

Remarks on pectoral fin. – With regard to this detailed agreement in the structure of the lower jaw, etc. it is suprising to find how different porolepiforms and osteolepiforms are in numerous important regards.

Before discussing these differences in the structure of the head attention may be called to the well-known fact that the pectoral fin in porolepiforms (fig. 59B) is long and narrow, externally somewhat suggestive of that in *Latimeria* and rather different from the paddle characteristic of osteolepiforms (fig. 59A). The endoskeleton of the pectoral fin has hitherto been unknown in porolepiforms but is partly shown in some specimens of *Glyptolepis groenlandica* (fig. 59C). It includes a kind of a central axis of at least four elements (*M1*, *M4*) rather suggestive of those in *Latimeria* (MILLOT & ANTHONY, 1958). Like in *Latimeria* these "stem elements" ("mesomeres") show some processes but the radials are still unknown and it is therefore not possible to use the pectoral fin in porolepiforms for discussions of the origin of the tetrapod limb. However, what is known is sufficient to show that indisputable porolepiforms both as to the external shape and the structure of the endoskeleton of the pectoral fin differ considerably from osteolepiforms (fig. 59A, JARVIK, 1964, 1965a, 1965b; ANDREWS & WESTOLL, 1970a, 1970b; as regards the endoskeleton of the pectoral fin in osteolepids, see JARVIK, 1959b, fig. 9; ANDREWS & WESTOLL, 1970b, fig. 3; cf. pl. 11:C,D).

Already from what has now been said I think it will be clear that we have to do with groups of a high systematic rank and because the differences between porolepiforms and osteolepiforms in the anatomy of the head, as we shall see, are profound the view (see JARVIK, 1965a, p. 120) that the differences are on a family or generic level is to be rejected as quite untenable. This applies also to the peculiar view (see JARVIK, 1966, pp. 42–43) that "the Osteolepidae differ from the Rhizodontidae as greatly as they differ from the Porolepidae and Holoptychidae combined". These views will not be further considered.

External dermal bones with discussion of certain bone homologies. – After these remarks we may turn to the external dermal bones and start with the exoskeletal shoulder-girdle. As mentioned above a remarkable fact is that the pectoral fin in porolepiforms (figs. 4, 5, 59B) arises higher up on the flank of the fish than it does in osteolepiforms

(JARVIK, 1948a, figs. 1, 2, 3G, 47, 57, 61, 64, 70, 76, 1950c, fig. 7, 1960, fig. 12). This difference is manifested in the structure of the cleithrum (figs. 52, 60). The ventral triangular portion of this bone is much longer than in osteolepiforms and sometimes a ventral portion of the bone (*Clm2*) may be separate. Other differences are that the area (*ar.e.sh*) on the inner side of the cleithrum for the attachment of the endoskeletal shoulder-girdle in porolepiforms is single, that the cleithrum is inserted in a groove in the posterior margin of the clavicle, and that the ascending process of the clavicle is a rodlike structure which continues downwards inside the vertical dorso-lateral plate and merges (*ri.vm*) on the dorsal side of the horizontal ventro-medial plate of the principal part of the bone. If it is added that the posttemporal (*Pt*, fig. 61B–D) does not meet the median extrascapular it is evident that there are considerable differences in the structure of the exoskeletal shoulder-girdle between the two groups.

In the extrascapular series (fig. 61) the median extrascapular (*Ext.m*) in porolepiforms overlaps the lateral extrascapulars (*Ext.l*) whereas it in osteolepiforms always is overlapped by these bones. Because of this surprising difference the lateral margin of the exposed part of the median extrascapular is convex in porolepiforms, but concave in osteolepiforms.

The parietal shield (fig. 61) in both groups covers the dorsal side of the otoccipital and has the same relations to the neural endocranium (fig. 104A,C). Postero-laterally there are an extratemporal (*Et*) and a supratemporal (*St*) but an important difference is that the area which in osteolepiforms is occupied by two bones, the parietal (*Pa*) and the intertemporal (*It*), in porolepiforms shows only one bone (*Pa It*). This difference has been much discussed (see e.g. LEHMAN, 1966, p. 31) and two rival theories have been set forth: 1) one of the bones has been lost and its territory has been invaded by the other bone (WESTOLL, 1937a, fig. 9c; MOY-THOMAS, 1938, p. 315, 1939, p. 90; PARRINGTON, 1949, 1956, 1967a; JARDINE, 1969, and others); 2) the two bones have fused into a compound parietointertemporal (HOLMGREN & STENSIÖ, 1936; JARVIK, 1948a, 1967b, and others). None of these theories which both rest on the assumption that the conditions in osteolepiforms are primitive can be proved but for several reasons the second theory is to be preferred and

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Fig. 59. Three photographs to demonstrate fundamental differences between, *A*, osteolepiforms and, *B*, *C*, porolepiforms in structure of pectoral fin. *A*, *Eusthenopteron foordi*. Specimen No. P. 222, Pal. Sect., Stockh. From JARVIK, 1964, fig. 25. *B*, *Holoptychius* sp. Same specimen as in fig. 6. *C*, *Glyptolepis groenlandica* n. sp. Specimen No. P. 1490, Min. Mus., Copenh. Same specimen as in pl. 19:2.

Clm, cleithrum; *E. sh*, endoskeletal shoulder-girdle; *Hu*, humerus; *M1*, *M4*, row of principal endoskeletal elements ("mesomeres") of pectoral fin; *Rr*, radius ray. *pf*, pectoral fin.

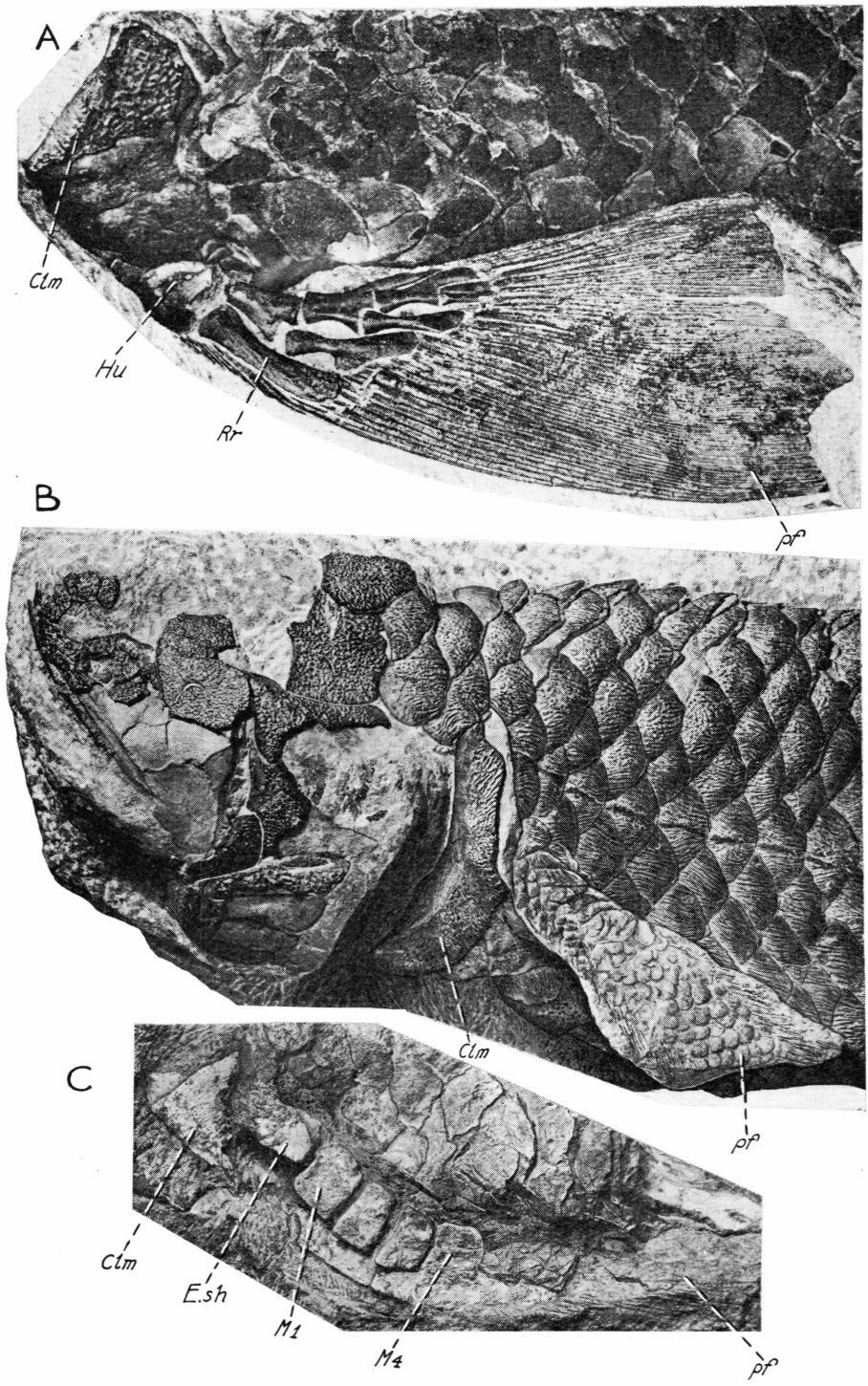


Fig. 59.

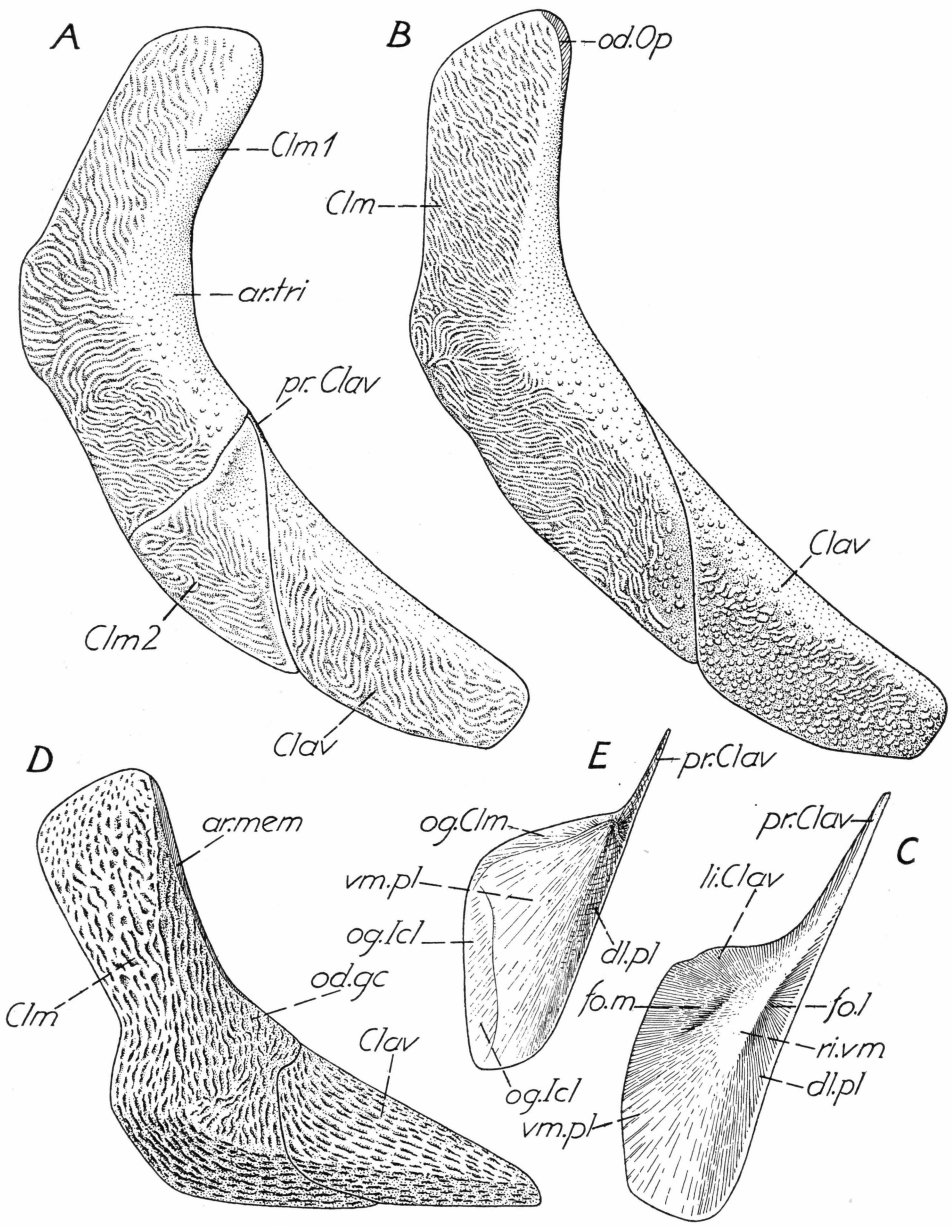


Fig. 60. Restorations of cleithrum and clavicle in lateral and of clavicle in anterodorsal aspects of *A–C*, *Holoptychius* sp., and *D*, *E*, *Eusthenopteron foordi*. *A* after specimen figured by JARVIK, 1950a, fig. 36; *D*, *E*, from JARVIK, 1944b, figs. 4, 7.

og. Clm, area of clavicle overlapping cleithrum; *og. Icl*, area of clavicle overlapping interclavicle.

For explanation of other index letters see fig. 52.

the name parietointertemporal (*Pa It*) for the large bone in porolepiforms is used in this paper.

Discussion. – When the supporters of theory 1 speak of "loss" of bones it is not easy to understand what is really meant. The dermal bones are mineralised integral parts of the skeletogenous tissue in which they are formed and when dealing with an *intact* skull-roof as in the case under discussion it is evident that no part of this tissue has got lost. What has happened is only that the intrinsic factors that govern the formation and growth of the bones have changed resulting in the formation of one bone instead of two within the same area, or we can perhaps say, in a recombination of the lepidomoria or other units of growth. When whole bones disappear as happens e.g. in the operculogular membrane at the transition from fish to tetrapod it is in the first hand the power of mineralisation of the skeletogenous tissue that disappears—an example of the general trend to a retrogressive development of the skeleton. Not until the operculogular membrane becomes partly or wholly reduced can we speak of a more substantial loss.

In favour of theory 1 reference is often made to the experiments by TATARKO (1934) which are attributed considerable importance and for PARRINGTON (1956, p. 390) "serve as a basis for discussion". TATARKO removed the subopercular in the head of the carp and found that its place was filled by further growth of the neighbouring dermal bones. What happened in this case is obviously only that the wound formed at the excision of the subopercular was healed by growth from the margins and in my opinion experiments of this kind (see also DEVILLERS & CORSIN, 1968) tell us very little of what happens under normal conditions in continuous and intact skeletogenous tissues. On the other hand, it is certainly true that dermal bones also in intact skulls may vary considerably in extent and in previous papers (1944a, p. 12, fig. 5, 1948a, pp. 61, 76–85) I have given examples of and discussed such variations. Unfortunately our knowledge of the origin and growth of dermal bones is still too incomplete to explain these variations and it is therefore to be welcomed that intense researches on these intricate subjects from morphological, histological, physiological, biochemical, and other aspects (see e.g. articles by DEVILLERS & CORSIN, LEBEDKINA, MOSS, and ØRVIG in "Nobel Symposium 4", ed. by T. ØRVIG, Stockholm 1968; see also STENSIÖ, 1961, 1964; ØRVIG, 1967) are now going on in many parts of the world. Maybe a profitable approach to these problem would be to pay more attention to the vascular system than has hitherto generally been done. After all it is the blood vessels that transport the material at the ossification of skeletogenous tissues and judging from the investigations by DZIALLAS (see JARVIK, 1967b, pp. 187–188, pl. 2) they play an important part at the formation of the centres of ossification and the growth of the dermal bones.

"Parrington's axiom 1" as recently formulated by WHITE (1965, p. 13; see also PANCHEN, 1967, p. 401) may now require some comments. This axiom says that "it is unwise to assume bone fusions without the evidence of multiple centres of radiation of either the ornament or the bone structure". A well-known fact emphasised already by GAUPP (1905, pp. 609–619; see also JARVIK, 1967b, pp. 190–191) is that *compound bones have only one centre of radiation.* Exoskeletal structures with two or more centres are to be regarded as two or more bones. More to the point, perhaps, would have been to stress the facts that the parietointertemporal in porolepiforms never has been found subdivided into its supposed components and that the intertemporal and parietal never have fused into a compound bone in osteolepiforms (as regards *Glyptopomus elginensis*, see JARVIK, 1950c, p. 13). To this more reasonable

objections to fusion I can only say that the parietal and frontal in anurans, although they arise independently in ontogeny, as far as I know, never have been found separate in the adult. Nor has the parietal in urodeles which like the frontoparietal in anurans has been proved to be a complex structure (see p. 263) been found subdivided in the adult.

A great dilemma for the supporters of theory 1 is to decide which of the bones that has grown large and replaced the other bone. Is it the intertemporal as claimed by MOY-THOMAS and WESTOLL or is it the parietal as maintained by PARRINGTON? No safe answer can be given and the different decisions made by these writers are conjectural. To base a nomenclature on a guess is certainly not very attractive and already for this reason the term parietointertemporal is to be preferred. This term tells at once that the area of the skull-roof which in osteolepiforms shows two bones in porolepiforms is occupied by a single ossification. The use of this term facilitates the comparison between the two groups and informs us that they in this particular regard differ from each other; and this irrespectively which of the two rival theories is correct or if—as is a third possibility seriously to be taken into consideration—the large bone in porolepiforms has arisen independently early in phylogeny in the same way as have other large bones (parietal, frontal, opercular, etc).

The bone pattern of the parietal shield in porolepiforms is surprisingly constant and only one case of subdivision (of the supratemporal) has been recorded. In the corresponding area of osteolepiforms, on the other hand, such occasional subdivisions are common and as is well known they occur more or less frequently also in other fishes and in tetrapods (JARVIK, 1944a, 1947, 1948a, 1950a,c; LEHMAN, 1961; STENSIÖ, 1969).

These occasional bones, often dismissed as curiosities, no doubt give us important clues as to the composition of the dermal bones and indicate that the bones which become subdivided are complex structures. The compound nature of dermal bones is also evidenced by a great number of embryological investigations which have shown that many adult dermal bones are the products of fusions of primordia that are independent in ontogeny. Recent anurans and urodeles provide good examples of such fusions.

A well-known fact is that the frontal and the parietal arise separate in anurans (see JARVIK, 1967b, p. 194) and that they soon fuse into a single bone, the frontoparietal. In previous papers (1942, 1963a, 1966, 1967b, 1968b) I have demonstrated a most close agreement in the structure of the head between anurans and osteolepiforms and of particular interest in this connection is that the frontal in the ontogeny of frogs appears in a place closely corresponding to that where the centre of radiation of the frontal in osteolepiforms is situated (fig. 104A, B). Moreover it has been shown that the parietal in the frog embryo first appears in a place which has exactly the same position in relation to the semicircular canals, the fossa bridgei, the occipital artery, the crista parotica and other structures lying close below the cranial roof, as has the centre of radiation of the parietal in osteolepiforms. Furthermore it has been shown that bones corresponding to the intertemporal, the supratemporal and the median extrascapular in osteolepiforms sometimes are developed in anuran tadpoles. This most remarkable condition that the pattern of dermal bones characteristic of osteolepiforms has been retained in anuran tadpoles can only mean that the primordia of the frontal, parietal, intertemporal, etc. in anuran ontogeny are of a phylogenetic importance. Moreover the very close agreement between osteolepiforms and anurans in numerous regards and the identical position of the dermal bones in relation to adjoining endoskeletal structures must imply that the frontal of osteolepiforms is homologous with the frontal of anurans and accordingly also with that in

reptiles and mammals and that the osteolepiform parietal is a true parietal. It is because of these facts and not on a direct comparison between osteolepiforms and the rabbit (PARRINGTON, 1967a, pp. 231–232) that I recently (1967b) in agreement with SCHMALHAUSEN (1950) has found it necessary to reject the nomenclature for the dermal bones of the cranial roof in fishes suggested by WESTOLL and to accept the nomenclature elaborated and adopted by a great number of distinguished anatomists and still used by most zoologists.

In urodeles, too, most interesting conditions with regard to the composition of the dermal bones have recently been discovered. When H. BJERRING in this institute some time ago studied serial sections of a 19.3 mm embryo of *Hynobius retardatus* he discovered a row of three separate ossifications in the posterior 3/4 of the lower jaw, so situated that they evidently correspond to infradentaries 2,3 and 4 in porolepiforms (and osteolepiforms). In later stages the primordia had fused into a single bone ("Angular", STADTMÜLLER, 1936, p. 654). Interesting conditions have been found also by LEBEDKINA. As demonstrated by her (1964b) the nasal in urodeles arises by fusion of originally separate nasal and postrostral primordia but of greater interest in this connection is her discovery that also the parietal in hynobiid urodeles (*Ranodon*) arises from separate primordia and is a complex structure (fig. 104D; SCHMALHAUSEN, 1968, pp. 221–222). The description given by SCHMALHAUSEN is a little indistinct but so much is clear that the urodele parietal includes equivalents also to the lateral extrascapular (called postparietal by SCHMALHAUSEN) and the supratemporal of the porolepiform ancestors (see also p. 263). The fact that the parietals of urodeles probably include equivalents not only to the whole parietal shield but also to the extrascapular series of porolepiforms is to be kept in mind when we use the term parietal with reference to urodeles (cf. JARVIK, 1948a, p. 81).

The examples now given show that the occurrence of several dermal bone primordia in the ontogeny of both anurans and urodeles is a recapitulation of ancestral conditions and no doubt these primordia are of phylogenetic importance. But these examples show also that fusions of bones in ontogeny are more common in tetrapods than has hitherto been known; and because fusions occur frequently in tetrapods it seems reasonable to assume that fusions have played an important part at the formation of the pattern of dermal bones in their piscine ancestors as well. These and many other facts support the view that the large bone in the parietal shield of porolepiforms is a complex structure and provided independent parietals and intertemporals have been present in their ancestors it most likely is a product of fusion of these bones and is a parietointertemporal.

This view is also supported by the position of the centre of radiation. In previous papers (1944a, 1947, 1948a) I have demonstrated many cases of fusions of bones both in fossil and recent fishes. In one skull of *Acipenser* (1948a, figs. 18C, 19C), for example, the area which generally is occupied by the right parietal and the median extrascapular shows only one bone, termed parietoextrascapular. The centre of radiation of this compound bone lies farther back than the centre of the parietal of the left side and antero-laterally to the place where the centre of the median extrascapular generally lies. In other words the new centre of the compound bone has been formed between the centres of its components and this is clearly what has happened also in porolepiforms. The centre of radiation of the parietointertemporal is situated farther antero-laterally in relation to the neural endocranium than the centre of the osteolepiform parietal and farther postero-medially than the centre of the osteolepiform intertemporal.

In this discussion of the porolepiform parietointertemporal hitherto only the membraneous components of the dermal bones have been considered. But dermal

bones may also contain another category of elements, the lateral sensory components (see JARVIK, 1967b, p. 191). These components which generally form bony gutters or cylinders arise independently, probably upon stimulation from the neuromasts and as demonstrated by the often quoted experiments by MOY-THOMAS (1941; see also DEVILLERS & CORSIN, 1968, p. 414) they do not develop if the primordia of the sensory canals are removed in early embryos. Later in ontogeny these gutters or cylinders often become incorporated into the underlying bone, and no doubt the osteolepiform intertemporal and the porolepiform parietointertemporal include such lateral sensory components. An interesting but still unexplained fact is that the sensory lines generally run through or close to the centres of radiation of the sensory line bones. This association with the centres of radiation is retained at the fusion of bones and the sensory lines of the bones that fuse will therefore move so as to pass close to the centre of radiation of the compound bone and this is true both of sensory canals and pit-lines (cf. PARRINGTON's axiom 2; White 1965, p. 13; see also below p. 152). Many examples of such displacements of sensory lines have been given in previous papers (1947, 1948a, 1967a, 1967b; see also pp. 136–137) and they are very distinct in the parietal shield of porolepiforms. At the fusion which in my opinion most likely has occurred between the parietal and the intertemporal the sensory canal of the latter bone has been dragged medially in the same way as has e.g. the supraorbital canal in the skull of *Acipenser* at the fusion between the lateral and medial frontals (see JARVIK, 1948a, figs. 18A, 19A, B), and the parietal pit-lines have moved antero-laterally. Quite naturally the supratemporal pit-line is generally not influenced but in the case it is continuous with the transverse parietal pit-line its medial part may be dragged forward as has happened in a specimen of *Porolepis* (fig. 57B) and in *Latimeria* (MILLOT & ANTHONY, 1958, pls. 19, 20).

In the fronto-ethmoidal shield (fig. 61) of porolepiforms independent dermosphenotic is lacking and most likely this element—if present in their ancestors—has fused with the frontal into a frontodermosphenotic (*FrD*). Pineal foramen is lacking in porolepiforms but between the anterior parts of the frontodermosphenotics is a single often distinctly domed pineal plate (*Pi. pl*). On the ventral side of that plate is a pit subdivided by a median ridge into unsymmetrical halves for the pineal and parapineal organs. In osteolepiforms the frontal (*Fr*) and dermosphenotic (*D* are independent and at any rate in the Devonian forms there is a pineal foramen surrounded by a ring of several small pineal plates (*Pin. pl*). The fact that pineal foramen may be lacking in post-Devonian osteolepiforms such as *Megalichthys* is a consequence of the same trend as we find in other groups of fishes, e.g. palaeoniscids.

The porolepiforms have a separate median rostral (*Rm*) pierced by the ethmoidal commissure whereas the lateral rostral has fused with the premaxillary forming a rostropremaxillary (*RP*, figs. 61,63). But in osteolepiforms there are medial rostrals that have fused with the premaxillary and generally also with the foremost nasal forming a nasorostropremaxillary (*NRP*). The lateral rostral (*Rl*) is independent. This bone (fig. 62A) which consists of three parts, pars facialis, pars palatina (*Rl.pal*), and processus dermintermedius (*pr. dim*) and is pierced by the infraorbital sensory canal forms the ventral margin of the fenestra exonarina

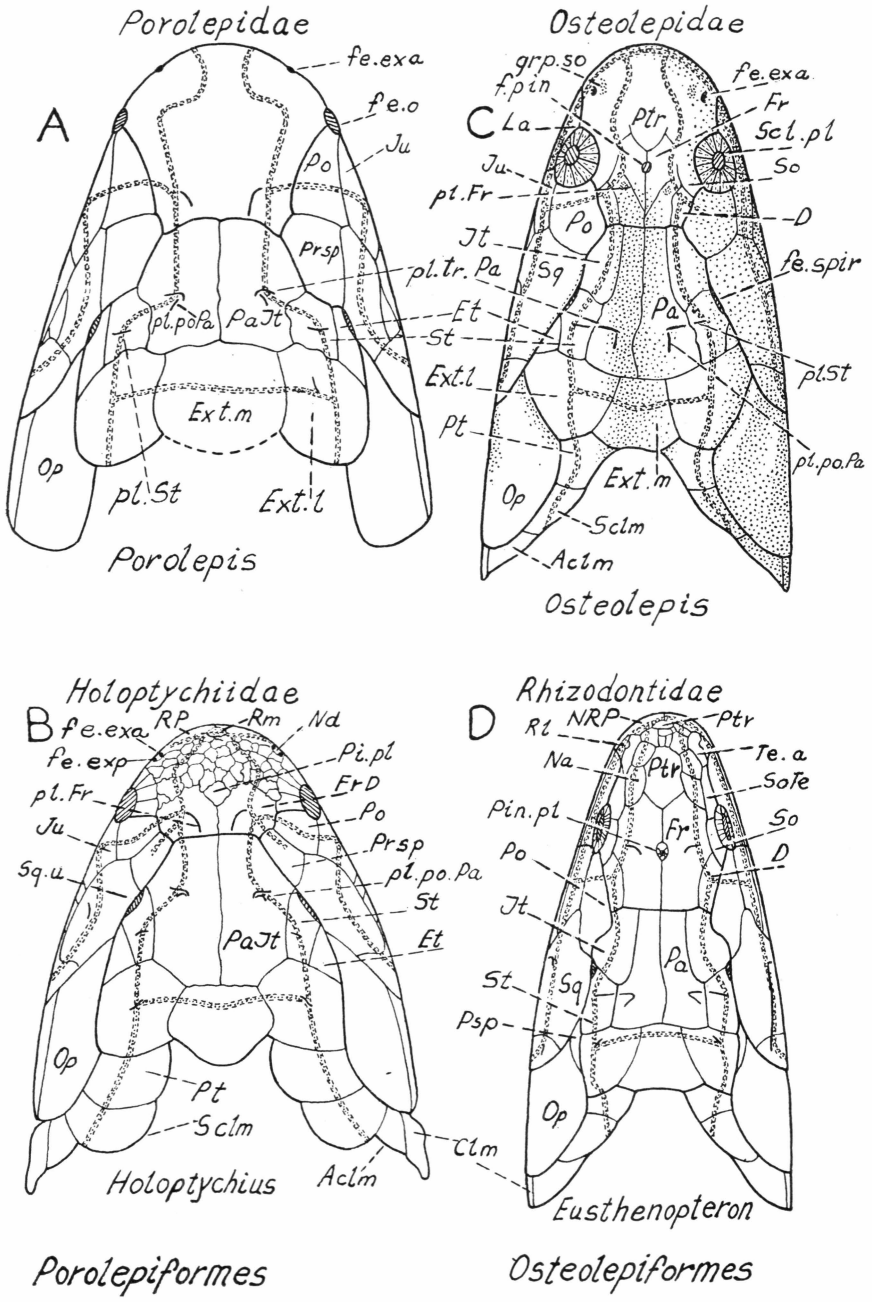


Fig. 61. Skulls in dorsal aspects to demonstrate differences in patterns of dermal bones and sensory lines between, *A*, *B*, porolepiforms and *C*, *D*, osteolepiforms and similarities between, *A*, porolepids and, *B*, holoptychiids and between, *C*, osteolepids, and, *D*, rhizodontids. *C*, after JARVIK, 1948a, figs. 32B, 37B. *D*, after JARVIK, 1944a, fig. 2C.

For explanation of index letters see fig. 63.

anterior. In porolepiforms the conditions are very different. In addition to the fenestra exonarina anterior (*fe. exa*) they have also a fenestra exonarina posterior (*fe. exp*) separated from the anterior aperture by a small guttershaped bone, the nariodal (*Nd*), with deep notches (*i. exa*, *i. exp*, fig. 62C) for the nasal tubes at its anterior and posterior ends. As demonstrated in previous papers (1964, 1966) the nariodal ("dermonariodal") corresponds to the bone which I (1942) have termed nariodal in urodeles whereas the septomaxillary of anurans and other eutetrapods (fig. 62B) is to be derived from the osteolepiform lateral rostral. These views have been generally accepted but several writers are of the opinion that the nariodal of urodeles is a true septomaxillary homologous with that in anurans. If true this must mean that the porolepiform nariodal is homologous with the lateral rostral.

Discussion. – In 1942 it was generally assumed that the nariodal of urodeles is an endoskeletal ossification and in accordance with this view I claimed that it is derived from the guttershaped part of the lateral wall of the nasal capsule in porolepiforms (fig. 77A) that is situated between the fenestra endonarina anterior and the fenestra endonarina posterior and which also in other regards agrees closely with the urodele nariodal. However, according to investigations carried out after 1942 by SCHMALHAUSEN (1958a, 1968) and many others the nariodal is a dermal bone and only for this reason it has been taken for granted that it must be homologous with the anuran septomaxillary, a dermal bone. But this is certainly a premature conclusion. It remains to be proved that the porolepiform nariodal and the osteolepiform lateral rostral are homologous, a problem that has recently been tackled by PANCHEN (1967).

PANCHEN first considers the fact that the lateral rostral in contrast to the nariodal is a sensory canal bone but accepting PARRINGTON's view (1956, p. 410) "that lateral line canals are not constant in their relations to dermal bones" he claims that the sensory canals are of no importance at the consideration of homology. However, a fact not so easily dismissed is that the osteolepiform lateral rostral includes lateral sensory components (cf. p. 150) and accordingly it no doubt is a more complex structure than the nariodal and already for this reason not strictly homologous with that bone. Moreover lateral sensory components more or less corresponding to those in the osteolepiform lateral rostral have become incorporated in the porolepiform rostropremaxillary but no explanation is given why the "precursors of the dermal bones attract the growing primordia of the lateral line system" ("PARRINGTON's axiom 2", WHITE, 1965, p. 13; PANCHEN, 1967, p. 401). Sensory lines, both canals and pit-lines, certainly may move but that this happens quite arbitrarily as PARRINGTON seems to believe is unlikely. As discussed above (p. 150) one case when sensory lines move is at the fusion of bones but they may of course move also for other reasons e.g. when the whole tissue to which they belong moves in connection with a remodelling of a part of the head. This is what has happened at the changes in the position of the nostrils.

As is well known one or both external nostrils may be situated close to the margin of the mouth, a condition which several writers (SÄVE-SÖDERBERGH, 1932, p. 98; SCHMALHAUSEN, 1964, 1968; PANCHEN, 1967) believe to be primitive. However, as I have strongly emphasised at several occasions (1942, pp. 278–280, 622, 1952, p. 80, 1968a, p. 232), in all cases when such a ventral position is found, e.g. in certain sharks, in holocephalians, in dipnoans and in ichthyostegids it is always associated

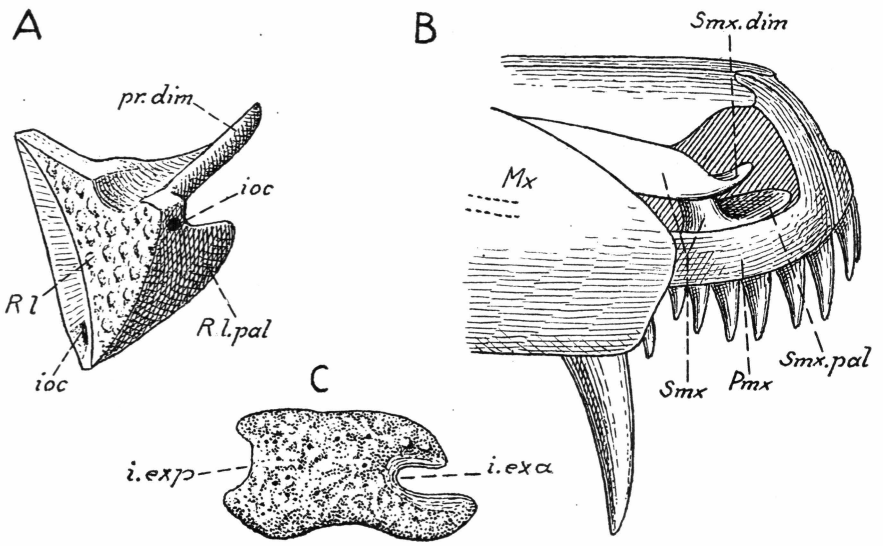


Fig. 62. Three representations to demonstrate similar development of lateral rostral in osteolepiforms and septomaxillary in primitive reptiles and different development of nariodal in porolepiforms. *A*, *Eusthenopteron foordi*, lateral rostral in lateral view. × 5/1. From JARVIK, 1942, fig. 86. *B*, *Scylacosaurus*, a Permian therocephalian reptile. Anterior part of the skull in antero-lateral view. After WEGNER from JARVIK, 1942, fig. 86. *C*, *Holoptychius* sp. Restoration of nariodal in lateral view. After specimen in fig. 6. × 6/1.

Mx, maxillary; *Pmx*, premaxillary; *Rl*, lateral rostral (pars facialis); *Rl. pal*, processus palatinus of lateral rostral; *Smx*, septomaxillary (pars facialis); *Smx. dim*, processus dermintermedius of septomaxillary; *Smx. pal*, processus palatinus of septomaxillary.

i. exa, *i. exp*, notches for anterior and posterior nasal tubes; *ioc*, infraorbital sensory canal; *pr. dim*, processus dermintermedius of lateral rostral.

with considerable modifications at the jaw margin below the nostrils, and this can only mean that the ventral position of the nostrils is secondary. Of particular interest in this connection is that the part of the infraorbital sensory canal that is situated below the nostrils, and which e.g. in osteolepiforms in which the external nostril lies well above the margin of the upper jaw has a straight course, has been pushed downwards and if not interrupted (holocephalians, dipnoans) it runs in a curve below the nostril. An interesting feature in porolepiforms is now that the infraorbital sensory canal in the anterior part of the lachrymal turns sharply ventrally (*iocv*, figs. 7, 79 D) to pass forwards ventrally to the posterior external nostril. This condition strongly suggests that the ventral position of that nostril in porolepiforms is secondary, and it is possible that it is the pressure exercised on the infraorbital canal at the ventral migration of the posterior nostril that has contributed to the incorporation of lateral sensory components into the rostropremaxillary. But let us now imagine that we remove the lateral sensory component—that is a cylindrical piece of bone similar to the lateral rostral in *Ichthyostega*—from the osteolepiform lateral rostral. As is readily seen this operation will result in a non-canal bone but it will not influence the shape of the bone. It will still consist of a pars facialis, a pars palatina and a

processus dermintermedius and it will be suggestive of the septomaxillary shown in fig. 62 B. We can now say that both this presumed non-canal bone and the porolepiform nariodal fall into the category of bones that I have termed anterior tectals. But as is well shown in particular in the material of *Holoptychius* from East Greenland (figs. 35–37; see also fig. 34 A; as regards osteolepiforms see WESTOLL, 1936; JARVIK, 1948 a, p. 50) the anterior tectals are subject to very strong variations as to number and extent and to establish safe homologies in this variable mosaic of bones is a hopeless task. Of greater importance than the question of homology is the fact that the porolepiform nariodal and the osteolepiform lateral rostral have become specialised in different fashions (see pp. 190–192). It is because of their different position in relation to the fenestra exonarina anterior and their very different structure and different relations to the associated nasal structures that these bones are to be kept apart under different names and it was because the urodele nariodal and the anuran septomaxillary differ in a corresponding way that I in 1942 found it necessary to introduce a new name for the bone previously called septomaxillary in urodeles.

In the external cheek-plate, too, porolepiforms and osteolepiforms differ considerably (fig. 63). The lachrymal (*La*) in porolepiforms is thickened and rests on the likewise thickened anterior end of the maxillary. Moreover it has a notch at its anterior end for the posterior external nasal tube, sometimes continued by a groove for that tube on the external side of the bone. In other respects the lachrymal resembles that

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Fig. 63. Skulls in lateral aspects to show differences in patterns of dermal bones and sensory lines between, *A*, *B*, porolepiforms and, *C*, *D* and osteolepiforms and similarities between, *A*, porolepids and, *B*, holoptychiids and between, *C*, osteolepids and, *D*, rhizodontids. *C*, after JARVIK, 1948 a, figs. 32 A, 37 A. *D*, after JARVIK, 1944 a, fig. 2 A.

Aclm, anocleithrum; *Clav*, clavicle; *Clm*, cleithrum; *D*, dermosphenotic; *De*, dentary; *Et*, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *Fr*, frontal; *FrD*, frontodermosphenotic; *G*, principal gular plate; *Gm*, median gular plate; *Gm1*, *Gm2*, anterior and posterior median gular plates; *Iclav*, interclavicle; *Id. 1*, *Id. 2*, *Id. 3*, *Id. 4*, infradentaries 1, 2, 3, and 4; *It*, intertemporal; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Nd*, nariodal; *NRP*, nasorostropremaxillary; *Op*, opercular; *Pa*, parietal; *PaIt*, parietointertemporal; *Pin. pl*, pineal plates of osteolepiforms; *Pi. pl*, single pineal plate of porolepiforms; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Psp*, postspiracular plate; *Pt*, posttemporal; *Ptr*, postrostral; *Qj*, quadratojugal; *Rbr*, branchiostegal rays; *Rl*, *Rm*, lateral and median rostrals; *RP*, rostropremaxillary; *SbmRbr*, submandibulobranchiostegal plate; *Sbm1–Sbm9*, submandibulars 1–9; *Sclm*, supracleithrum; *Scl. pl*, sclerotic plates; *So*, supraorbital; *Sop*, subopercular; *SoTe*, supraorbitotectal; *Sq*, squamosal; *Sq. l*, *Sq. u*, lower and upper squamosals; *St*, supratemporal, *Sy*, symphysial dermal bones; *Te. a*, anterior tectal.

fe. exa, *fe. exp*, fenestra exonarina anterior and posterior; *fe. o*, orbital fenestra; *fe. spir*, spiracular fenestra; *f. pin*, pineal foramen; *grp. so*, group of pores for special sensory organs; *pl. Fr*, frontal pit-line; *pl. G*, *pl. Gm*, pit-lines of principal and median gulars; *pl. Id. 2*, pit-line of infradentary 2; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. Qj*, quadratojugal pit-line; *pl. Sbm7*, *pl. Sq*, *pl. St*, pit-lines of submandibular 7, squamosal and supratemporal; *pl. tr. Pa*, transverse parietal pit-line.

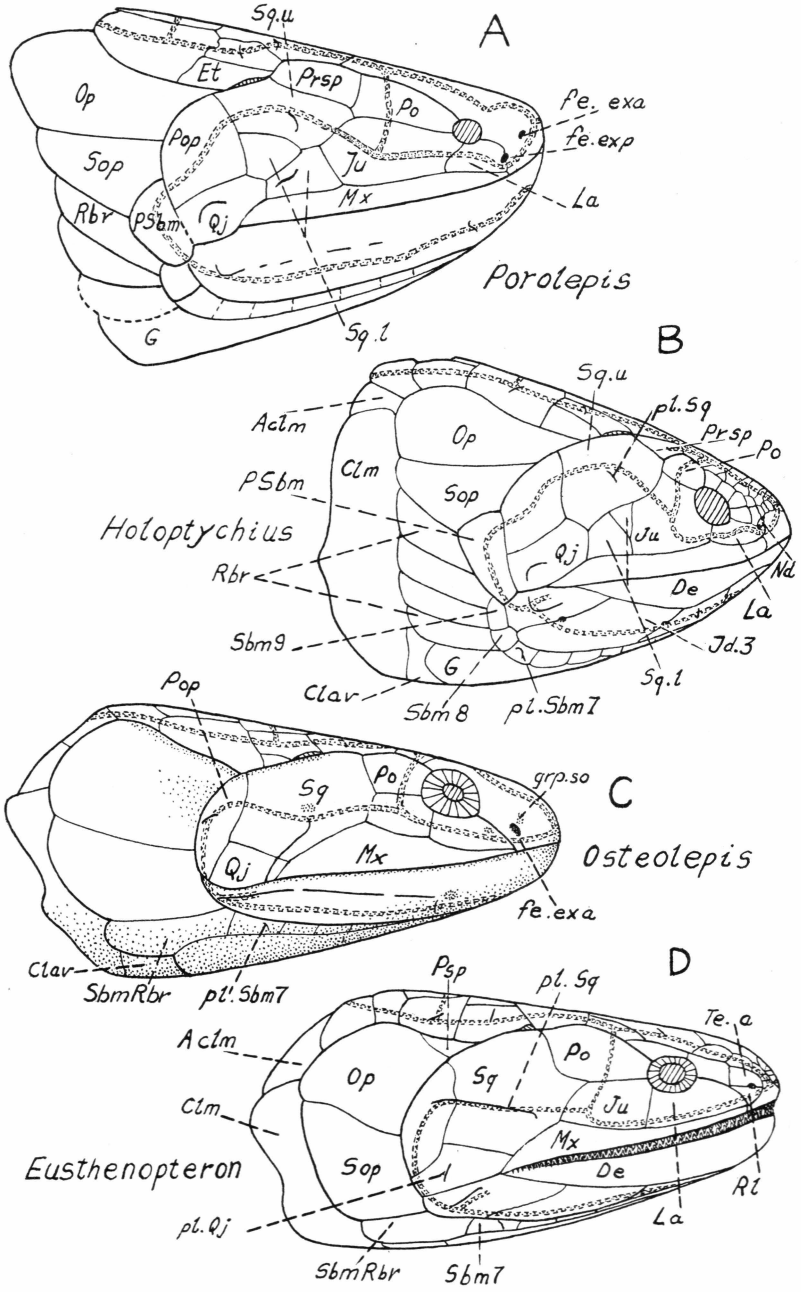

A
Sq.u
Et
Prsp
Op
Po
Pe. exa
Pop
fe.exp
Sop
Ju
Mx
La
Rbr
PSbm
Qj
Porolepis
G
Sq.l
B
Sq.u
pl.Sq
Aclm
Op
Prsp
Po
PSbm
Clm
Sop
Holoptychius
Ju
Qj
Rbr
Nd
De
La
Sbm9
Jd.3
G
Clav
Sbm8
pl.Sbm7
Sq.l
Pop
Sq
Po
grp.so
C
Osteolepis
Qj
Mx
fe.exa
Clav
SbmRbr
pl.Sbm7
D
Psp
pl.Sq
Te.a
Aclm
Op
Sq
Po
Clm
Ju
Mx
Eusthenopteron
Sop
De
Rt
La
pl.Qj
SbmRbr
Sbm7

Fig. 63.

in osteolepiforms and the jugal (*Ju*), the postorbital (*Po*), the preopercular (*Pop*) and the quadratojugal (*Qj*) require no special comments. The maxillary (*Mx*) is, as seen in external view, suggestive of that in osteolepiforms, but it lacks the anterior ascending process characteristic of that group (see JARVIK, 1966, p. 77) and, moreover, it has a palatal lamina. An important difference between the two groups is that porolepiforms have a prespiracular plate (*Prsp*). This plate which like the other dermal bones of the cheek is situated outside the palatoquadrate must not be confused with the supratemporal, intertemporal or dermosphenotic of the osteolepiforms which belong to the cranial roof and cover the dorsal side of the braincase (cf. PARRINGTON, 1949, fig. 1, 1956, p. 408, fig. 7, 1967a, p. 238; JARDINE, 1969). Moreover porolepiforms have an upper (*Sq.u*) and several lower squamosals (*Sq.l*) and the jugal sensory canal runs in a curve through the centre of radiation of the upper squamosal to join the infraorbital canal in the jugal at a characteristic acute angle. In osteolepiforms there is always a single squamosal (*Sq*) and the jugal canal runs almost straight forwards to the infraorbital canal. This difference is easily accounted for if we assume that the porolepiform squamosals fuse into a single bone. The centre of this compound bone will be situated farther ventrally than that of the upper squamosal and the jugal canal will be straighthened out and run as in osteolepiforms. A most important difference is, finally, that preopercular lateral sensory components in porolepiforms very likely have fused with submandibulars forming a preoperculosubmandibular (*PSbm*). As a consequence of this fusion the preopercular canal has been dragged out backwards forming a characteristic loop.

The preoperculosubmandibular which has no equivalent in osteolepiforms is situated wholly behind the palatoquadrate, outside the symplectic, and belongs to the bones of the operculogular membrane rather than to the cheek. Ventrally to this bone porolepiforms show one or two independent submandibulars (*Sbm 8*, *Sbm 9*) which have no equivalents in osteolepiforms or possibly enter into the bone in them which I have termed the submandibulobranchiostegal plate (*SbmRbr*; JARVIK, 1963a, p. 13). The operculogular series, too, is distinctly different in the two groups (figs. 63, 64). The opercular and the subopercular have a characteristic shape in porolepiforms and below the subopercular are several independent branchiostegal rays (*Rbr*). Moreover, the gular plate posteriorly extends higher up on the side of the head than in osteolepiforms and one of the gular plates is overlapped by that of the other side, whereas in osteolepiforms the two gular plates meet in the median line without overlapping.

With regard to the external dermal bones of the head it may finally be mentioned that disregarding small patches of cosmine in one specimen

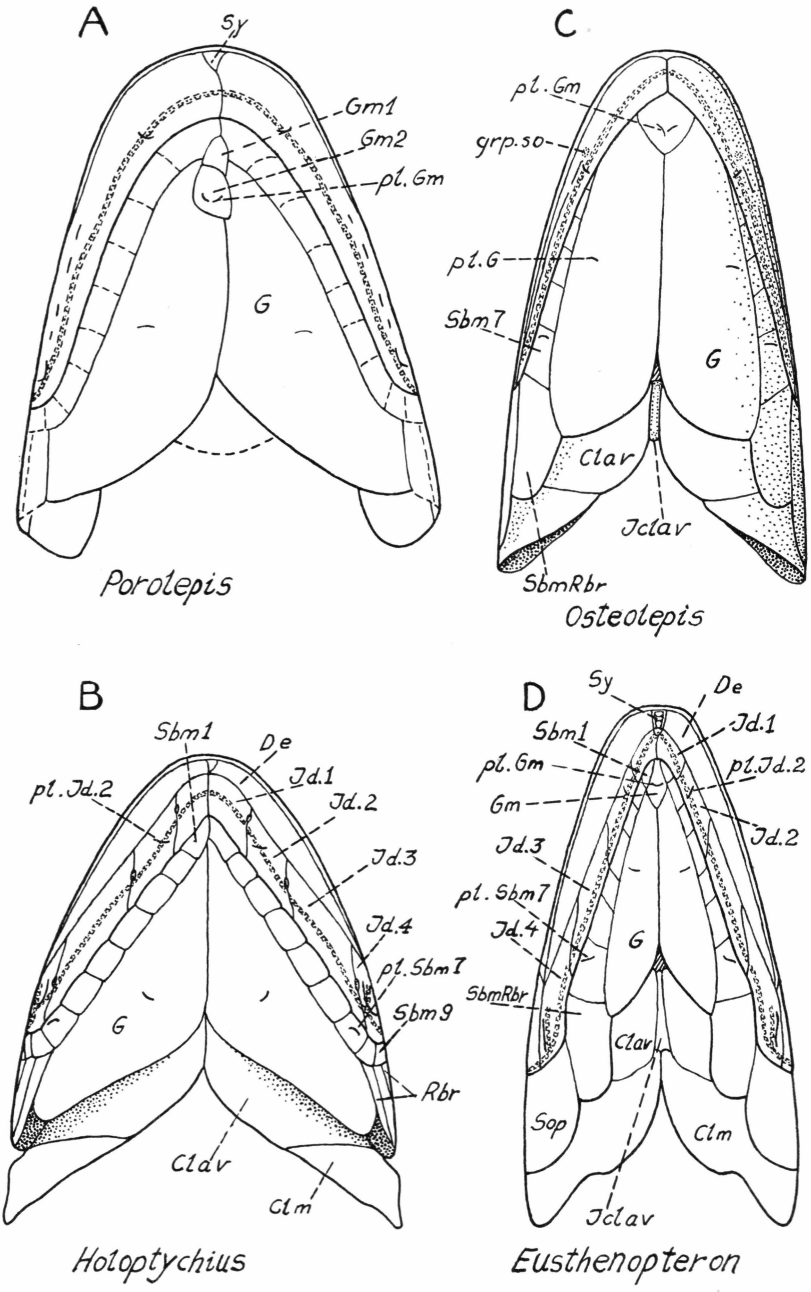


Fig. 64. Skulls in ventral aspects to show differences and similarities in patterns of dermal bones and sensory lines between *A*, *B*, porolepiforms and *C*, *D*, osteolepiforms. *C*, after JARVIK, 1948a, figs. 32C, 37C. *D*, after JARVIK, 1944a, fig. 2D.

For explanations of index letters see fig. 63.

of *Porolepis* (pl. 8:4) no blisters have been observed in the head of porolepids (as regards blisters on scales see ØRVIG, 1969a, pp. 248–249, fig. 2).

Sensory lines. – The tubes of the sensory canals branch richly even in the Lower Devonian porolepids and certain sensory canals and pit-lines have become displaced in connection with fusion of bones but in other respects no differences of any importance have been observed. A remarkable fact, however, is that no groups of small pores for special sensory organs have been found in the cosmine layer of porolepids (see JARVIK, 1966, p. 77).

Dermal bones of mouth cavity. – The vomer and the parasphenoid will be discussed below (pp. 166, 171–172) and at this place should only be mentioned: 1) that the parasymphysial dental plate in porolepiforms as compared with that in osteolepiforms is a highly specialised structure carried by the modified anterior part of the dentary (figs. 47–50), 2) that the entopterygoid and the lateral tooth-bearing bones of the palatoquadrate overlap each other in different ways (fig. 32), 3) that porolepiforms have upper and lower oral dental plates in the anterior part of the mouth cavity (figs. 24E–G, 30, 72, 73, 102E), 4) that the dental plates of the

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Fig. 65. Two photographs to illustrate some fundamental differences in snout structure between osteolepiforms and porolepiforms. *A*, *Eusthenopteron foordi*. Anterior part of divisio cranialis anterior in ventral aspect. Specimen No. P. 341, Pal. Sect., Stockh. Same specimen as figured by JARVIK, 1942, pl. 8:1, 1966, fig. 18A. *B*, *Porolepis brevis*. Holotype. Divisio cranialis anterior in ventral aspect. From JARVIK, 1942, pl. 4:1.

Enpt, entopterygoid; *P*, parasphenoid; *Vo*, vomer.

art.ap, area articulating with processus apicalis of palatoquadrate; *art.e*, area articulating with ethmoid articular process of palatoquadrate; *ar.Vo*, vomeral area; *cav. in*, cavum internasale; *cav. nc*, cavity of nasal capsule; *c. iv*, intervomerine canal; *c. nbv*, ventral branch of naso-basal canal; *co*, posterior corner of postnasal wall; *c.o.lat*, canal for r. ophthalmicus lateralis; *c.orp*, posterior canal of orbito-rostral passage; *c.palal*, *c.pall*, *c.palm*, antero-lateral, lateral and medial branches of palatine canal of vomer; *c. pna*, anterior palato-nasal canal; *c. pr*, profundus canal; *c. prl*, lateral profundus canal; *d. pnc*, ventral side of divisio prenasalis communis of ethmosphenoid exposed in anterior palatal fenestra; *fe. ench*, fenestra endochoanalis; *fe. exch*, fenestra exochoanalis; *fe. pal*, anterior palatal fenestra; *fe.vl*, fenestra ventro-lateralis; *fo.ap*, fossa apicalis; *fo.aup*, fossa autopalatina; *fo. iv*, intervomerine pit; *fo. nc*, pit for anterior end of notochord; *fo. pren*, prenasal pit; *gr. orp*, posterior groove of orbito-rostral passage; *i. exp*, notch in margin of fronto-ethmoidal shield for posterior nasal tube; *ioc*, infraorbital sensory canal; *lal.Vo*, rostro-caudal part of ventral tooth-bearing lamina of vomer; *la.pal*, palatal lamina of fronto-ethmoidal shield; *lat.Vo*, transverse part of ventral tooth-bearing lamina of vomer; *od. La*, area overlapped by lachrymal; *pr. bp*, basipterygoid process; *pr. conn*, processus connectens; *pr. vl*, ventro-lateral process of postnasal wall; *pr.Vo*, antero-lateral process of vomer; *pr.Vop*, posterior process of vomer; *ri. in*, internasal ridge; *ri. P*, tooth-bearing ridge of parasphenoid; *te. o*, tectum orbitale; *vot*, vomerine tusk; *w. pn*, postnasal wall.

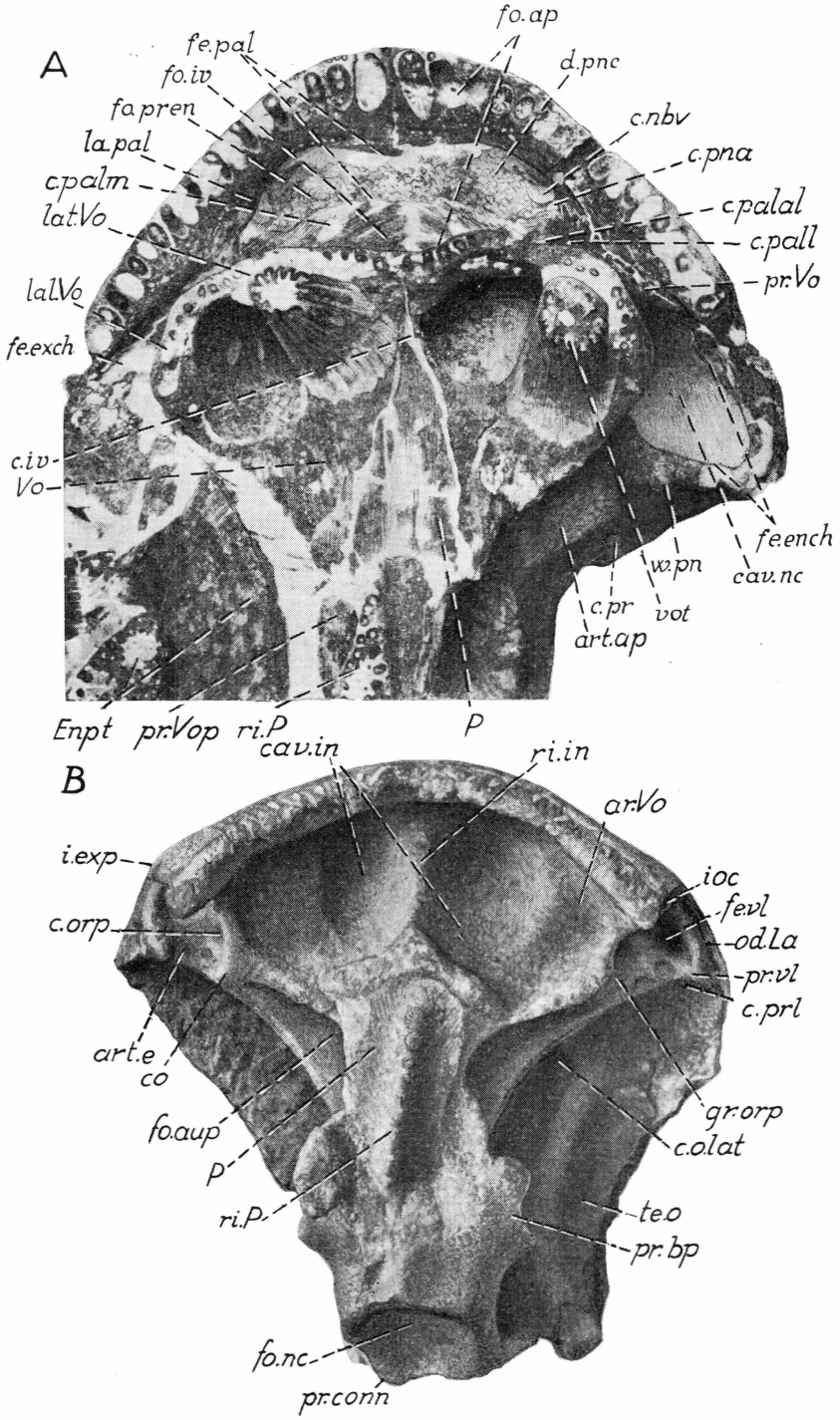

A
fo.ap
fe.pal
fo.iv
d.pnc
fa.pren
c.nbv
la.pal
c.pna
c.palm
c.palal
lat.Vo
c.pall
pr.Vo
lal.Vo
fe.exch
c.iv-
Vo
fe.ench
w.pn
cav.nc
c.pr
vot
art.ap
Enpt
pr.Vop
ri.P
P
B
cav.in
ri.in
ar.Vo
i.exp
ioc
fe.vl
c.orp
od.La
pr.vl
c.prl
art.e
co
gr.orp
fo.aup
c.o.lat
P
ri.P
te.o
pr.bp
fo.nc
pr.conn

Fig. 65.

visceral arches are weakly developed and 5) and that porolepiforms lack spiracular and ceratohyal dental plates.

Neural endocranium and certain adjoining dermal bones. – As demonstrated in 1942 porolepiforms and osteolepiforms differ widely from each other in the structure of the ethmoidal region and the snout as a whole. The differences were in fact found to be so great that if "we were to judge solely from the snout we should probably regard *Osteolepiformes* and *Porolepiformes* as fairly remote groups, which must be classified far apart" (JARVIK, 1942, p. 493). Later investigations of *Glyptolepis* with the aid of Sollas' grinding method and other studies of both porolepiforms and osteolepiforms (see also JARVIK, 1962, 1963a, 1965a, 1966) have fully confirmed the results gained in 1942; but they have also added several new data and as is now clear osteolepiforms and porolepiforms are even more distinct from each other than there was reason to suspect in 1942. The main differences in the structure of the braincase may be summarised as follows (cf. JARVIK, 1942, pp. 489–493).

1) The nasal cavity in osteolepiforms is subdivided anteriorly and antero-laterally into a recessus superior, a recessus medius and a recessus inferior. The nasal cavity in porolepiforms shows no signs whatever of a subdivision into such compartments. The subdivision in osteolepiforms is effected by several processes and crests, viz. the processus intermedius (*pr. im*) of the lamina nariochoanalis, the lateral horizontal ridge (*ri. lh*),

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Fig. 66. Four almost transverse sections through, *A*, *B*, fenestra exonarina anterior and, *C*, *D*, fenestra exochoanalis to show fundamental differences in these parts of snout between, *A*, *C*, porolepiforms (*Glyptolepis groenlandica*) and, *B*, *D*, osteolepiforms (*Eusthenopteron foordi*), *A*, *C*, sections Nos. 35 and 58 of grinding series of *Glyptolepis groenlandica* (see also fig. 8). × 3/10. *B*, *D*, sections Nos. 44 and 32 of grinding series 1 of *Eusthenopteron foordi* (see also JARVIK, 1942, pls. 11–13). × 3/10.

La, lachrymal; *Mx*, maxillary; *NRP*, nasorostropremaxillary; *Ptrm*, posterior median postrostral; *Rl*, lateral rostral; *Rl. pal*, palatal lamina of lateral rostral; *RP*, rostropremaxillary; *Vo*, vomer.

cav. in, internasal cavity; *cav. nc*, cavity of nasal capsule; *c. cut. v*, canal for cutaneous vessel; *c. nb*, naso-basal canal; *c. nta*, canal for anterior nasal tube; *c. o. lat*, canal for r. ophthalmicus lateralis; *cr. rc*, crista rostro-caudalis; *fe. ench*, fenestra endochoanalis; *fe. exa*, fenestra exonarina anterior; *fe. exch*, fenestra exochoanalis; *fe. exp*, fenestra exonarina posterior; *fe. vl*, fenestra ventro-lateralis; *gr. mn*, groove for r. medialis narium; *ioc*, infraorbital sensory canal; *la. nch*, lamina nariochoanalis; *la. pal*, palatal lamina; *la. Vo*, vertical tooth-bearing lamina of vomer; *pr. dim*, processus dermintermedius of lateral rostral; *pr. im*, processus intermedius of lamina nariochoanalis; *pr. Te*, medial process of anterior tectal; *re. jo*, recess probably for Jacobson's organ; *re. l*, lateral recess of nasal cavity; *re. vm*, ventro-medial recess, probably for Jabobson's organ; *ri. in*, internasal ridge; *sn*, septum nasi; *soc*, supraorbital sensory canal; *sol. n*, solum nasi; *vot*, tusk of vomer; *w. in*, internasal wall; *w. lic*, ventral, medially curved part of lateral nasal wall; *w. mn*, medial wall of nasal cavity; *w. pren*, prenasal wall.

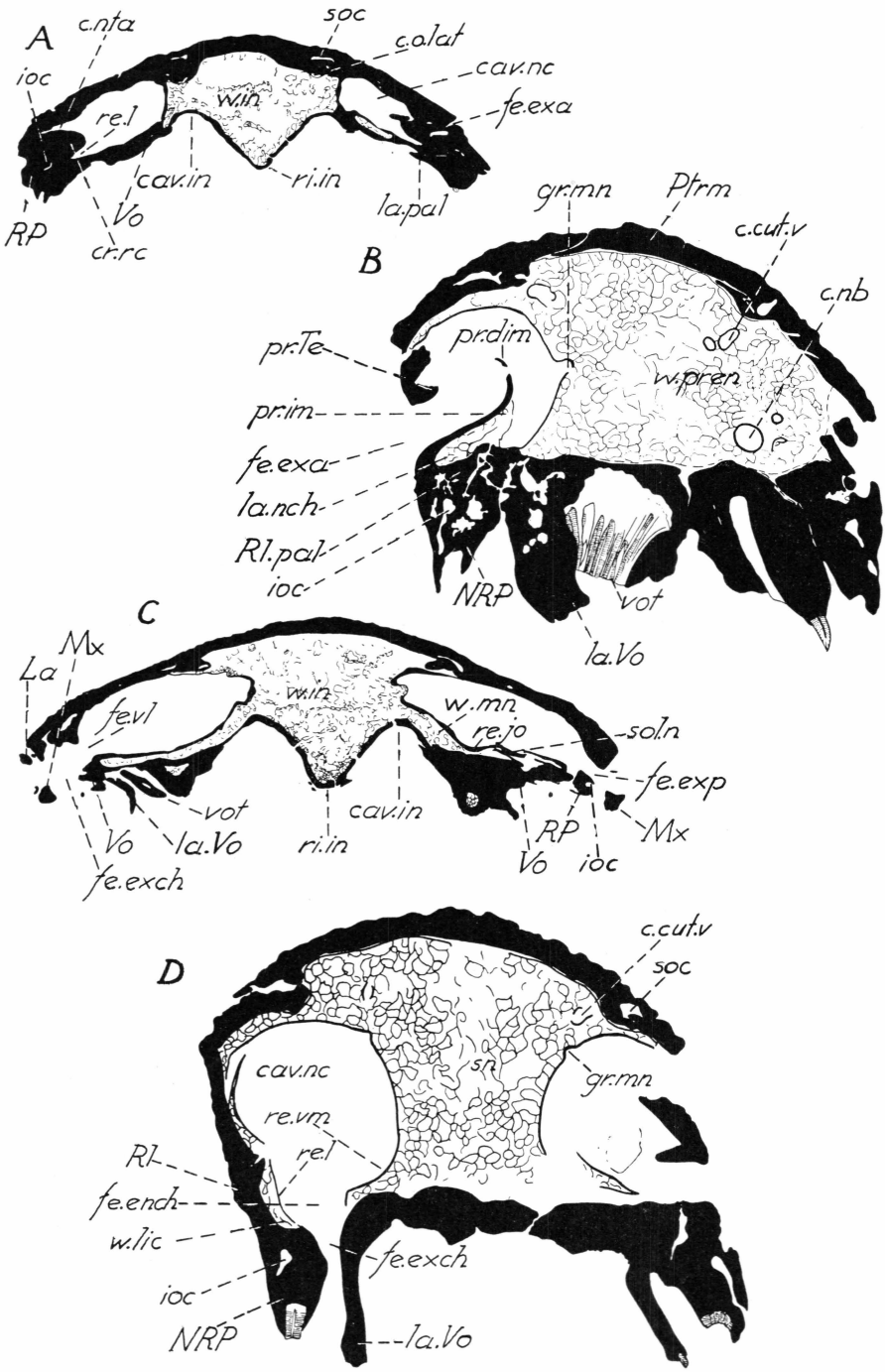

A
c.nta
soc
c.alat
ioc
cav.nc
w.in
fe.exa
re.l
cav.in
ri.in
la.pal
RP
Vo
cr.rc
B
gr.mn
Ptrm
c.cut.v
c.nb
pr.Te
pr.dim
w.pren
pr.im
fe.exa
la.nch
Rl.pal
ioc
NRP
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C
Mx
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w.in
fe.vl
w.mn
re.jo
sol.n
fe.exp
vot
cav.in
Vo
la.Vo
ri.in
RP
Mx
Vo
ioc
fe.exch
D
c.cut.v
soc
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rel
Rl
fe.ench
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ioc
NRP
la.Vo

Fig. 66.

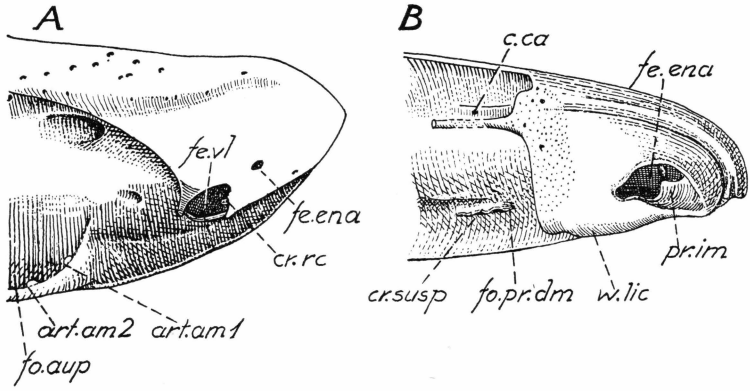


Fig. 67. Ethmoidal region and anterior part of orbito-temporal region of neural endocranium in lateral aspects to show differences between, *A*, porolepiforms and, *B*, osteolepiforms. *A*, *Glyptolepis groenlandica* n. sp. After fig. 21. *B*, *Eusthenopteron foordi*. From JARVIK, 1942, fig. 67.

art.am1, *art.am2*, anterior and posterior articular areas for antero-medial articular lamina of pars autopalatina; *c. ca*, canal for v. cerebralis anterior; *cr. rc*, crista rostro-caudalis; *cr. susp*, crista suspendens; *fe. ena*, fenestra endonarina anterior; *fe.vl*, fenestra ventro-lateralis; *fo.aup*, fossa autopalatina; *fo.pr.dm*, pit receiving dorso-medial process of pars autopalatina; *pr. im*, processus intermedius of lamina nariochoanalis; *w. lic*, ventral, medially curved part of lateral nasal wall.

Fig. 68. Representations to illustrate differences in structure of ethmoidal region between, *A1–A4*, porolepiforms and, *B1–B4*, osteolepiforms. *A1*, *B1*, ethmoidal region in posterior aspect. *A2*, *B2*, posterior half in anterior and, *A3*, *B3*, anterior half in posterior aspects. *A4*, *B4*, ethmoidal region and anterior part of orbitotemporal region in ventral aspect. *A1*, *A4*, *Porolepis brevis*, *A2*, *A3*, *Porolepis spitsbergensis*. Same as in fig. 9. *B1–B4*, *Eusthenopteron foordi*. After JARVIK, 1942, figs. 48, 49, 51, 52 A.

art. am, areas in floor of fossa autopalatina articulating with antero-medial articular lamina of palatoquadrate; *art. ap*, area articulating with processus apicalis of palatoquadrate; *art. e*, area articulating with ethmoidal articular process of palatoquadrate; *art. pl*, postero-lateral ethmoidal articular area; *ar. Vo*, vomeral area; *cav. in*, cavum internasale; *cav. nc*, cavity of nasal capsule; *c. cut*, canal for profundus branch and cutaneous vessels; *c.cut.v*, canal for cutaneous vessel; *c.nb*, naso-basal canal; *c. nbv*, ventral branch of naso-basal canal; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. ora*, *c. orp*, anterior and posterior canals of orbito-rostral passage; *c. pr*, profundus canal; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. prt*, canals for terminal twigs of n. profundus; *cr. im*, crista intermedia; *cr. rc*, crista rostro-caudalis; *fe. ena*, fenestra endonarina anterior; *fe. ench*, fenestra endochoanalis; *f. enp*, foramen in postnasal wall for posterior nasal tube and certain nerves and vessels; *fe.vl*, fenestra ventro-lateralis; *fo. aup*, fossa autopalatina; *fo. pr. dm*, pit for dorso-medial process of pars autopalatina; *fo. pren*, prenasal pit; *gr. et. com*, groove for ridge housing ethmoidal commissural canal; *gr. mn*, groove for r. medialis narium; *gr. ntp*, groove in cavity of nasal capsule for posterior nasal tube; *gr. orp*, posterior groove of orbito-rostral passage; *gr. pnt*, groove in anterior part of orbit for posterior nasal tube (nasolachrymal duct); *i.ech*, incisura ectochoanalis; *i. enp*, notch for posterior nasal tube; *i. m. lb*, insertion for m.levator bulbi; *la. nch*, lamina nariochoanalis; *pr. im*, processus intermedius of lamina nariochoanalis; *pr.pv*, *pr vl*, postero-ventral and ventro-lateral processes of

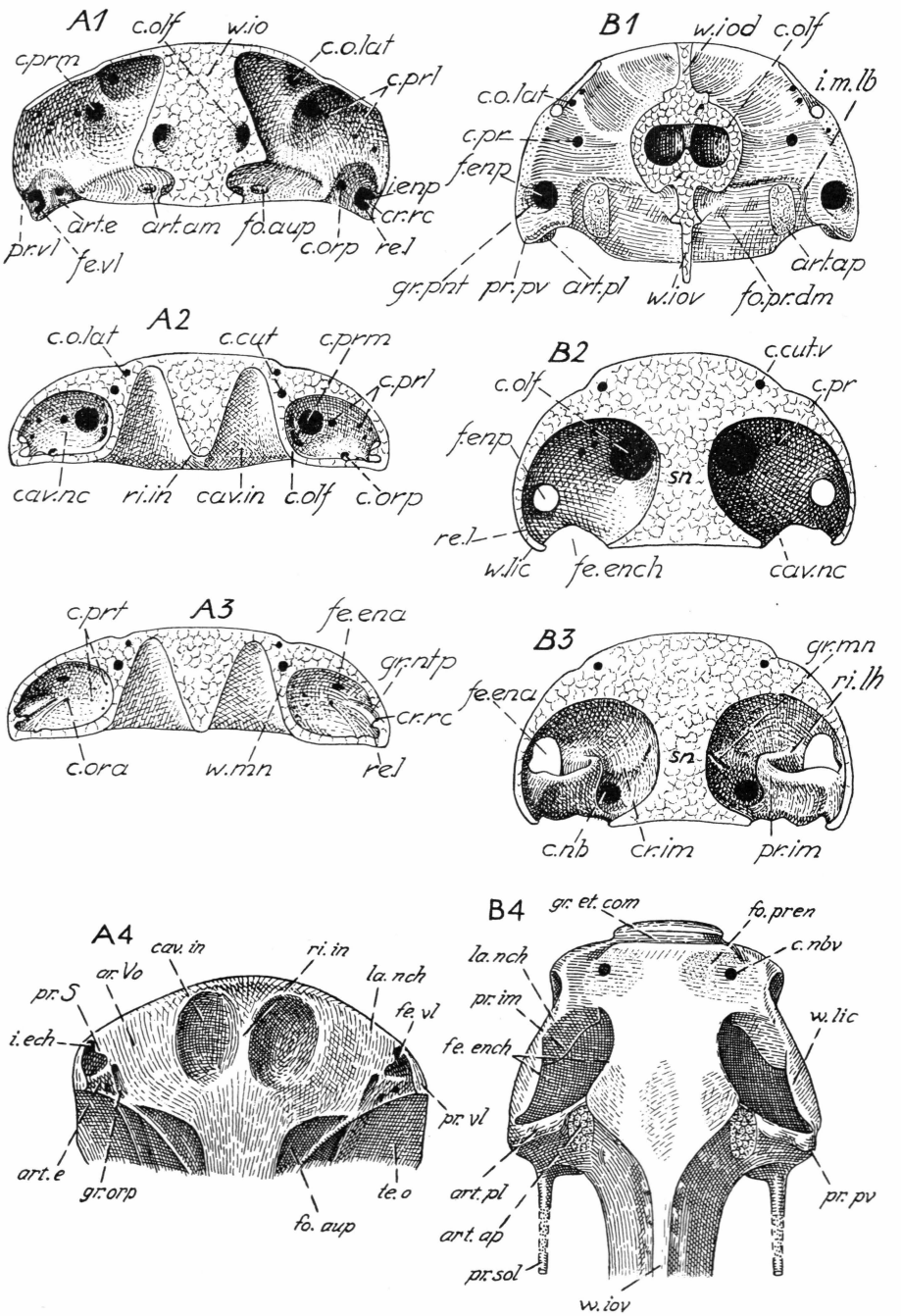


Fig. 68.

postnasal wall; *pr. S*, Seydel's palatal process; *pr. sol*, processus supraorbitalis lateralis; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *ri. lh*, lateral horizontal ridge; *sn*, septum nasi; *te. o*, tectum orbitale; *w. io*, interorbital wall; *w. iod*, *w. iov*, dorsal and ventral thin portions of interorbital wall; *w. lic*, ventral, medially curved part of lateral nasal wall forming wall of lateral recess; *w. mn*, medial nasal wall.

the crista intermedia (*cr. im*), the processus dermintermedius (*pr. dim*) of the lateral rostral and the inwardly directed process (*pr. Te*) of the anterior tectal. The porolepiforms are completely devoid of equivalents to these processes and crests (figs. 66–68).

2) The fenestra endonarina anterior (*fe. ena*) and the fenestra endochoanalis (*fe. ench*) are much larger in osteolepiforms than in porolepiforms.

3) The fenestra endochoanalis in porolepiforms is confluent with the fenestra endonarina posterior, forming a fenestra ventro-lateralis (*fe.vl*). Such a fenestra is lacking in osteolepiforms.

4) The fenestra endonarina posterior is in porolepiforms (*i. enp*) situated in the lateral nasal wall inside the fenestra exonarina posterior (*fe.exp*, *i.exp*). The latter, probably due to a secondary migration (see p. 153), lies closer to the margin of the upper jaw than the fenestra exonarina anterior (*fe. exa*) and in the case the posterior external nasal tube (*ntp*) continued behind the posterior opening it made a sharp bend (*b*) at that opening and ran in a groove (*gr. La*) on the external side of the lachrymal towards the orbital fenestra. In osteolepiforms there is no fenestra exonarina posterior. The osteolepiform fenestra endonarina posterior (*f. enp*) lies in the postnasal wall and behind that opening the posterior external nasal tube (nasolachrymal duct) went straight backwards to the orbital fenestra, first in an endoskeletal groove (*gr. pnt*, fig. 68B1) directed towards that fenestra and behind that inside the dermal bones that form the lateral boundary of the anterior part of the orbit (figs. 7, 65–68, 79A–D).

5) In front of the fenestra endonarina posterior the posterior nasal tube in porolepiforms ran in a groove (*gr. ntp*) on the inner side of the lateral nasal wall, bounded ventrally by a distinct ridge, the crista rostrocaudalis (*cr. rc*). This groove and crest are lacking in osteolepiforms (fig. 68).

6) The rostro-caudal crest in porolepiforms forms the dorsal boundary of the lateral recess (*re. l*) of the nasal cavity. This recess is bounded laterally by the lateral nasal wall and ventrally by the postero-lateral part of the solum nasi which at least sometimes protrudes backwards into a small process known as Seydel's palatal process (*pr. S*). In osteolepiforms the lateral recess is bounded by the medially curved ventral part (*w. lic*) of the lateral nasal wall only. The postero-lateral part of the solum nasi is not developed and accordingly also Seydel's palatal process is lacking (fig. 68).

7) The internasal wall (*w. in*) in osteolepiforms is solid and forms a nasal septum (*sn*) which is narrow when the nasal cavities lie close together (*Eusthenopteron*) and broad when they are far apart (*Megalichthys*). In porolepiforms the internasal wall contains a paired internasal cavity

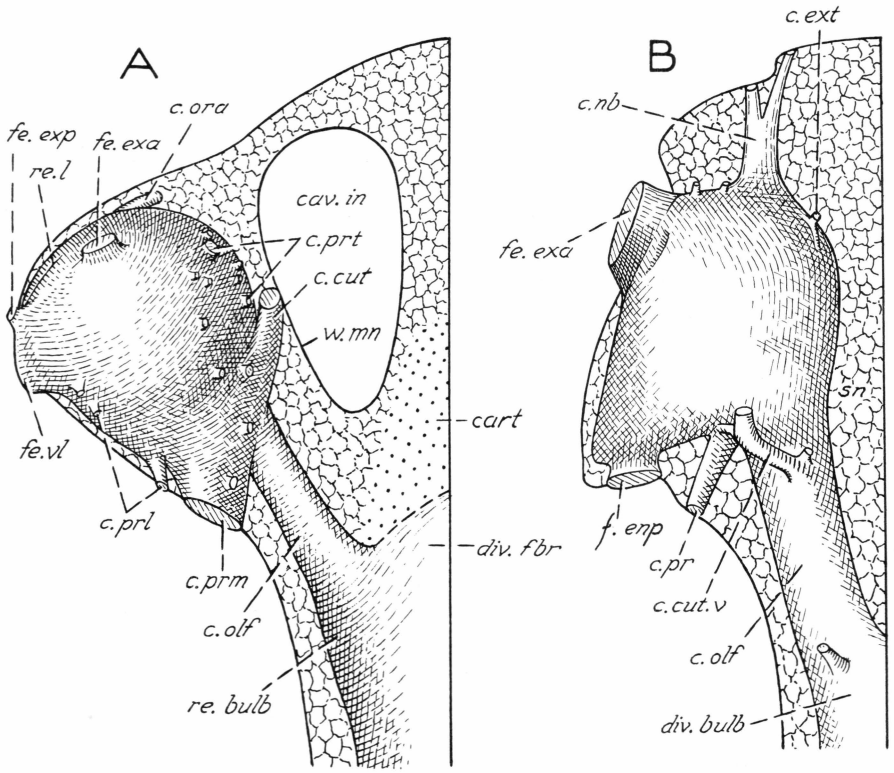


Fig. 69. Diagrams to illustrate differences between porolepiforms and osteolepiforms in position and development of nasal cavities. Left half in dorsal view. Dorsal parts of ethmosphenoid removed so that casts of nasal cavities, olfactory canals and anterior part of cranial cavity are exposed. *A*, *Porolepis spitsbergensis* (cf. figs. 14A, 70A). *B*, *Eusthenopteron foordi* (cf. fig. 70B and JARVIK, 1942, fig. 57A).

cart, part of internasal wall possibly formed by cartilage; *cav. in*, internasal cavity; *c. cut*, canal probably for branch of n. profundus and cutaneous vessels; *c. cut. v*, canal for cutaneous vessels; *c. ext*, canal for r. externus narium of n. ophthalmicus profundus; *c. nb*, naso-basal canal; *c. olf*, canalis olfactorius; *c. ora*, anterior canal of orbito-rostral passage; *c. pr*, canal for n. ophthalmicus profundus; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. prt*, canals for twigs of medial terminal profundus branch; *div. bulb*, division of cranial cavity for bulbus olfactorius; *div. fbr*, forebrain division of cranial cavity; *fe. exa*, fenestra exonarina anterior; *fe. exp*, fenestra exonarina posterior; *f. enp*, foramen in postnasal wall for posterior nasal tube and certain nerves and vessels; *fe. vl*, fenestra ventro-lateralis; *re. bulb*, recess for bulbus olfactorius; *re. l*, lateral recess of nasal cavity; *sn*, septum nasi; *w. mn*, medial nasal wall.

(*cav. in*) which is without equivalent in osteolepiforms. The internasal cavities which are separated from each other by a median internasal ridge (*ri. in*) and from the nasal cavity by a medial nasal wall (*w. mn*) open ventrally through an opening (*fe. pal*) in the exoskeleton bounded laterally by the vomers (figs. 65, 66, 68–70, 73).

8) The vomers (*Vo*) in porolepiforms are somewhat rectangular in shape, they lie far apart and they diverge forwards. The vomers in osteolepiforms are triangular structures with a pointed posterior process (*pr. Vop*). Anteriorly they meet in the median line and they diverge slightly backwards (fig. 73).

9) The transverse parts (*lat. Vo*) of the tooth-bearing laminae of the vomers in osteolepiforms form the posterior wall of a large exoskeletal fossa, the fossa apicalis (*fo. ap*). This fossa, the intervomerine pit (*fo. iv*), the intervomerine canal (*c. iv*) and the prenasal pit (*fo. pren*) have no equivalents in porolepiforms. The prenasal pit which is situated in the lateral part of the fossa apicalis, in front of the tooth-bearing lamina of the vomer and partly on the ventral side of the anterior part of the horizontal plate of that bone, must not be confused with the internasal cavity of porolepiforms (figs. 65, 73).

10) The canals and other passages for nerves and vessels are also very different in the two groups. The postnasal wall in osteolepiforms is pierced by a single and not particularly wide profundus canal (*c. pr*); in porolepiforms by a wide medial (*c. prm*) and one or several narrower lateral (*c. prl*) profundus canals (figs. 68, 69).

11) In osteolepiforms there is a single nerve-canal (*c. ext*) leading upwards from the nasal cavity to the dorsal side of the ethmoidal region; in porolepiforms a great many canals (*c. prt*) ascend from the nasal cavity to the dorsal side of the ethmoidal region piercing the dorsal part of the medial nasal wall, the prenasal wall and the medial part of the tectum nasi (figs. 68–70).

12) No canal corresponding to the naso-basal canal (*c. nb*) of osteolepiforms exists in porolepiforms. On the other hand, the orbito-rostral passage (*gr. orp*, *c. orp*, *gr. ora*, *c. ora*) of porolepiforms has no equivlent in osteolepiforms (fig. 68).

13) In osteolepiforms there are well developed continuous passages for nerves and vessels in the ventro-lateral part of the snout (palato-nasal canal, buccalis canal, JARVIK, 1942, fig. 58). No such continuous passages are present in porolepiforms.

14) The vomer in osteolepiforms is traversed by a palatine canal which within the bone divides into three anterior branches (*c. palal*, *c. pall*, *c. palm*). No such canal exists in porolepiforms (figs. 65, 73).

15) In porolepiforms a descending canal from the nasal cavity in the bony mass medially to the fenestra endochoanalis meets an ascending canal from the palate (*c. pald*) and at the junction a strong canal (*c. pr-p*) running forwards to the internasal cavity is given off. These canals which probably carried the profundus-palatine anastomosis lack equivalents in osteolepiforms. In them the profundus-palatine anastomosis was probably formed in the fossa apicalis between nerve-branches which entered that fossa through canals *c. nbv* and *c. palm* (fig. 73).

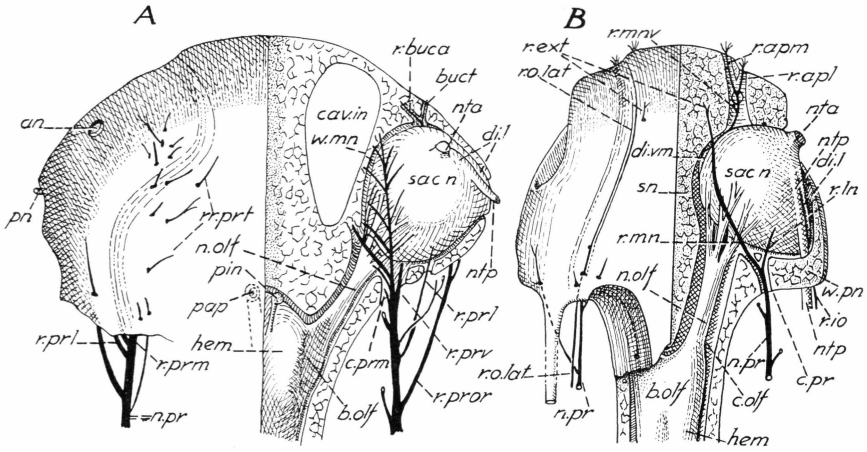


Fig. 70. Restorations of nerves and certain other soft parts in snout of, *A*, porolepiform, *Porolepis brevis* (see fig. 15) and, *B*, osteolepiform, *Eusthenopteron foordi* (from JARVIK, 1942, fig. 59).

an, anterior nostril; *b. olf*, bulbus olfactorius; *buct*, twig of r. buccalis to neuromast of infraorbital sensory canal; *cav. in*, cavum internasale; *c. olf*, canalis olfactorius; *c. pr*, profundus canal; *c. prm*, medial profundus canal; *di. l*, *di. vm*, lateral and ventro-medial diverticles of nasal sac; *hem*, forebrain hemisphere; *n. olf*, nervus olfactorius; *n. pr*, n. ophthalmicus profundus; *nta*, *ntp*, anterior and posterior nasal tubes; *pap* parapineal organ; *pin*, pineal organ; *pn*, posterior nostril; *r. apl*, *r. apm*, lateral and medial terminal branches of r. medialis narium; *r. buca*, anterior branch of r. buccalis lateralis; *r. ext*, r. externus narium of n. ophthalmicus profundus; *r. io*, r. infraorbitalis of r. maxillaris V; *r. ln*, *r.mn*, r. lateralis and r. medialis narium of n. ophthalmicus profundus; *r. mnv*, ventral terminal branch of r. medialis narium; *r. o. lat*, r. ophthalmicus lateralis; *r. prl*, *r. prm*, lateral and medial terminal profundus branches; *r. pror*, terminal profundus branch passing through orbito-rostral passage; *r. prv*, ventral terminal profundus branch anastomosing with r. palatinus VII; *rr. prt*, twigs of medial terminal profundus branch; *sac n*, nasal sac; *sn*, septum nasi; *w.pn*, postnasal wall; *w.mn*, medial nasal wall.

These very great differences between osteolepiforms and porolepiforms in the structure of the skeleton of the snout and in the course and position of canals and other passages for nerves and vessels and several other differences not recorded in this brief summary can only mean that also the nasal sac, the course and mode of branching of the nerves and vessels and other details in the soft anatomy were fundamentally different (fig. 70; see also fig. 15 and JARVIK, 1966, fig. 19B, D).

In the development of the postethmoidal part of the ethmosphenoid, that is in the main the orbitotemporal region, as well as the parasphenoid, porolepiforms and osteolepiforms also differ considerably (as regards osteolepiforms see also WATSON, 1926, 1954, figs. 27, 28; HOLMGREN & STENSIÖ, 1936; SÄVE-SÖDERBERGH, 1936; ROMER, 1937; JARVIK, 1937, 1942, 1952, 1954, 1966; STENSIÖ, 1963b; BJERRING, 1967, 1968, 1971).

The interorbital wall (*w. io*) in osteolepiforms consists of a thin dorsal part (*w. iod*), a thickened middle part which lodges the olfactory canals (*c. olf*) and the anterior part of the cranial cavity, and a thin ventral part. The suborbital ledge (*le. so*) is narrow and the tectum orbitale incomplete (*pr. sol*). In porolepiforms the dorsal part of the interorbital wall is broad and the tectum orbitale (*te. o*) is generally well developed. Ventrally to the middle portion the interorbital wall also in porolepiforms is thin but this thin part forms the medial wall of a deep characteristic pocket, the fossa autopalatina (*fo. aup*), which extends forwards into the ethmoidal region. This fossa is bounded ventrally by the suborbital ledge (*le.so*) which forms a thin broad lamina. On the dorsal side of that lamina there are one, or most often, two areas (*art. am1*, *art. am2*) where the antero-medial articular lamina of the palatoquadrate has fused with or was in synchondrotic connection with the neural endocranium. In osteolepiforms the interorbital wall presents a special crest, the crista suspendens (*cr. susp*), and in front of that a shallow pit (*fo. pr. dm*), which received a small articular process of the palatoquadrate (figs. 67, 68, 71, 105A, B).

In the development of the lateral side of the postethmoidal part of the ethmosphenoid there are also other differences. The canal for the n. opticus (*c. II*) in porolepiforms is wide and the presence of a wide descending groove (*gr. v. o*, fig. 20B) in its posterior part suggests that it transmitted also a vein. In osteolepiforms no such groove has been found and antero-dorsally to the opening of the opticus canal which is of moderate size lies the aperture of the canal (*c. ca*) for the anterior

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Fig. 71. Transverse sections through skull in anterior part of orbitotemporal region of, *A*, porolepiform and, *B*, osteolepiform. *A*, section No. 102 of grinding series of *Glyptolepis groenlandica*. × 3/1 approx. *B*, section No. 85 of grinding series 2 of *Eusthenopteron foordi*. × 3/1 approx.

Co, coronoid; *De*, dentary; *Dpl*, dermopalatine; *Enpt*, entopterygoid; *Fr-et. sh*, fronto-ethmoidal shield; *G*, principal gular plate; *Gm*, median gular plate; *Hh*, hypohyal; *Id*, infradentary; *La*, lachrymal; *Mb*, meckelian bone; *Mx*, maxillary; *Mxp*, palatal lamina of maxillary; *P*, parasphenoid; *Pq. aup*, pars autopalatina of palatoquadrate; *Prart*, prearticular; *Sbm1*, submandibular 1; *Scl. pl*, sclerotic plates.

art. am1, anterior area of fusion between antero-medial articular lamina of pars autopalatina and dorsal side of suborbital ledge; *c. olf*, canalis olfactorius; *cot1*, tip of tusk coronoid 1; *c. prm*, medial profundus canal; *cr. susp*, crista suspendens; *dp*, dental plates; *dplt*, dermopalatine tusk; *fe. o*, orbital fenestra; *fo. aup*, fossa autopalatina; *ioc*, infraorbital sensory canal; *la. am*, antero-medial articular lamina of palatoquadrate; *la. Co*, *la. Dpl*, vertical tooth-bearing laminae of coronoid and dermopalatine; *le. so*, suborbital ledge; *mmdp*, medial mandibular dental plates; *om*, margin of orbital fenestra; *p-mc*, preoperculo-mandibular sensory canal; *pr. sol*, processus supraorbitalis lateralis; *pr. Vop*, posterior process of vomer; *ri. P*, median tooth-bearing ridge of parasphenoid; *soc*, supraorbital sensory canal; *te. o*, tectum orbitale; *uodp*, upper oral dental plates; *w. io*, interorbital wall; *w. iod*, *w. iov*, dorsal and ventral thin portions of interorbital wall.

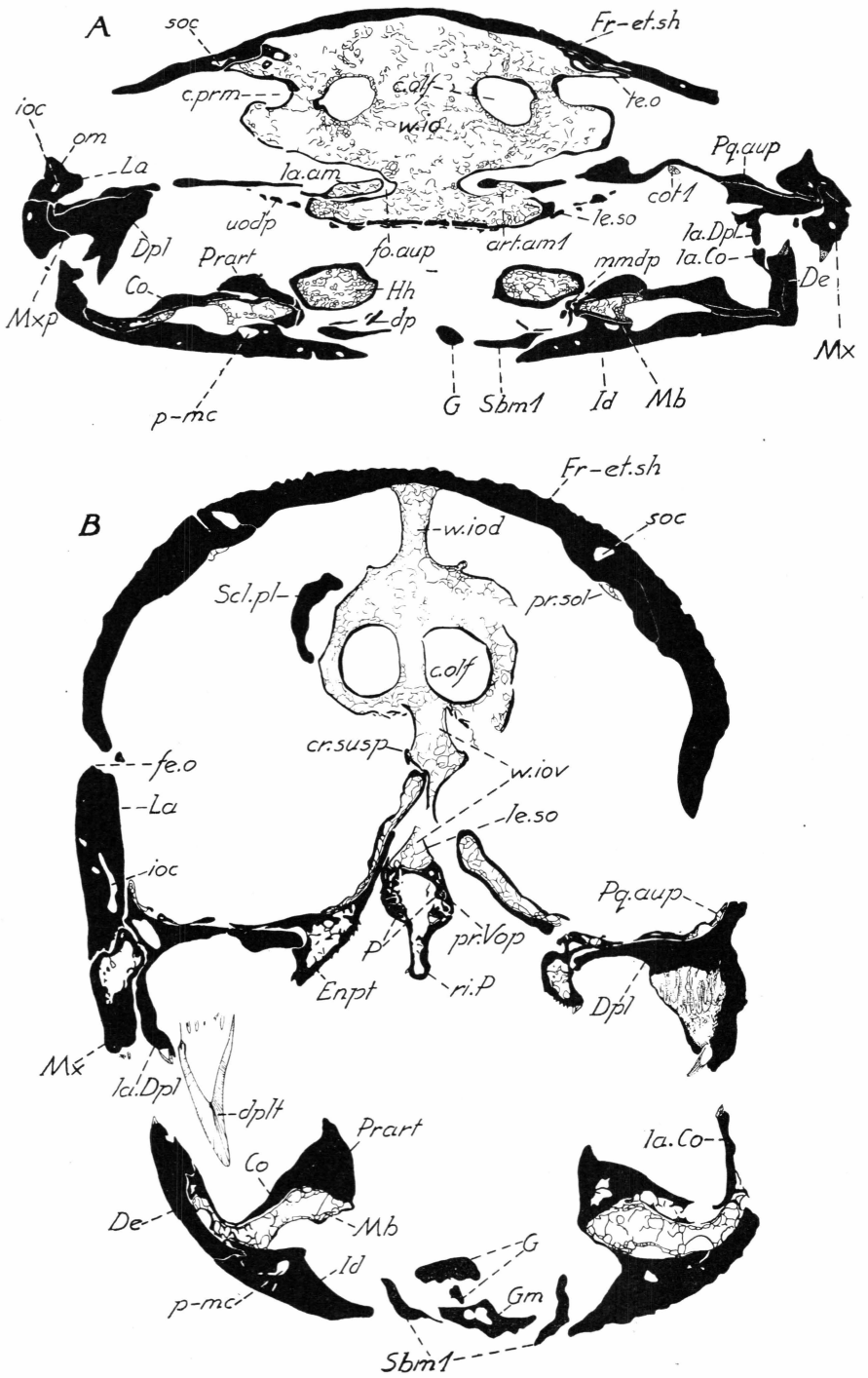

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Fig. 71.

cerebral vein. In porolepiforms, this canal generally seems to be lacking (cf. p. 54). The suprapterygoid process (*pr. sp*) is differently developed and the articular area of the processus connectens (*pr. conn*) is in porolepiforms directed ventro-laterally, in osteolepiforms laterally (figs. 67, 105A,B). Certain other differences will be discussed below.

The shape of the anterior part of the cranial cavity is different. In porolepiforms there is a ventro-lateral recess (*re. bulb*) continued forwards by the canalis olfactorius (*c. olf*) and separated from the forebrain division (*div. fbr*) by a distinct groove. This configuration can only mean that each bulbus olfactorius (*bulb*) was situated close ventro-laterally to the forebrain hemisphere (*hem*) of its side. In osteolepiforms, on the other hand, the olfactory canals run forwards from the anterior end of the cranial cavity which most anteriorly (*div. bulb*) lodged the olfactory bulbs and farther back (*div. fbr*) the hemispheres. Consequently the olfactory bulbs were in osteolepiforms, as in most other vertebrates (cf. p. 199), situated in front of the hemispheres, either close together (*Eusthenopteron*) or rather far apart (*Megalichthys*) and very likely each bulb was connected with the hemisphere of its side by a short tractus olfactorius (figs. 69–72, 80A,C, 83A; see also STENSIÖ, 1963b, figs. 47, 48, 50–52; BJERRING, 1971, figs. 9C, 17).

Another important difference is that porolepiforms have separate pineal and parapineal canals (*c.pin*, *c.pap*), the former situated close to the right and the latter close to the left of the median line, whereas osteolepiforms have a single median canal (*c.papi*). The pineal canal in porolepiforms is situated a little farther back than the parapineal canal and it ascends to the right and posterior half of the pit on the ventral side of the pineal plate, whereas the parapineal canal opens into the left and anterior half of that pit. In osteolepiforms the single canal runs to the pineal foramen (*f.pin*) which no doubt housed the pineal organ but the fact that the canal widens dorsally forming a recess (*re. pap*) in the dorsal side of the interorbital wall indicates that it also carried the parapineal tract and that the parapineal organ was situated in that recess in front of the pineal organ, below the dermal cranial roof (figs. 70, 72, 80A,C; see also JARVIK, 1967b, fig. 2C,D).

In the development of the fossa hypophyseos, too, porolepiforms and osteolepiforms differ considerably. This fossa (*fo. hy*) is in porolepiforms comparatively large, it bends more strongly forwards in its ventral part than in osteolepiforms and consists of a posterior vertical (*fo. hyv*) and a long antero-ventral and almost horizontal portion (*fo. hyh*). The latter is anteriorly continued upwards and backwards by a strong paired canal (*c.p.tub*) probably for the pars tuberalis of the adenohypophysis. The latter canal is situated far in front of the vertical portion of the fossa and in the interspace between that portion and canal *c.p.tub* there are

two other paired canals which connect the anterior horizontal portion of the fossa with the cranial cavity. The anterior of these canals (*c. a. cer*) almost certainly transmitted the arteria cerebralis, whereas the posterior one (*c. port*) probably conveyed portal vessels. In osteolepiforms there is only one paired canal (*c. a. cer*) situated close in front of the fossa hypophyseos and it is generally assumed that this is the canal for the cerebral artery. Another distinctive feature of the fossa hypophyseos in porolepiforms is that its antero-ventral portion anteriorly widens considerably and forms a median canal-like portion and a low paired lateral recess (*re. lhy*). The median part is divided ventrally into two halves by a median endoskeletal crest (*cr. m*) and an important fact is that the buccohypophysial canal due to this crest is paired (*c. bhy*, *c. bhd*, *c. bhs*). In osteolepiforms there is a single median canal for the buccohypophysial duct. This canal (*c. hyp*) has a long exoskeletal portion piercing the parasphenoid which in this part is thick (*ri. P*). In porolepiforms, on the other hand, the part of the parasphenoid underlying the fossa hypophyseos is thin and the buccohypophysial canals of both sides have a common median opening (*f. P*) in that bone (figs. 17–19, 31, 72, 73; see also Stensiö, 1963b; Bjerring, 1971).

In addition to the paired buccohypophysial canal there are in porolepiforms four paired canals that lead outwards from the antero-ventral portion of the fossa hypophyseos. Three of these canals, one probably for the pituitary vein (*c. v. pit*), one for the a. carotis interna (*c. a. ci*) and one for the a. ophthalmica magna (*c. a. om*) are present also in osteolepiforms but have a somewhat different position and course. Most remarkable is perhaps that the external opening of the canal for the pituitary vein in osteolepiforms is situated in front of the posterior vertical portion of the basipterygoid process but in porolepiforms dorsally to that portion. The fourth canal (*c. a. pal*), probably for the palatine artery, has been found only in porolepiforms which show also another canal (*c. a. cib*) which pierces the parasphenoid and runs forwards towards the ventral part of the fossa hypophyseos. A characteristic feature of porolepiforms is moreover that besides the latter canal also the canals for the internal carotid artery and the a. palatina pierce the parasphenoid and run for a fairly long distance within this bone or between it and the overlying part of the neural endocranium. In osteolepiforms the canal for the a. carotis interna sometimes pierces the thin dorso-lateral part of the parasphenoid or runs dorsally to that bone (figs. 20, 72, 73, 85D, 105A, B; see also Jarvik, 1965a; Bjerring, 1971).

The parasphenoid (*P*) of porolepiforms is characterised by the canals that pierce it but is also in several other regards very different from that in osteolepiforms. In contrast to that group it is a short broad plate ending anteriorly about at the transition between the orbitotemporal

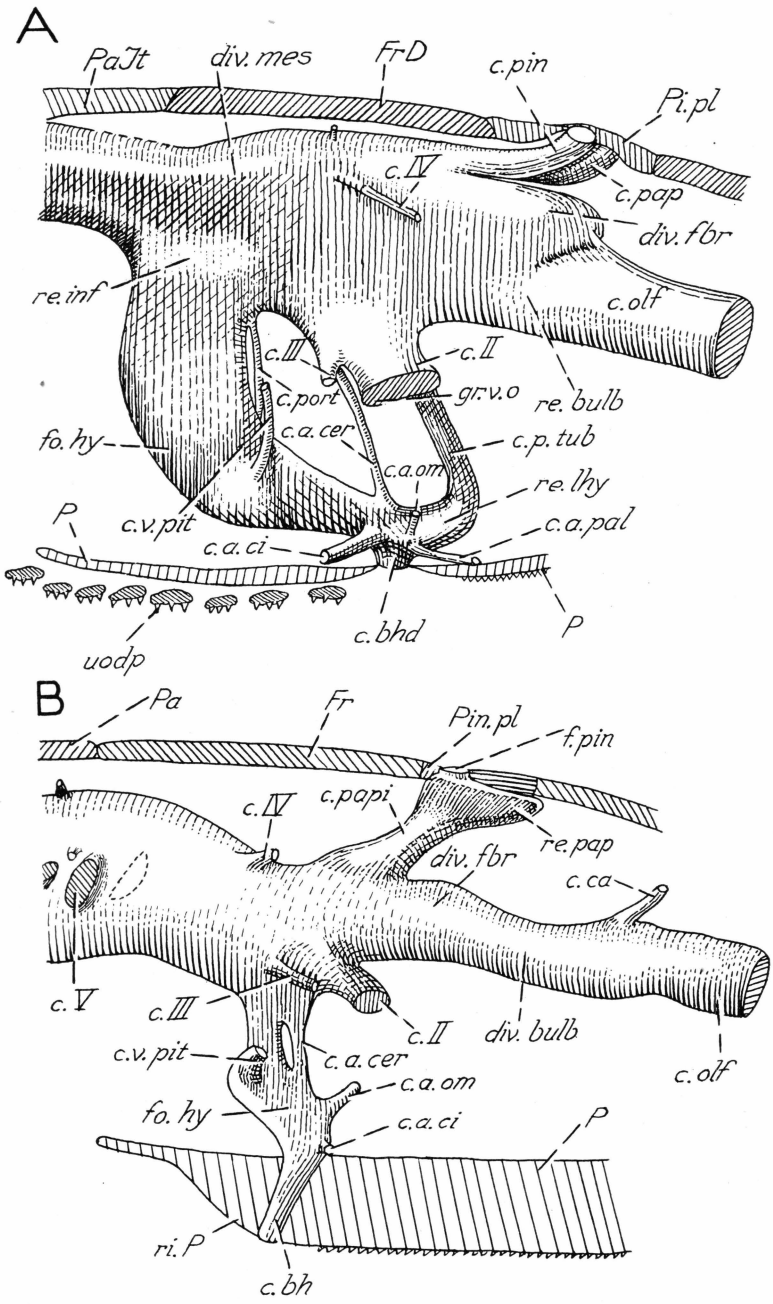


Fig. 72. Casts of anterior part of cranial cavity with fossa hypophyseos in lateral aspect to illustrate differences between, *A*, porolepiforms and, *B*, osteolepiforms. Adjoining dermal bones of cranial roof and palate in median section. × 6/1 approx. *A*, *Glyptolepis groenlandica* (cf. fig. 17). Graphical restoration after grinding series. *B*, *Eusthenopteron foordi*. After wax-model and serial sections of grinding series 2 (cf. JARVIK, 1942, fig. 57, 1967b, fig. 2; STENSIÖ, 1963b, figs. 50A, 52).

and ethmoidal regions and usually without contact with the vomer. Its dorsal side which covers the ventral sides of the internasal wall and the broad suborbital ledge is convex as seen in transverse sections. In osteolepiforms the bone is long and narrow extending far forwards underneath the ethmoidal region and a long anterior part of the bone is laterally in close contact with the vomeres. Its dorsal side is in the middle part of the bone concave and forms a gutter with encloses the ventral part of the interorbital wall. Posteriorly the bone in both groups forms a processus ascendens anterior (*pr. asc. I*) but characteristic for porolepiforms is that the groove for the prespiracular gill-slit (*gr. psp*) is very distinct and is lined with teeth or teeth modified into ridges. This groove which in porolepiforms extends to close behind the opening (*f. P*) for the buccohypophysial ducts is very indistinct in osteolepiforms and lacks teeth. The dentition of the parasphenoid in osteolepiforms forms a shagreen carried by a high median ridge (*ri. P*) which in its posterior part is pierced by the buccohypophysial canal (*c. hyp*). Postero-laterally to the ridge there is a distinct paired pocket (*fo. m. sc*), very likely for the insertion of the subcranial muscle. In porolepiforms this muscle was most probably inserted into a groove-like endoskeletal depression (*i. m. sc*) found close dorsally to the processus ascendens. The tooth-bearing area, which as to its shape differs considerably from that in osteolepiforms, is moderatly raised and a remarkable fact is that the part of the bone situated outside this area is covered by independent dental plates (*uodp*), which have no equivalents in osteolepiforms (figs. 71–73).

The otoccipital in porolepiforms is still imperfectly known and a detailed comparison with osteolepiforms is to be postponed until the grinding series of *Glyptolepis* has been finished and wax-models have been made. It may, however, be mentioned that there is no articular area

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Fr, frontal; *FrD*, frontodermosphenotic; *P*, parasphenoid; *Pa*, parietal; *PaIt* parietointertemporal; *Pin. pl*, pineal plates; *Pi. pl*, pineal plate.

c. a. cer, *c. a. ci*, *c. a. om*, *c. a. pal*, canals for a. cerebralis, a. carotis interna, a. ophthalmica magna and a. palatina; *c. bh*, single buccohypophysial canal; *c. bhd*, right buccohypophysial canal; *c. ca*, canal for vena cerebralis anterior; *c. olf*, canalis olfactorius; *c. pap*, canal for parapineal tract; *c. papi*, common canal for parapineal and pineal tracts; *c. pin*, canal for pineal tract; *c. port*, canal probably for portal vessels; *c. p. tub*, canal for pars tuberalis of adenohypophysis; *c. v. pit*, canal for pituitary vein; *c. II*, *c. III*, *c. IV*, *c. V*, canals for n. opticus, n. oculomotorius, n. trochlearis and n. trigeminus; *div. bulb*, division of cranial cavity for bulbus olfactorius; *div. fbr*, *div. mes*, forebrain and mesencephalon divisions of cranial cavity; *fo. hy*, fossa hypophyseos; *f. pin*, pineal foramen; *gr. v. o*, groove for optic vein; *re. bulb*, ventro-lateral recess of cranial cavity for bulbus olfactorius; *re. inf*, recess for infundibulum of diencephalon; *re. lhy*, lateral recess of fossa hypophyseos for lateral lobe of adenohypophysis; *re. pap*, recess for parapineal organ; *ri. P*, median tooth-bearing ridge of parasphenoid; *uodp*, upper oral dental plates.

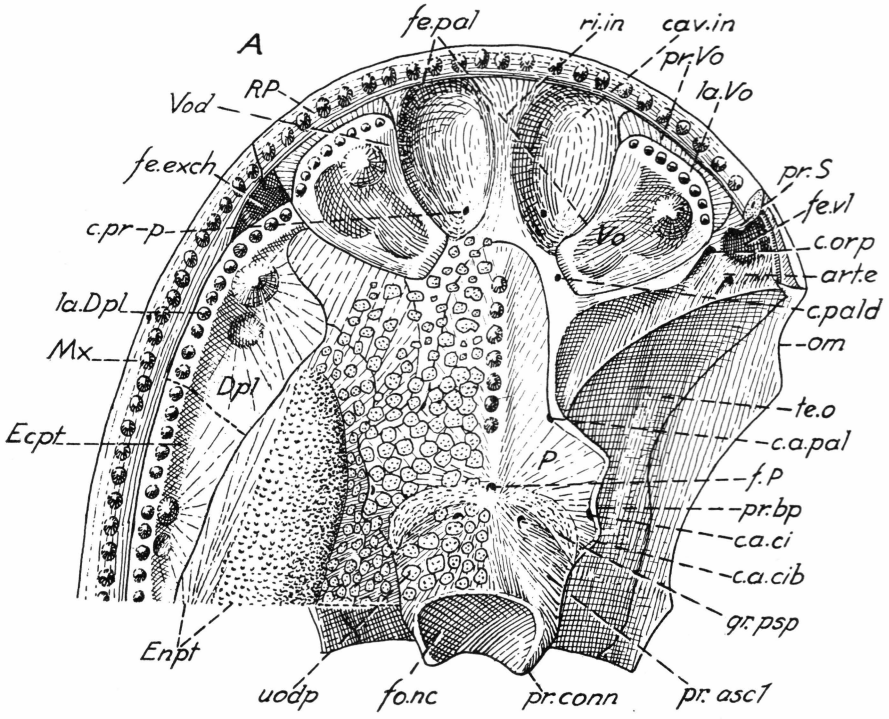


Fig. 73. Divisio cranialis anterior with adjoining part of palatoquadrate-cheek complex of right side in ventral aspect of, *A*, porolepiform, *Porolepis brevis* and, *B*, osteolepiform, *Eusthenopteron foordi*. Slightly modified from JARVIK, 1966, figs. 3 H and 17 B.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Mx*, maxillary; *NRP*, nasorostropremaxillary; *P*, parasphenoid; *RP*, rostropremaxillary; *Vo*, vomer; *Vod*, ascending lamina of vomer.

art. ap, area of postnasal wall articulating with processus apicalis of palatoquadrate; *art. e*, area of postnasal wall articulating with ethmoidal articular process of palatoquadrate; *c. a. ci*, canal for a. carotis interna; *c. a. cib*, canal for medial branch of a. carotis interna; *c. a. pal*, canal for a. palatina; *cav. in*, cavum internasale; *c. hyp*, canal in parasphenoid for buccohypophysial duct; *c. iv*, intervomerine canal; *c. nbv*, ventral branch of naso-basal canal; *c. orp*, posterior canal of orbitorostral passage; *c. palal*, antero-lateral branch of palatine canal in vomer; *c. pald*, canal for ascending branch of r. palatinus anastomosing with ventral branch of n. ophthalmicus profundus; *c. pall*, *c. palm*, lateral and medial branches of palatine canal of vomer; *c. pr-p*, canal for combined profundus-palatine nerve; *c. II*, *c. III*, canals for n. opticus and n. oculomotorius; *fe. ench*, fenestra endochoanalis; *fe. exch*, fenestra exochoanalis; *fe. pal*, anterior palatal fenestra; *fe. vl*, fenestra ventrolateralis; *fo. ap*, fossa apicalis; *fo. iv*, intervomerine pit; *fo. m. sc*, pit of parasphenoid for insertion of subcranial muscle; *fo. nc*, pit for anterior end of notochord; *fo. pren*, prenasal pit; *f. P*, foramen in parasphenoid for buccohypophysial duct; *gr. psp*, prespiracular groove; *la. Dpl*, vertical tooth-bearing lamina of dermopalatine; *lal. Vo*, *lat. Vo*, rostro-caudal and transverse parts of tooth-bearing lamina of vomer; *la. Vo*, vertical, tooth-bearing lamina of vomer; *om*, margin of orbital fenestra; *pr. asc1*, processus ascendens anterior of parasphenoid; *pr. bp*, basipterygoid process; *pr. conn*,

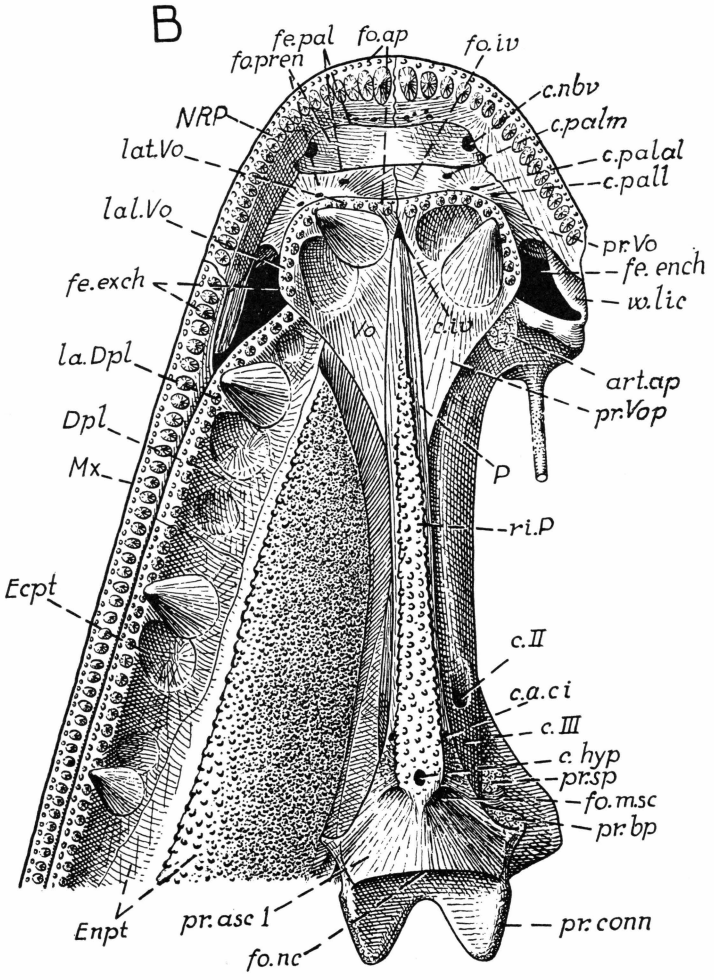


Fig. 73 B.

processus connectens; *pr. S*, Seydel's palatal process; *pr. sp*, suprapterygoid process; *pr. Vo*, *pr. Vop*, antero-lateral and posterior processes of vomer; *ri. in*, internasal ridge; *ri. P*, ventral tooth-bearing ridge of parasphenoid; *te. o*, tectum orbitale; *uodp*, upper oral dental plates; *w. lic*, ventral, medially curved part of lateral nasal wall.

(*art. ptm*) for the palatoquadrate on the lateral side of the otical shelf in porolepiforms and no canal for the occipital artery (*c. a. occ*) has been observed. If this canal is absent this is an important difference. Another difference is that the basicranial fenestra in porolepiforms is continued backwards by a median slit and on the whole the arcual elements which probably form the main part of the posterior ossification seem to be less consolidated in porolepiforms than in osteolepiforms, a condition which explains why this ossification is lacking in most specimens of porolepiforms that have been prepared (figs. 31, 92A, 93D, E, 104A, C).

The ventral side of the otoccipital is in both groups covered by numerous dental plates, but whereas there in osteolepiforms are two large paired plates (paraotic and subotic) there is only one large plate in porolepiforms. This plate, the paraotic plate (*Podp*), is in porolepiforms provided with a distinct ridge (*ri. dp*) on its inner side. The position of the independent dental plates which in porolepiforms are situated laterally and antero-laterally to the paraotic plate, the presence of a pocket (*pl*) in the roof of the mouth between the palatoquadrate and the neural endocranium and the absence of both spiracular dental plates and spiracular cartilage bones indicate that there were considerable differences between the two groups with regard to the anterior extent of the spiracular gill-slit and if there is a spiracular canal in porolepiforms is unknown (figs. 24E–G, 30; as regards osteolepiforms see JARVIK, 1954).

Visceral endoskeleton and subbranchial series. – The palatoquadrate in porolepiforms differs from that in osteolepiforms mainly in the following respects. The pars autopalatina (*Pq. aup*) in porolepiforms is anteriorly divided by a notch into an ethmoidal articular process (*pr. e*) and an antero-medial articular lamina (*la. am*). According to the new interpretations suggested in this work (pp. 35, 71, 220–221) the ethmoidal articular process corresponds to the processus apicalis (*pr. ap*) in osteolepiforms, and like that it was joined—in most cases probably synchondrotically—to the postnasal wall postero-medially to the fenestra endochoanalis (antero-medial ethmoidal articulation, JARVIK, 1954, p. 27). In porolepiforms the ethmoidal process forms the lateral wall of a canal which is the posterior part of the orbito-rostral passage and on its postero-medial side is a distinct groove (*gr. buca*), presumably for the r. buccalis lateralis. In osteolepiforms the processus apicalis forms the medial boundary of a pit (*i.m.lb*), presumably for the insertion of a portion of the m. levator bulbi, and postero-laterally to that pit the pars autopalatina for a rather long distance (*art. pl*, lateral ethmoidal articular area, JARVIK, 1942, p. 453) lies close underneath the postnasal wall which in this part is formed mainly by the skeletal bridge ventrally to the wide foramen (*f.enp*) which transmitted the posterior external nasal tube. In porolepiforms this articulation (postero-lateral ethmoidal articulation, JARVIK, 1954, p. 27) is possibly represented by a contact between the pars autopalatina and the inner side of the processus ventro-lateralis (*pr.vl*) of the postnasal wall (cf. fig. 92B). Postero-medially to the processus apicalis the pars autopalatina in osteolepiforms is bent upwards and the margin of this part shows a process (*pr. dm*) which fits into a pit (*fo.pr.dm*) on the lateral side of the interorbital wall (JARVIK, 1942, pp. 437–439; orbital articulation, JARVIK, 1954, p. 27). In porolepiforms the corresponding part of the pars autopalatina, the antero-medial articular lamina (*la.am*), is a horizontal plate which occupies the fossa auto-

palatina. The ventral side of that plate has fused, or articulates, with the dorsal side of the suborbital ledge in one or, most often, two places (*art 1*, *art 2*). Other differences in the structure of the palatoquadrate are that there is no notch (*iV*) for the rr. maxillaris and mandibularis V in porolepiforms and that paratemporal process (*pr. pt*) and paratemporal articulation are lacking (figs. 25, 26 D, 67, 68, 71; see also JARVIK, 1942, figs. 54, 55, 1954, figs. 16 C, 23 B).

The hyomandibula (*Hy*) in porolepiforms is imperfectly known but one difference seems to be that the ventral proximal articular head (*ahv*) differs in shape from the dorsal head (*ahd*) and that it is situated farther back than that head. In osteolepiforms the two articular heads are similar in shape and the ventral one lies straight ventrally to the dorsal head. In both groups the proximal part of the hyomandibula rests in the spiraculo-hyomandibular recess (*re. sh*) but of great interest is that the ventral end of the hyomandibula in porolepiforms is situated rather far behind the pars quadrata (*Pq. qu*) of the palatoquadrate and that there between the ventral end of the hyomandibula and the palatoquadrate is a separate bone, the symplectic (*Sym*), which has no equivalent in osteolepiforms. The fact that the preoperculosubmandibular (*PSbm*) which is situated outside the symplectic is also lacking in osteolepiforms lays further stress upon the importance of this difference (figs. 27, 86, 87 A, 92 A; JARVIK, 1954, figs. 16 A, B, 23–25).

The dorsal parts of the branchial arches are too incompletely known in porolepiforms to be considered. In the development of the hyobranchial skeketon and the subbranchial series the two groups differ very much (JARVIK, 1963 a). The most important differences may be summarised as follows:

1) The osteolepiforms possess two basibranchials (*Bb 1*, *Bb 2*), the anterior with a wide median canal (*c. Bb 1*) in its anterior part. The porolepiforms have only one basibranchial (*Bb*); no median canal.

2) In osteolepiforms the branchial arches extend independently of each other downwards to, and articulate with, the basibranchial series. In porolepiforms only the three foremost arches articulate with the basibranchial series and hypobranchial III (*Hb III*) articulates both with hypobranchial II (*Hb II*) and hypobranchial IV (*Hb IV*).

3) The ceratohyal (*Ch*) in osteolepiforms carries dental plates (*chl*) on it external (ventro-lateral) side. In porolepiforms such dental plates are lacking and the external side of the ceratohyal shows impressions (*m. sar Ia*, *m. bhe. a*, *m. iha. a*) indicating that this side was occupied by muscles (*m. sar I*, *m. bhe*, *m. iha*).

4) The subbranchial series in osteolepiforms includes two large endoskeletal (endomesodermal) elements, the sublingual rod (*Sl*) and the urohyal (*Uh*). In porolepiforms there is only a urohyal.

5) The urohyal (*Uh*) has become specialised in different ways. In porolepiforms its main posterior part forms a horizontal plate, bifurcated posteriorly; in osteolepiforms it is a large vertical plate.

An important difference in the development of the intermandibular skeleton is finally that porolepiforms show a horseshoe-shaped median field of dental plates, the prolingual field (*plf*), situated in the floor of the mouth close behind the symphysis of the lower jaws. This field is lacking in osteolepiforms as is also the medial mandibular field (*mmf*) of dental plates of porolepiforms (figs. 29, 101 B, D, 102 E).

Comparison with urodeles

Principles for establishing relationships

The anatomy of the head in larval and adult urodeles has attracted a considerable interest during the last few decades and in addition to the well known papers by WIEDERSHEIM (1877), DRÜNER (1901, 1903, 1904), COGHILL (1901, 1902), GAUPP (1905) and the comprehensive accounts by STADTMÜLLER (1924, 1936) and FRANCIS (1934; for further references see JARVIK, 1942) valuable contributions have been made more recently by MATTHEWS (1950), RYKE (1950), THERON (1952), SCHMALHAUSEN (1953a, b, 1955a, b, 1956a, b, 1957a, b, 1958a, b, 1964, 1968), FOX (1954, 1959, 1965), PAPENDIECK (1954), MEDVEDEVA (1959, 1960, 1961, 1964, 1968), LEBEDKINA (1960, 1963, 1964a, b, 1968a, b), CLOETE (1961), JOUBERT (1961), REGEL (1961, 1962, 1964a, b, 1968), SRINIVASACHAR (1962), EYAL-GILADI & ZINBERG (1964), SEWERTZOFF (1968), BJERRING (1970, 1971), and others. However, these papers generally serve special purposes and there is not always easy to find exactly those pieces of information that are needed for a safe interpretation of the fossil structures. It is therefore often necessary to supplement the information in the literature by investigations of recent material and for the present study microtomised series of larval stages of *Hynobius* which on my account have been investigated by H. C. BJERRING have been of a great value.

But if we want to argue in favour of a close relationship between porolepiforms and urodeles we have to consider carefully also the other groups of lower vertebrates, which is a most time-consuming task. And as I have recently emphasised (1968b, pp. 499–501) we have to rely only on such specialisations that are common to the two groups thought to be related and which are not shared with any other groups; and "only when all available data, morphological as well as embryological, fit into the picture are we justified to claim relationship". Because of the great wealth of structural details that may be obtained from the fossil material

with the aid of Sollas' grinding method and other reliable methods of investigation and the anatomical complexity in extant forms it is hardly possible any more for one scientist to consider the whole body. To base far-reaching conclusions as to relationship on lists of similarities chosen more or less at random from different parts of the animal and often without critical examination of their reliability is a frequently used but certainly most doubtful method (cf. JARVIK, 1965a, pp. 101, 124). Quite naturally nobody can be a specialist on all organ systems implying that nobody has the possibility to judge correctly the used characters. If we want to obtain reliable results in a reasonable time I think the only way is to concentrate on a limited part which can be treated thoroughly according to the rather rigorous principles for establishing relationship outlined above; and it was with this in mind that I first (1942) chose the snout and later (1963a) the intermandibular division as the subject for a more comprehensive analysis.

In the middle of the thirties when I started my studies of the snout very little was known about the differences in this part of the head between the various groups of lower gnathostomes; and as to urodeles and anurans it was hardly more than one difference that had been more thoroughly discussed: the anurans have a solid nasal septum whereas there in urodeles is an internasal cavity bordered laterally by the medial nasal wall. In the fossil material at my disposal it was easy to see that porolepiforms in this respect are as urodeles, whereas osteolepiforms agree with anurans, but it was in fact another condition that first attracted my attention. When studying material of *Eusthenopteron wenjukowi* (1937) I found that the anterior part of the nasal cavity is subdivided by endoskeletal crests and by a strong process, the processus dermintermedius, of the dermal bone that was shown to be a lateral rostral, and it was pointed out that a similar subdivison occurs in anurans.

Later (1942) I could give a detailed description of these crests and processes on the basis of two grinding series and other excellent material of *Eusthenopteron foordi*. The discovery of minor and at the beginning seemingly insignificant structural details in the fossil material brought about a search for corresponding details in recent anurans; conversely, the presence of structural features in larval or adult anurans, which could be suspected to be of phylogenetic importance caused further still more detailed studies and, if necessary, further preparation of the fossil material. By this method one detail was added to the other, and the fact that every new piece of evidence fitted in and tallied well with the view that osteolepiforms and anurans are closely akin made me more and more convinced that I was on the right track. In this way the equivalents of the crista intermedia, the lamina superior, the lamina inferior and the

shanks of the septomaxillary in anurans could be easily identified in osteolepiforms; the evolution of the recessus superior, the recessus medius, and the recessus inferior in the phylogeny of anurans could be made out; and the formation of the prenasal processes supporting the premaxillary and of the cavum prenasale could be explained. Moreover, under a never-ceasing consideration of the conditions in porolepiforms, urodeles and other groups of lower gnathostomes, it could be shown that the n. profundus, the r. maxillaris V and the r. palatinus VII in the snout of osteolepiforms ran and branched exactly in the way that is characteristic of anurans, and that the nerve-anastomoses of anurans very likely were developed already in osteolepiforms. Furthermore it was shown that there are striking similarities as to the position of the intermaxillary gland, and in the development of the parasphenoid, the vomer, the nasolachrymal duct, the boundaries of the lateral recess of the nasal cavity, and other particulars. With the aid of embryological data it could, in addition, be explained why the dermopalatine, which in osteolepiforms is a dermal bone of the palatoquadrate, in anurans is found on the ventral side of the postnasal wall, and why the proximal part of the nasolachrymal duct in anurans lies ventrally to the septomaxillary but dorsally to the corresponding part of the processus dermintermedius of the lateral rostral in osteolepiforms.

When it had been shown 1) that osteolepiforms in a great number of characters show exactly the same specialisations as anurans, 2) that they agree with anurans also in characters (e.g. the presence of the nasal septum) which are shared with other groups, 3) that osteolepiforms in important regards agree better with larval than with adult anurans and finally 4) that the differences that exist and which to a considerable extent are a consequence of the retrogressive development of the skeleton in phylogeny could be satisfactory explained, the only reasonable conclusion was that anurans are closely related to osteolepiforms and descendants of osteolepiforms or osteolepiform-like ancestors. It may be added that these results have been confirmed by studies carried out later (1963a, 1964, 1965a,b, 1966, 1967b; STENSIÖ, 1963b) of other parts, a condition which shows that the methods used in 1942 were reliable and that it is possible to gain safe results as to relationships by comparative studies of a limited region such as the snout.

Structure of snout

After these general remarks let us now turn to the comparison between porolepiforms and urodeles. When comparing these two groups in my studies of the snout (1942) the methods for establishing relationship mentioned above were used and by collecting evidence alternately

from the fossils and the embryological and anatomical descriptions of urodeles it could be shown that porolepiforms and urodeles agree closely in the structure of the snout and show exactly the same partly rather strange specialisations. However, the porolepiform-material at my disposal in 1942, consisting mainly of *Porolepis*, was less complete than that of osteolepiforms and it was not until new material (of *Glyptolepis*) was obtained allowing investigations by means of Sollas' grinding method that the final proof for the view expressed in 1942 that the urodeles are descendants of primitive porolepiforms could be presented (JARVIK, 1962, 1963a, 1966).

As pointed out above urodeles agree with porolepiforms but differ from osteolepiforms and anurans in the development of the internasal wall and in the complete absence of equivalents to the crests and processes that cause the subdivision of the anterior part of the nasal cavity in osteolepiforms and anurans (figs. 66–68). But there are also many other most distinct differences between porolepiforms and urodeles, on the one hand, and osteolepiforms and anurans, on the other.

Nerve passages and innervation. – As first clearly expressed by COGHILL (1901, 1902; cf. JARVIK, 1964, p. 58) there are considerable differences between urodeles and anurans in the innervation of the snout. One most striking fact is that the n. ophthalmicus profundus in urodeles is strong and has taken over the innervation of those parts of the snout which generally are supplied by the r. maxillaris V, which accordingly is weakly developed and hardly reaches the snout. The strong profundus nerve (*n.pr*) in urodeles divides in the orbit into three terminal branches (*r.prl*, *r.prm*, *r.prv*) which pass into the nasal cavity through a large medial (*c.prm*) and one or more smaller lateral (*c.prl*) profundus foramina in the postnasal wall. Within the nasal cavity the medial terminal branch (*r.prm*) breaks up into numerous twigs (*rr.prt*) which penetrate the cartilaginous or membraneous walls of the nasal cavity and supply the dorsal and anterior parts of the snout. In the fossil material of porolepiforms available in 1942 it was easy to see that the conditions must have been exactly the same (JARVIK, 1942, pp. 393–394). In porolepiforms, too, the postnasal wall is pierced by a wide medial and one or more lateral profundus foramina and in front of the medial one the tectum nasi is pierced by numerous foramina obviously for twigs of the medial terminal profundus branch. It was also established that the r. ophthalmicus lateralis (*r.o.lat*) went forwards dorsally to the nasal capsule, as in urodeles, and it was pointed out (1942, pp. 253–254, 302) that the r. ophthalmicus superficialis V (*rd. V*, fig. 88), as far as known, does not participate in the innervation of the preorbital part of the head in any gnathostomes (figs. 74–76; as regards osteolepiforms and anurans see figs. 68–70; JARVIK, 1964, fig. 20).

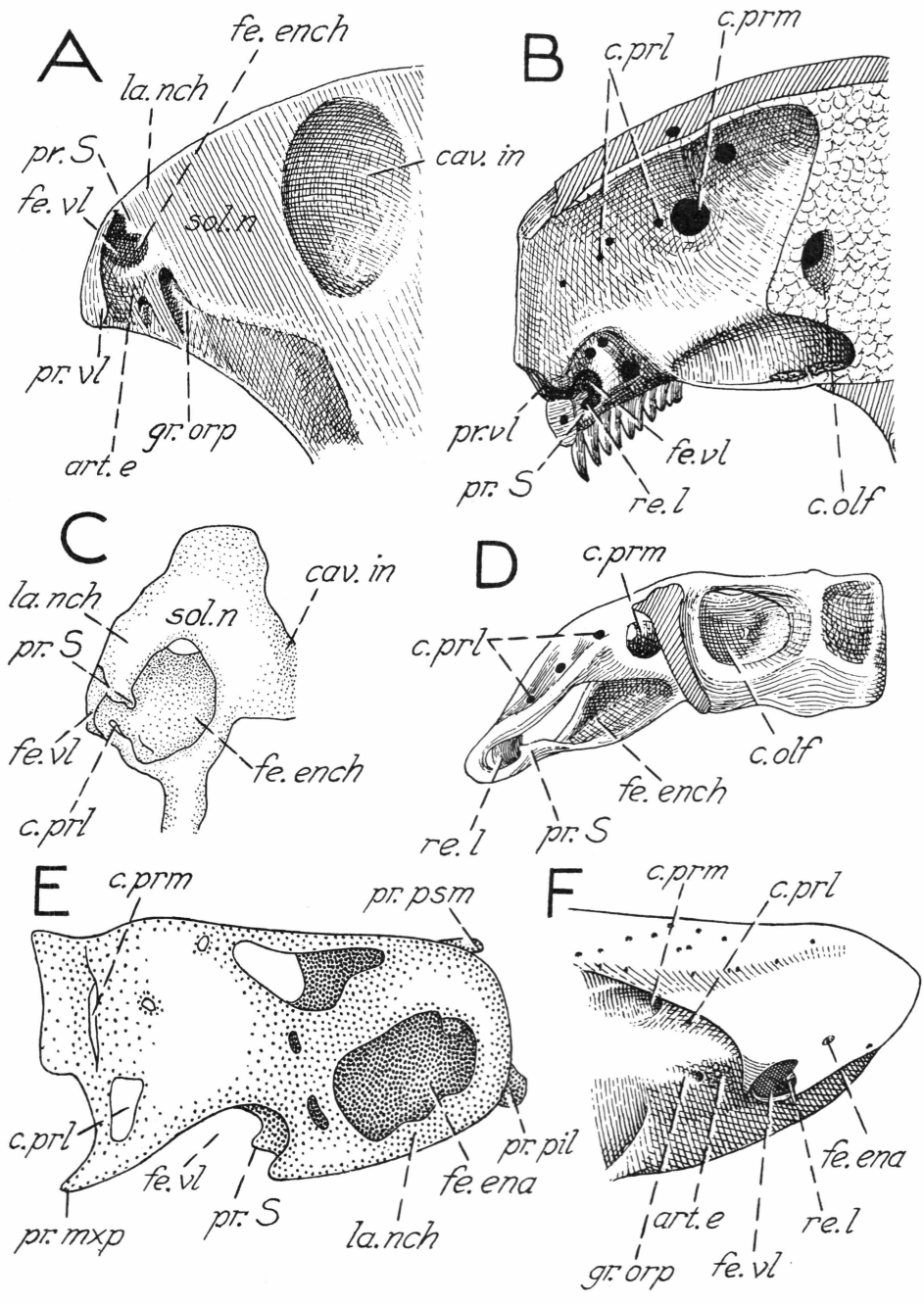

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Fig. 74.

The presence of a wide medial profundus foramen suggesting that the n. ophthalmicus profundus was strong in porolepiforms, too, the important fact that the canals which pierce the lateral parts of the postnasal wall or the grooves on the posterior side of the postnasal wall leading to them (*c. orp*, *gr. orp*) have such a direction that they obviously transmitted nerves (or vessels) coming from the medial parts of the orbit, and the absence of canals in the lateral parts of the snout that could have transmitted the r. maxillaris V, indicate that the latter also in porolepiforms was weakly developed. But because also buccalis canal is lacking in the proper place I assumed (1942, p. 394) that a buccalis branch (*r. buca*) probably ran forwards through the orbito-rostral passage, and thus medially to the choana, to innervate the foremost neuromasts of the infraorbital sensory canal. This assumption was supported by the conditions in *Siren* (Norris, 1913; see Jarvik, 1942, p. 305) but later Schmalhausen (1957a, 1968) has shown that also in hynobiids a buccalis branch (*r. buca*) destined to the foremost infraorbital neuromasts runs forwards medially to the choana. Of great interest was the discovery in the sections of *Glyptolepis* that a fine canal (*c. buct*) obviously for a buccalis twig (*buct*) connects the anterior part of the orbito-rostral passage (*c. ora*) with the infraorbital canal and because, in addition, a groove (*gr. buca*) obviously for the r. buccalis was searched—and found—just where it was to be expected, namely at the posterior end of the orbito-rostral passage on the postero-medial side of the ethmoidal articular process of the palatoquadrate, I think it can be safely concluded that the r. buccalis innervated the most anterior part of the infraorbital canal in

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Fig. 74. Drawings to illustrate similarities in snout structure between *A*, *B*, *F*, porolepiforms and, *C–E*, urodeles. *A*, *B*, *Porolepis brevis*. Half of ethmoidal region in ventral and posterior aspects. In *B* with dermal bones. *C*, *Pleurodeles waltlii*, larva, 65 mm. Half of ethmoidal region in ventral aspect. From Eyal-Giladi & Zinberg, 1964, fig. 12. *D*, *Salamandra salamandra*, metamorphosed stage, 82 mm. Half of ethmoidal region in posterior aspect. From Stadtmüller, 1924, fig. 26. *E*, *Ranodon sibiricus*, larva, 75 mm. Ethmoidal region in lateral aspect. From Regel, 1968, fig. 34. *F*, *Glyptolepis groenlandica*. Ethmoidal region in lateral aspect.

art. e, area of postnasal wall articulating with ethmoidal articular process of palatoquadrate; *cav. in*, cavum internasale; *c. olf*, canal or foramen for n. olfactorius; *c. prl*, *c. prm*, lateral and medial profundus canals; *fe. ena*, fenestra endonarina anterior; *fe. ench*, part of fenestra ventro-lateralis representing fenestra endochoanalis; *fe. vl*, fenestra ventro-lateralis; *gr. orp*, posterior groove of orbito-rostral passage; *la. nch*, lamina nariochoanalis; *pr. mxp*, processus maxillaris posterior, probably corresponding to ventro-lateral process of postnasal wall in porolepiforms; *pr. pil*, processus prenasalis inferior lateralis; *pr. psm*, processus prenasalis superior medius; *pr. S*, Seydel's palatal process; *pr. vl*, ventro-lateral process of postnasal wall; *re. l*, lateral recess of cavity of nasal capsule; *sol. n*, solum nasi.

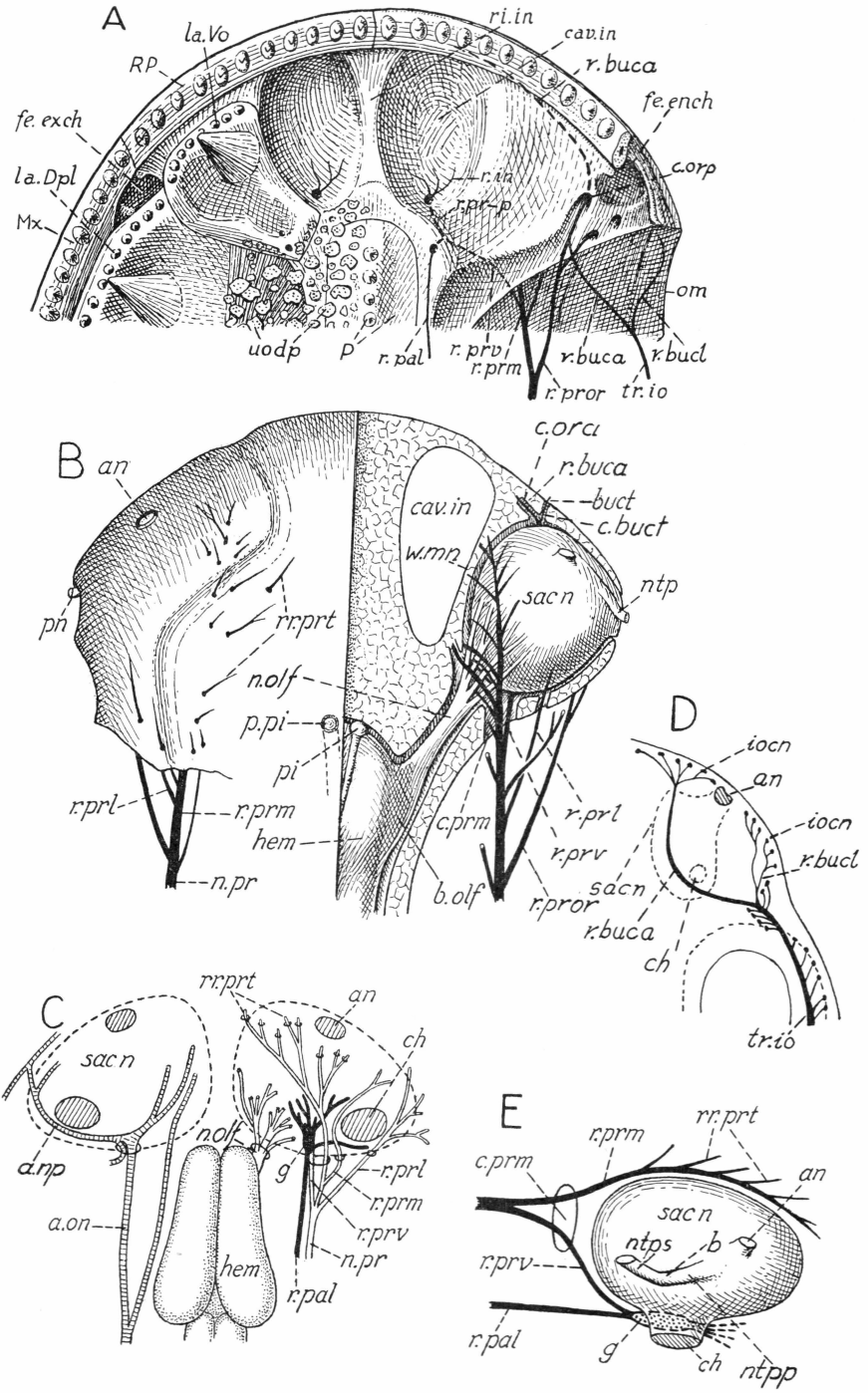

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Fig. 75.

the rather strange way that is characteristic of urodeles. Moreover there was in porolepiforms as in urodeles a lateral buccalis branch (*r. bucl*) which supplied the neuromasts of the part of the infraorbital canal situated ventrally to the anterior nostril (figs. 25, 75, 76).

The course of the r. palatinus VII (*r. pal*) in the snout of porolepiforms could not be made out in 1942. In urodeles this nerve, medially to the choana, forms a characteristic anastomosis with the ventral terminal branch (*r. prv*) of the n. ophthalmicus profundus and the combined nerve thus formed (*r. pr-p*) runs forwards and supplies (*r. in*) the internasal ("intermaxillary") gland (see JARVIK, 1966, fig. 3). A most remarkable fact is that in exactly the place where such an anastomosis was to be expected in porolepiforms, the serial sections of *Glyptolepis* show an ascending canal (*c. pald*) from the palate which joins a descending canal (*c. prv*) from the nasal cavity and where they meet a rather strong canal (*c. pr-p*) is given off forwards to the postero-medial part of the internasal cavity (figs. 73A, 75).

Internasal gland. – The facts now given demonstrate not only that there was a profundus-palatine anastomosis in the area medially to the choana in porolepiforms, too, but also that a compound nerve (*r. pr-p*) entered the internasal cavity. This nerve cannot possibly have had another function than to innervate a gland homologous with the complex internasal gland in urodeles. Because the internasal cavity in porolepiforms no doubt received at least the tips of one or more of the tusks of the parasymphysial dental plate (see JARVIK, 1966, p. 52) it is evident that this gland (*gl. in*) was rather small at any rate in primitive porolepiforms. Most likely it was housed in the posterior part of the internasal cavity, that is where the compound nerve supplying it entered that cavity (figs. 15B, 31, 73A, 75; see also JARVIK, 1966, figs. 1, 2B). It seems also likely that the gland originally arose in this part of the roof of the mouth cavity, presumably by a congreation of single glands in the mucous membrane. Because the internasal gland is innervated by nerves

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Fig. 75. Diagrammatic representations to illustrate fundamental similarities in innervation of snout between, *A*, *B*, porolepiforms and, *C*, *D*, urodeles. *A*, *B*, *Porolepis brevis*. See fig. 15. *C*, *Salamandra salamandra*. After FRANCIS, from JARVIK, 1942, fig. 21, 1964, fig. 20D. *D*, hynobiid urodele. After SCHMALHAUSEN, from JARVIK, 1966, fig. 2C. *E*, nasal sac and certain nerves in lateral aspect to show profundus-palatine anastomosis in urodeles and porolepiforms. From JARVIK, 1964, fig. 20F.

a. np, posterior nasal artery; *a. on*, a. orbitonasalis; *b*, bend of posterior nasal tube; *c. buct*, canal for twig of r. buccalis; *ch*, choana; *c. ora*, anterior canal of orbitorostral passage; *g*, ganglion; *iocn*, neuromasts of infraorbital sensory line; *ntpp*, *ntps*, primary and secondary portions of posterior nasal tube.

For explanation of other index letters see fig. 15.

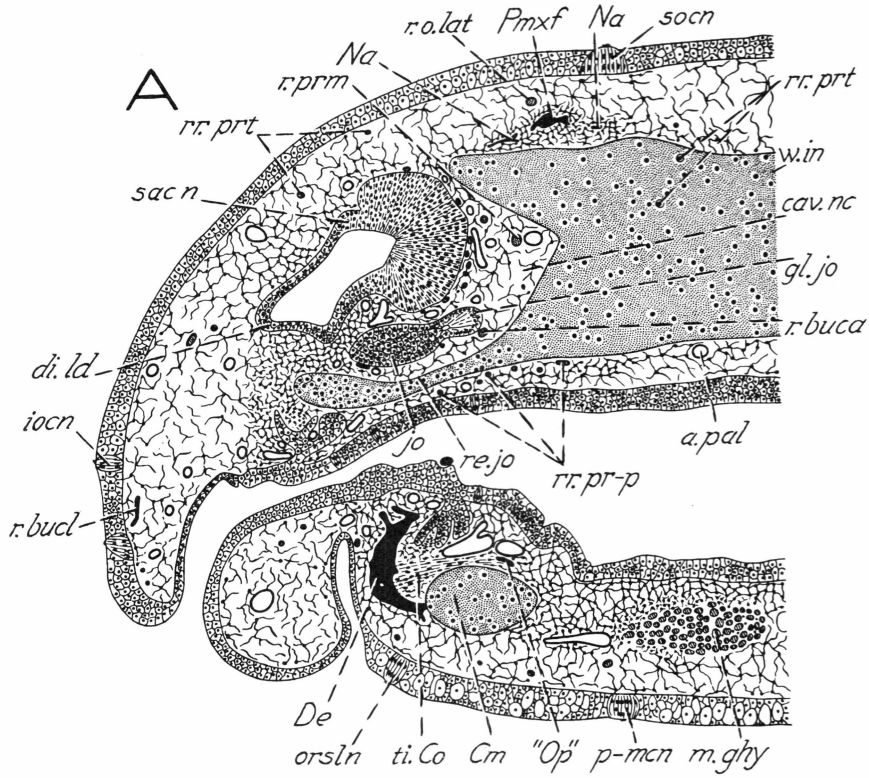


Fig. 76. *A*, *Hynobius retardatus*, larva, 33 mm. Transverse section of left half of snout in region of Jacobson's organ. From BJERRING (unpublished). × 57/1. *B*, *Glyptolepis groenlandica*. Transverse section of left half of snout in region of presumed recess for Jacobson's organ. Section No. 61 of grinding series. × 15/2.

Cm, ceratomandibular (meckelian bone or cartilage); *Co1*, coronoid 1; *De*, dentary; *Fr-et. sh*, fronto-ethmoidal shield; *Id.1*, infradentary 1; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; "*Op*", "operculare"; *Pmxf*, pars facialis of premaxillary; *Vo*, vomer.

a. pal, a. palatina; *cav. in*, internasal cavity; *cav. nc*, cavity of nasal capsule; *c. o. lat*, canal for r. ophthalmicus lateralis; *di. ld*, antero-dorsal portion of lateral diverticle of nasal sac; *fe. exch*, fenestra exochoanalis; *fe. exp*, fenestra exonarina posterior; *fe. vl*, fenestra ventro-lateralis; *gl. jo*, Jacobson's gland; *iocn*, neuromast of infraorbital sensory canal; *jo*, Jacobson's organ; *la. Vo*, vertical tooth-bearing lamina of vomer; *m. ghy*, musculus geniohyoideus; *mmdp*, medial mandibular dental plates; *orsln*, neuromast of oral sensory line; *p-mc*, preoperculo-mandibular sensory canal; *p-mcn*, neuromast of preoperculo- mandibular sensory canal; *pr. Vo*, antero-lateral process of vomer; *psyt*, tusks of parasymphysial dental plate; *r. buca*, *r. bucl*, anterior and medial buccalis branches; *re. jo*, recess in floor of nasal capsule for Jacobson's organ; *r. o. lat*, r. ophthalmicus lateralis; *r. prm*, medial terminal profundus branch; *rr. pr-p*, twigs of combined profundus-palatine nerve; *rr. prt*, twigs of medial terminal profundus branch; *sac n*, nasal sac; *soc*, supraorbital sensory canal; *socn*, neuromast of supraorbital sensory canal; *ti. Co*, strand of dense connective tissue between "operculare" and dentary probably representing vestige of coronoid series; *uodp*, upper oral dental plates; *w. in*, internasal wall.

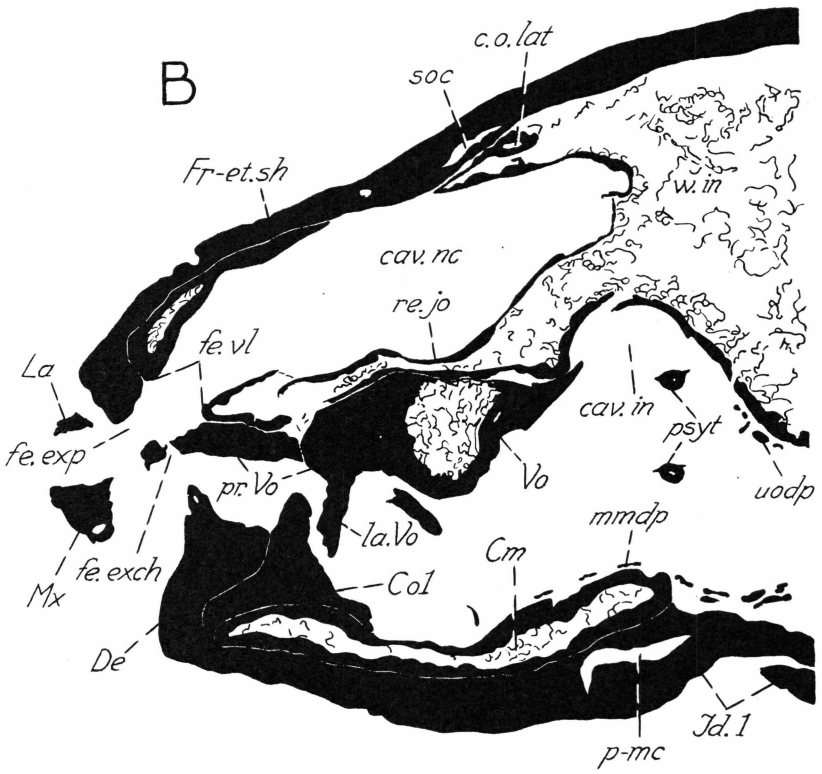


Fig. 76 B.

from both sides of the head it is evident that it must be a paired structure (cf. JARVIK, 1942, pp. 400–401) which tallies well with conditions in porolepiforms in which the internasal cavity is paired (the paired structures interpreted by REGEL, 1968, figs. 30, 46, as the primordia of the internasal gland are most likely blastemata of vomeral teeth; BJERRING, unpublished).

The internasal gland of porolepiforms and urodeles must not be confused with the intermaxillary gland of osteolepiforms and anurans (see also JARVIK, 1966, pp. 87–91). This gland, too, is certainly derived from single glands in the mucous membrane of the roof of the mouth cavity, but probably it arose in another part of that membrane, and it is innervated in a different fashion. More precisely this gland probably arose in the prenasal pit (*fo. pren*) of osteolepiforms, which is situated in the lateral part of the fossa apicalis (*fo. ap*), in front of the nasal cavities and in front of the transverse portion (*lat. Vo*) of the tooth-bearing lamina of the vomer. The differences in the position of the areas of origin of the internasal and intermaxillary glands are clearly coordinated with the peculiar differences in their innervation. In urodeles and certainly in

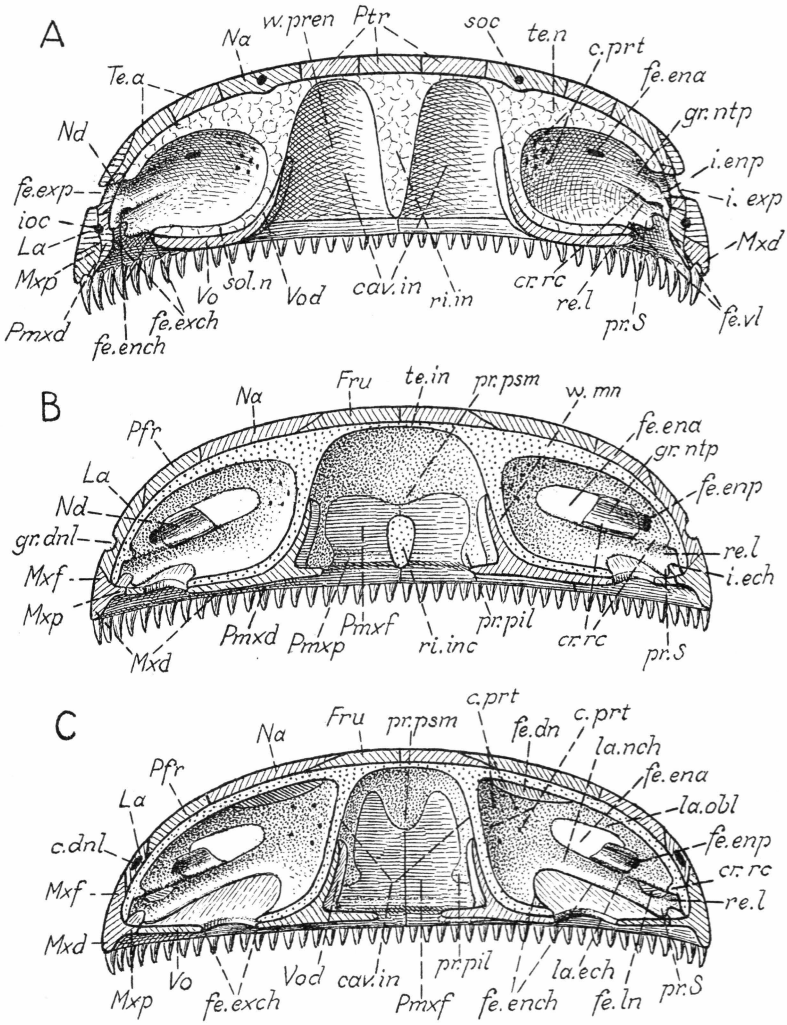


Fig. 77. Three diagrammatic drawings to illustrate probable development of snout in urodeles from one of *Porolepis*-like type. All figures show snout from behind with hindmost part including postnasal wall removed. Cross-sections through endocranial bony tissue reticulated, through dermal bones ruled. Cartilage dotted. *A*, *Porolepis spitsbergensis*, but with sutures of dermal cranial roof and certain other details after *Glyptolepis* and *Holoptychius*. *B*, primitive urodele stage. *C*, more advanced urodele stage. From JARVIK, 1942, fig. 46, slightly modified.

Fru, urodele frontal; *La*, lachrymal; *Mxd*, *Mxf*, *Mxp*, pars dentalis, pars facialis and pars palatina of maxillary; *Na*, nasal; *Nd*, nariodal; *Pmxd*, *Pmxf*, *Pmxp*, pars dentalis, pars facialis and pars palatina of premaxillary (rostropremaxillary); *Pfr*, prefrontal; *Ptr*, postrostral; *Te. a*, anterior tectal; *Vo*, vomer; *Vod*, ascending lamina of vomer.

cav. in, cavum internasale; *c. dnl*, canalis nasolacrimalis; *c. prt*, canals for twigs of medial terminal profundus branch; *cr. rc*, crista rostro-caudalis; *fe. dn*, fenestra dorsalis nasi; *fe. ena*, fenestra endonarina anterior; *fe. ench*, fenestra endo-

porolepiforms as well the anastomosing branch of the n. ophthalmicus profundus is the *ventral* terminal branch which enters the nasal cavity through the wide medial profundus foramen and passes down behind the nasal sac to anastomose with the r. palatinus *ventral* to the posterior part of that sac, medial or rather postero-medial to the choana. In osteolepiforms and anurans the anastomosing profundus branch—in sharp contrast to conditions in porolepiforms and urodeles—is the r. medialis narium (*r. mn*) which within the nasal cavity runs forwards *dorsal* to the nasal sac and even dorsal to the olfactory nerve and it passes downwards in front of the nasal sac to anastomose with the r. palatinus in the prenasal part of the snout. In osteolepiforms this anastomosis probably occurred in the prenasal pit, that is where the intermaxillary gland probably arose (figs. 15B, 65, 70, 73, 75; JARVIK, 1966, fig. 19).

An interesting fact is also that a vestige, the cartilago infranasalis (*ri. inc*), of the internasal ridge (*ri. in*) of porolepiforms is retained in several urodeles (figs. 77B, 92B; JARVIK, 1942, pp. 286, 397; REGEL, 1964a, pp. 49–50, fig. 14, 1968, p. 69). In previous papers (1942, pp. 396–401, 421–423, 496–508, 1966, pp. 83–91) I have discussed the evolution of the internasal and intermaxillary glands and the modifications in the internasal wall and the divisio prenasalis communis in the phylogeny of urodeles and anurans and with the aid of conditions in primitive forms and in larvae I have tried to explain what has happened both in the evolution from porolepiforms to urodeles and from osteolepiforms to anurans.

Crista rostro-caudalis and nariodal. – In the lateral parts of the snout, too, important similarities between porolepiforms and urodeles have been demonstrated. In porolepiforms the fenestra endonarina posterior (*i. enp*) and the fenestra endochoanalis (*fe. ench*) are confluent forming a fenestra ventro-lateralis (*fe. vl*). A corresponding opening may be present in urodeles, too, and an important common feature is the

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choanalis; *fe. enp*, fenestra endonarina posterior; *fe. exch*, fenestra exochoanalis; *fe. exp*, fenestra exonarina posterior; *fe. ln*, fenestra lateralis nasi; *fe. vl*, fenestra ventro-lateralis; *gr. dnl*, groove for posterior (secondary) portion of ductus nasolacrimalis; *gr. ntp*, groove for posterior external nasal tube (anterior or primary portion of ductus nasolacrimalis); *i. ech*, incisura ectochoanalis; *i. enp*, notch in margin of fenestra ventro-lateralis for posterior external nasal tube (fenestra endonarina posterior proper); *i. exp*, notch in posterior margin of nariodal for posterior nasal tube; *ioc*, infraorbital sensory canal; *la. ech*, lamina ectochoanalis; *la. nch*, lamina nariochoanalis; *la. obl*, lamina obliqua; *pr. pil*, processus prenasalis inferior lateralis; *pr. psm*, processus prenasalis superior medius; *pr. S*, Seydel's palatal process; *re. l*, lateral recess of nasal cavity; *ri. in*, internasal ridge; *ri. inc*, cartilaginous vestige of internasal ridge (cartilago infranasalis); *soc*, supraorbital sensory canal; *sol. n*, solum nasi; *te. in*, tectum internasale; *te. n*, tectum nasi; *w. mn*, medial nasal wall; *w. pren*, prenasal wall.

presence of a crista rostro-caudalis (*cr. rc*) which in both groups forms the dorsal boundary of the lateral recess (*re. l*) of the cavity of the nasal capsule. Laterally this recess is bounded by a part of the lateral nasal wall and ventrally by the solum nasi which in both groups may be produced backwards into a process situated laterally to the choana. This process, Seydel's palatal process (*pr. S*), which lies in and supports the plica palatina must not be confused with the processus lingularis in anurans which is a part of the lateral nasal wall situated dorsally to the plica palatina (see JARVIK, 1965a, p. 117, fig. 4). Dorsally to the rostro-caudal crest is a groove (*gr. ntp*) which in urodeles carried the naso-lachrymal duct and in porolepiforms its equivalent, the posterior external nasal tube (*ntp*). This groove is in *Porolepis* formed by a portion of the lateral nasal wall which I in 1942 considered to be homologous with the nariodal in urodeles, at that time generally held to be a cartilage bone. However, as now seems to be well established (see p. 152) the nariodal of urodeles is a dermal bone and under these circumstances it must correspond to the "dermonariodal" (JARVIK, 1964, p. 61) first found in *Holoptychius* but probably present also in other porolepiforms. This dermal bone (*Nd*) which like its equivalent in urodeles most properly is termed nariodal is obviously situated outside and covers that portion of the lateral nasal wall which I in 1942 interpreted as the nariodal. What has happened in phylogeny is probably only that the ossified lateral nasal wall of the primitive porolepiforms—as a consequence of the general trend to a retrogressive development of the skeleton—has become cartilaginous (as possibly in *Holoptychius*) and later membraneous (figs. 74, 77, 78A,B, 92).

When in 1942 (p. 249) I introduced the new name nariodal for the bone in urodeles which earlier had been called septomaxillary (or nariale) I stated that it was because it is a cartilage bone and therefore not homologous with the septomaxillary of anurans and other eutetrapods which is a dermal bone. But this was certainly not the only reason. It was also because of the obvious differences in position, structure and morphological relations.

The nariodal (*Nd*) in porolepiforms and urodeles has a characteristic oblique position. It is situated far behind the prenasal wall, behind the anterior external nasal tube, and it extends postero-ventrally to the fenestra exonarina posterior, an opening which is lacking in osteolepiforms and anurans. Moreover it forms a gutter outside the posterior nasal tube or, in urodeles (and *Glyptolepis groenlandica*), the proximal part (*ntpp*) of the nasolachrymal duct. In *Onychodactylus* (fig. 79G) in which the nariodal forms a cylinder it anteriorly is provided with a medial process which behind the external nostril (*an*) extends inwards close to the diverticulum laterale of the nasal sac (SCHMALHAUSEN, 1968, p. 176,

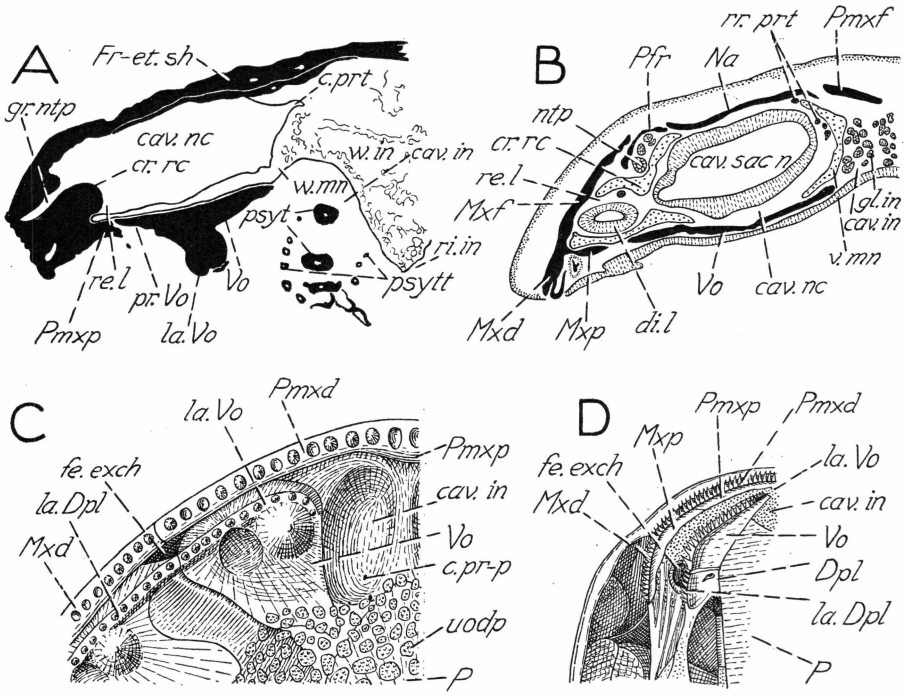


Fig. 78. Drawings to illustrate similarities in snout structure between, *A*, *C*, porolepiforms and, *B*, *D*, urodeles. *A*, *Glyptolepis groenlandica*. Transverse section in region of crista rostro-caudalis. Section No. 42 of grinding series. *B*, *Ambystoma maculatum*, adult. Transverse section in region of crista rostro-caudalis. From THERON, 1952, fig. 4b. *C*, *Glyptolepis groenlandica*. Right half of snout in ventral aspect. *D*, *Ambystoma tigrinum*, permanent larva (axolotl, 6 years old, 22 cm). Right half of snout in ventral aspect. From WINTREBERT, 1922, fig. 32.

Dpl, dermopalatine; *Fr-et. sh*, fronto-ethmoidal shield; *Mxd*, *Mxf*, *Mxp*, pars dentalis, pars facialis and pars palatina of maxillary; *Na*, nasal; *P*, parasphenoid; *Pfr*, prefrontal; *Pmxd*, *Pmxf*, *Pmxp*, pars dentalis, pars facialis and pars palatina of premaxillary; *Vo*, vomer.

cav. in, internasal cavity; *cav. nc*, cavity of nasal capsule; *cav. sac n*, cavity of nasal sac; *c. pr-p*, canal for combined profundus-palatine nerve innervating internasal gland; *c. prt*, canal for twig of medial terminal profundus branch; *cr. rc*, crista rostro-caudalis; *di. l*, ventral portion of lateral diverticle of nasal sac situated in lateral recess; *fe. exch*, fenestra exochoanalis; *gl. in*, internasal ("intermaxillary") gland; *gr. ntp*, groove for posterior external nasal tube; *la. Dpl*, *la. Vo*, vertical tooth-bearing laminae of dermopalatine and vomer; *ntp*, nasolachrymal duct (posterior nasal tube); *pr. Vo*, antero-lateral process of vomer; *psyt*, tusks of parasymphysial dental plate; *psytt*, lateral and medial rows of small teeth of parasymphysial dental plate; *re. l*, lateral recess of cavity of nasal capsule; *ri. in*, internasal ridge; *rr. prt*, twigs of medial profundus branch; *uodp*, upper oral dental plates (forming posterior process of vomer in many urodeles); *w. in*, internasal wall; *w. mn*, medial nasal wall.

fig. 103). This process which most likely is a secondary formation must not be confused with the processus dermintermedius (*pr. dim*) of the

lateral rostral in osteolepiforms or with the septomaxillary of anurans which originates mainly from that process. The processus dermintermedius and the septomaxillary have no relations whatever to the diverticulum laterale. They are situated farther forward in the snout than the nariodal, ventrally and in front of the anterior external nasal tube and close to the prenasal wall. Moreover they extend far into the nasal cavity and are intimately connected with the processus intermedius (*pr. im*) and the lateral horizontal ridge (*ri. lh*) of the prenasal wall in osteolepiforms or their equivalents (lamina inferior and lamina superior) in anurans, structures that are completely lacking in urodeles and porolepiforms. Furthermore the nasolachrymal duct in osteolepiforms and anurans is associated only with the most posterior part of the processus dermintermedius or the corresponding part of the septomaxillary and the proximal portion of the duct lies dorsal to that part both in osteolepiforms and in larval anurans (in the ontogeny of anurans the duct migrates through the septomaxillary to its ventral side). In view of these great differences (figs. 7 D, 62, 66, 68, 77, 79; JARVIK, 1942, figs. 68–72) it is impossible to accept the view held by SCHMALHAUSEN, PANCHEN, and others that the nariodal in urodeles and porolepiforms is homologous with the septomaxillary (lateral rostral) in osteolepiforms, anurans and other eutetrapods (see also pp. 152–154).

Nasal muscles. – In support of the presumed homology PANCHEN (1967, p. 400) claims that "the relations of the bone ("the septomaxillary") to the muscles of the nostril are identical in urodeles and anurans". This statement seems to be a little premature. As a matter of fact GAUPP (1904, p. 670) found the conditions in urodeles and anurans to be so different that it was necessary to introduce new names for the muscles in anurans, viz. the m. lateralis narium for the muscle which BRUNER (1901) had considered to be homologous with the m. constrictor naris in urodeles and m. medialis narium for the m. dilatator naris (BRUNER). The m. lateralis narium (constrictor, BRUNER) in anurans has no relations at all to the septomaxillary, whereas the constrictor in urodeles is attached to the nariodal (SCHMALHAUSEN, 1968, p. 176).

In the fossil forms it is of course difficult to say anything with certainty as to the existence and development of such small structures as the nasal muscles. However, in osteolepiforms there are two small but distinct recesses (JARVIK, 1942, pp. 449, 539, figs. 52, 57, *re.m.ln*, *re.m.mn*; see also 1966, p. 72) so situated that they very well may have served as the areas of origin of two muscles, one corresponding to the m. lateralis narium in anurans and like that without relations to the processus dermintermedius (septomaxillary), and one equivalent to the m. medialis narium in anurans and attached to a part of the processus dermintermedius that corresponds to the part of the postero-lateral

shank of the septomaxillary to which this muscle is attached in anurans. As regards the nasal muscles in porolepiforms very little could be said in 1942 (pp. 369–370) but it was pointed out that the small postero-ventral and antero-dorsal pocket-like recesses found in the wall of the canal (*c. nta*) for the anterior external nasal tube possibly had served as places of origin for such muscles. New material of *Porolepis* shows that the postero-ventral recess (*re.m.cn*, fig. 13B) is larger than the antero-dorsal one and in a specimen of *Glyptolepis?* cf. *paucidens* (fig. 10B) there was space enough behind the nasal tube for a muscle corresponding to the semicircular m. constrictor naris in urodeles (FRANCIS, 1934, pl. 24:82). This muscle, if present, must have been situated close to, and was probably also attached to, the ventro-lateral wall of the canal for the anterior external nasal tube (*c. nta*), formed in its lateral part by the anterior margin of the nariodal and inside that by the margin of the fenestra endonarina anterior. This means that the muscle probably was attached in the same way as in urodeles in which it "becomes attached to the edge of the fenestra narina and in part to the narial bone also" (SCHMALHAUSEN, 1968, p. 176). There is thus some evidence that the nasal muscles in osteolepiforms were as in anurans and in porolepiforms as in urodeles.

Nasolachrymal duct. – The nasolachrymal duct in larvae of hynobiid urodeles has a remarkable course (fig. 79F,G). Its proximal or primary portion (*ntpp*), partly situated in the groove on the inner side of the nariodal (*Nd*) and the first portion of the duct to arise in ontogeny, runs in a postero-ventral direction towards the postero-ventro-lateral corner of the nasal capsule. It passes out from the nasal capsule through a notch in the postero-ventral end of the nariodal and between that notch and the lachrymal (*La*) there is an opening in the exoskeleton (*fe. exp*) which corresponds to the fenestra exonarina posterior in porolepiforms. However, the duct does not end in this opening, but makes a characteristic sharp bend (*b*) and runs obliquely upwards to the eye, in early larval stages in a groove on the outside of the lachrymal. This groove for the distal or secondary portion (*ntps*) of the nasolachrymal duct is later converted into a canal. In porolepiforms (figs. 7, 75E, 79B–D) the conditions are very similar and it was in fact this striking agreement that in 1942 (pp. 405–409) made me convinced that urodeles are not only closely related to but most probably also descendants of primitive porolepiforms. Judging from the fossil material available at that time—in fact only one specimen of *Holoptychius* showing the external side of the lachrymal (pl. 29:3)—the posterior external nostril (*pn*) must have been situated in the fenestra exonarina posterior. However, as demonstrated by the material of *Porolepis* the posterior nasal tube running to that fenestra must have had the same oblique direction as the

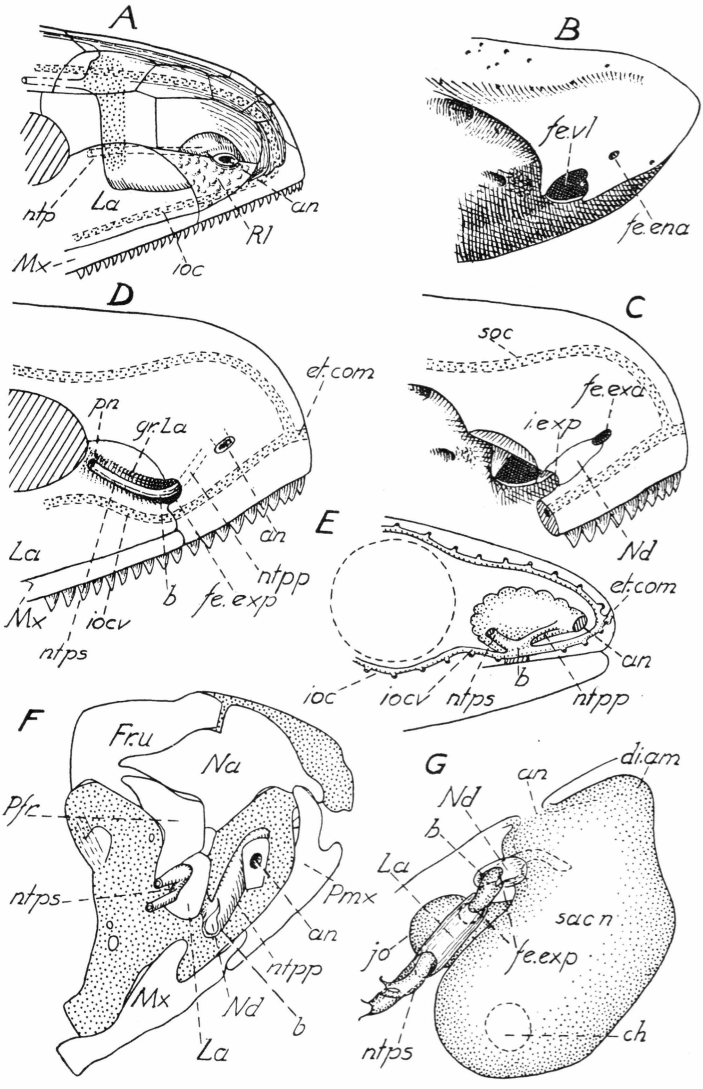


Fig. 79. Drawings to illustrate similarities between porolepiforms and urodeles in development of nariodal and in course of nasolacrymal duct (posterior external nasal tube) and adjoining part of infraorbital sensory canal and different conditions in osteolepiforms. *A*, Osteolepiformes, *Eusthenopteron foordi*. Snout in lateral view. From JARVIK, 1964, fig. 21A. *B–D*, Porolepiformes, *Glyptolepis groenlandica*. *B*, anterior part of ethmosphenoid in lateral aspect. Cf. fig. 21. *C*, same with dermal bones. *D*, anterior part of external cheek-plate added to show groove of lachrymal. *E*, hypothetical rhipidistid to illustrate SCHMALHAUSEN's theory of origin of choana. From SCHMALHAUSEN, 1958b, fig. 5. Communication between nasolacrymal duct and infraorbital sensory canal does not exist. *F*, Urodela, *Onychodactylus japonicus*. Snout in dorso-lateral aspect. After CHUNG & YATABE, from JARVIK, 1964, fig. 21F. *G*, Urodela, *Onychodactylus fischeri*, larva, 85 mm. Reconstruction of nasal sac in dorsal aspect. From SCHMALHAUSEN, 1958a, fig. 14 (1964, fig. 103).

proximal portion (*ntpp*) of the nasolachrymal duct in larval urodeles and like that it was situated in a groove on the inner side of the lateral wall of the nasal capsule—if this groove is formed by the endoskeletal lateral nasal wall as in *Porolepis* or, as a consequence of the retrogressive development of the skeleton, by the adjoining dermal bone (nariodal) is of little importance. The only possible conclusion from this and other similarities was that the short posterior external nasal tube in *Porolepis* (and *Holoptychius*) is homologous with the proximal and first formed portion (*ntpp*) of the nasolachrymal duct in urodeles. But because the fenestra exonarina posterior in *Porolepis* lies antero-ventrally to the orbital fenestra I in 1942 found it necessary to assume that the posterior external tube at the transformation into a nasolachrymal duct, in order to reach the eye, made a sharp bend at the fenestra exonarina posterior and grew obliquely upwards across the external side of the anterior part of the lachrymal, causing a groove on that side corresponding to that found in early larvae of urodeles. That this is actually what has happened has later been confirmed by the new material of *Glyptolepis groenlandica* (see 1964, pp. 62–64). When I some years ago made a graphical restoration of the lateral aspect of the snout in that form on the basis of the serial sections I found that the fenestra exonarina posterior is continued by a deep groove (*gr. La*) on the external side of the lachrymal running in a postero-dorsal direction (1966, fig. 21 D) and later it was discovered in another specimen (pl. 17) that this groove, exactly as postulated in 1942 (p. 408), runs to or almost to the orbital fenestra (figs. 7, 77, 79).

The peculiar bend (*b*) of the nasolachrymal duct (posterior external nasal tube) in larvae of urodeles and in *Glyptolepis* (fig. 79) is clearly associated with the fact that the fenestra exonarina posterior (with the original posterior external nostril), as explained above (p. 153), secondarily has migrated in a ventral direction to be situated postero-ventral to the anterior external nostril (*an*) and fairly close to the margin of the upper jaw. In connection with this migration both the nasolachrymal duct and the infraorbital sensory canal (*ioc*) have been pushed downwards and the latter makes a sharp bend downwards (*iocv*) in the anterior

Fr. u, urodele frontal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *Nd*, nariodal; *Pfr*, prefrontal; *Pmx*, premaxillary; *Rl*, lateral rostral.

an, anterior nostril; *b*, bend of posterior external nasal tube (nasolacrymal duct); *ch*, choana; *di. am*, antero-medial diverticle of nasal sac; *et. com*, ethmoidal commissural canal; *fe. ena*, fenestra endonarina anterior; *fe. exa*, fenestra exonarina anterior; *fe. exp*, fenestra exonarina posterior; *fe. vl*, fenestra ventro-lateralis; *gr. La*, groove of lachrymal for secondary portion of posterior nasal tube; *i. exp*, notch for posterior nasal tube; *ioc*, infraorbital sensory canal; *iocv*, ventrally curving portion of infraorbital sensory canal; *jo*, Jacobson's organ; *ntp*, posterior external nasal tube (nasolacrymal duct); *ntpp*, *ntps*, primary and secondary portions of posterior external nasal tube; *pn*, posterior nostril; *sac n*, nasal sac; *soc*, supraorbital sensory canal.

part of the lachrymal, as does also the infraorbital sensory line in the corresponding place in urodeles. As a result of these modifications the nasolachrymal duct at the sharp bend in the fenestra exonarina posterior will be situated fairly close to the infraorbital sensory canal (line). Moreover the distal part of the duct on its way towards the eye will be situated close to, and will run almost parallel with, that part (*iocv*) of the infraorbital sensory canal (line) that runs downwards in the anterior part of the lachrymal in porolepiforms or in the corresponding place in larval urodeles. With regard to these morphological relations and in view of the still unexplained fact that a branch of the r. buccalis passes forwards medially to the choana it is understandable that the ideas occurred to SCHMALHAUSEN (1957a, 1958a, 1958b, 1964, 1968; see also MEDVEDEVA, 1959, 1960, 1961) that a portion of the infraorbital sensory canal has been utilised at the formation of the distal or secondary portion (*ntps*) of the nasolachrymal duct and that the choana has arisen by a subdivision of the original posterior external nostril (fig. 79E). As is now well established both in porolepiforms and osteolepiforms the nasolachrymal duct and the adjoining part of the infraorbital sensory canal coexist, they are quite separate and the infraorbital canal is never interrupted in the area below the nostrils (cf. p. 153; JARVIK, 1964, pp. 64–65; BERTMAR, 1966, 1969; PANCHEN, 1967).

Nasal sac. – As discussed in 1942 (p. 402, fig. 19B) the shape of the cavity of the nasal capsule indicates that the nasal sac in porolepiforms (fig. 15A), like that in urodeles, consisted of a main part and a lateral diverticle (*di. l*) and that the latter was divided into two divisions, a dorsal one (*di. ld*) which lay above the anterior part of the crista rostro-caudalis and was continued backwards by the posterior external nasal tube, and a ventral one (*di. lv*) situated in the lateral recess (*re. l*). However, the presence of an antero-medial recess (*re. am*) in new material of both *Porolepis* and *Glyptolepis* (figs. 10, 13) demonstrates that the main part of the nasal sac in porolepiforms, in front of the anterior external nasal tube, had an antero-medial bulge (*di.am*), similar to that in urodeles (fig. 79G). Moreover the presence in the sections of *Glyptolepis* of a distinct recess (*re. jo*, fig. 76B) on the dorsal side of the solum nasi antero-medially to the fenestra endochoanalis suggests that the main part of the nasal sac had also a medial diverticle corresponding to that recently found by BJERRING in larval stages of *Hynobius* (fig. 76A) and interpreted as Jacobson's organ (*jo*; as regards this organ, often called the vomero-nasal organ, in urodeles see also MEDVEDEVA, 1968; BERTMAR, 1969).

Vomer. – Also with regard to the vomer (*Vo*) important similarities have been demonstrated previously (1942, pp. 415–417, 1966, fig. 3). In urodeles this bone undergoes considerable modifications in ontogeny,

but at any rate in certain larval stages (figs. 78D, 91, 92C,D) it agrees well with that in porolepiforms (figs. 31, 73A, 78A,C) as to shape and position, and it may be composed of a horizontal plate and a vertical tooth-bearing lamina (*la. Vo*) which latter medial to the fenestra exochoanalis (*fe. exch*) is continued backwards by the corresponding lamina (*la. Dpl*) of the dermopalatine. In *Glyptolepis* (fig. 78A) the anteromedial part of the bone extends a little into the cavum internasale (*cav. in*) in much the same way as in *Ambystoma* (fig. 78B) or *Rhyacotriton* (Cloete, 1961, fig. 4). In *Holoptychius* in which the cavum internasale secondarily has increased in size, this part of the vomer forms an ascending lamina (*Vod*, fig. 77) similar to the vertical lamina of the vomer in several urodeles (see Jarvik, 1942, p. 416) and like that lining the lateral wall of the cavum internasale. In several urodeles also dermal bones of the cranial roof may secondarily form vertical laminae which extend into the cavum internasale, a condition seriously misinterpreted by some supporters of the theory of a monophyletic origin of the "Amphibia" (see Jarvik, 1965a, pp. 115–117, fig. 4). An interesting fact with regard to the vomer in urodeles is also that it undergoes a progressive development in a posterior direction by a successive addition of tooth-plates (see Jarvik, 1966, p. 42, fig. 3). By this process a tooth-bearing posterior process extending more or less far backwards underneath the parasphenoid is often formed (see e.g. Wiedersheim, 1877; Wintrebert, 1922; Stadtmüller, 1936, p. 638). In certain urodeles (plethodontids) these tooth-plates retain their independence and form patches on the ventral side of the parasphenoid. Because of the very great agreement shown to exist between urodeles and porolepiforms in numerous other respects I found it reasonable to assume (1942, pp. 416–417) that the corresponding tooth-plates were present underneath the parasphenoid already in porolepiforms. The serial sections of *Glyptolepis* (1962, p. 93) revealed that these presumed tooth-plates (*uodp*, fig. 30; see also *tp*, fig. 92B) actually exist.

Orbitotemporal region

But it is of course not only in the snout that porolepiforms agree closely with urodeles. As we now shall see there are important resemblances also in the orbitotemporal region (the otical and occipital regions are still too incompletely known in porolepiforms to be considered. (As regards the occipital artery in anurans and the a. palatonasalis in urodeles see p. 282 No. 32 and Jarvik, 1967b, pp. 194–196, fig. 8).

Bulbus olfactorius. – An important fact discussed already in 1942 (p. 395) and later confirmed by the serial sections of *Glyptolepis* (1965a, pp. 112–113; see also Stensiö, 1963b) is that the olfactory canal

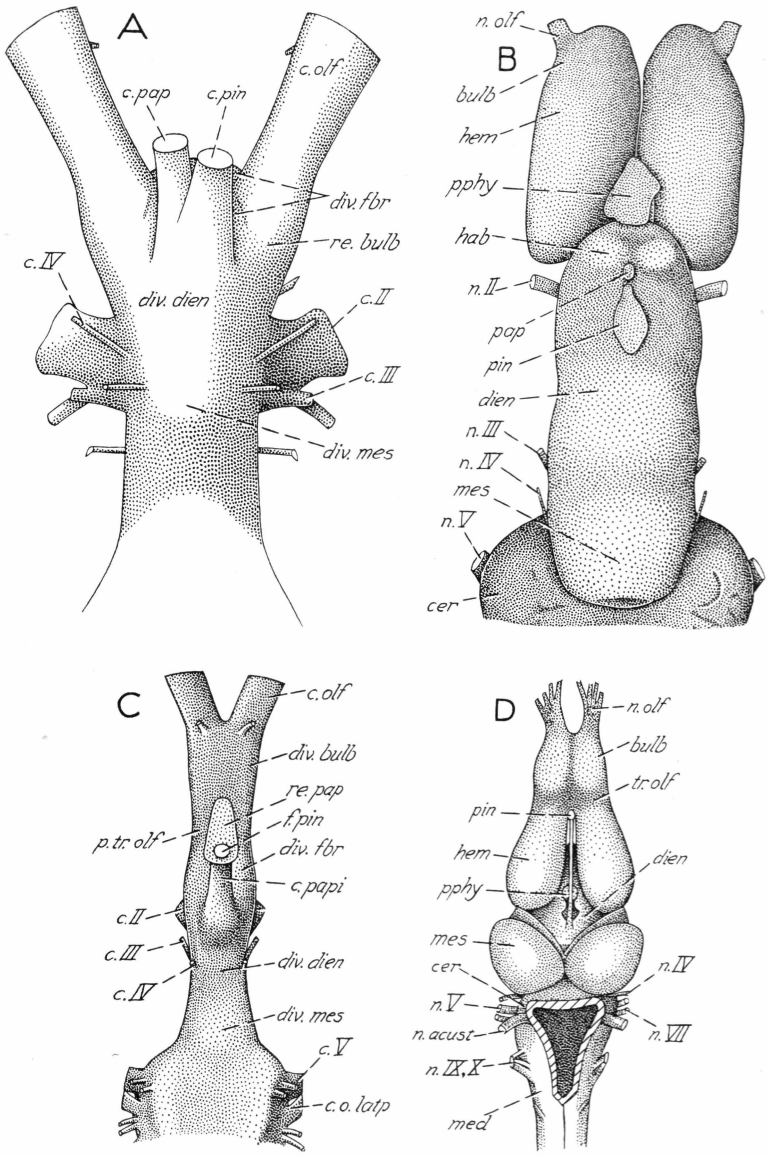


Fig. 80. Representations to show similarities in development of anterior parts of cranial cavity and brain between, *A*, *B*, porolepiforms and urodeles and, *C*, *D*, between osteolepiforms and anurans. *A*, *Glyptolepis groenlandica*. Anterior part of cranial cavity with adjoining canals. Same as in fig. 17 A. *B*, *Hynobius retardatus*, larva 33 mm. Drawing of anterior part of brain after model in wax made by H. C. BJERRING. *C*, *Eusthenopteron foordi*. Anterior part of cranial cavity with adjoining canals. Drawing after wax-model from grinding series 2. *D*, *Rana*. Main anterior part of brain. From WIEDERSHEIM, 1909, fig. 203; slightly modified.

bulb, bulbus olfactorius; *cer*, cerebellum; *c. o. latp*, canal for r. ophthalmicus lateralis; *c. olf*, canalis olfactorius; *c. pap*, canal for parapineal tract; *c. papi*, common canal for parapineal and pineal tracts; *c. pin*, canal for pineal tract; *c. II*, *c. III*,

(*c. olf*) enters the ventro-lateral part of the cranial cavity and that there is a recess (*re. bulb*) so situated that it no doubt housed the bulbus olfactorius (*bulb*, figs. 17, 69A, 70, 80A, 83A). This is of great interest because a characteristic feature of urodeles (figs. 80B, 84A; see also BINDEWALD, 1914; NEIMANIS, 1931; JARVIK, 1942, pp. 301–302; HERRICK, 1948, pp. 20, 54; STENSIÖ, 1963b; NOWAK, 1967) is just that the bulbus olfactorius is incorporated in the ventro-lateral part of the hemisphere (*hem*) in the same way as it must have been in porolepiforms. In this respect porolepiforms and urodeles differ not only from anurans (fig. 80D) and other eutetrapods in which the bulbus like in osteolepiforms (figs. 70B, 72B, 80C; see also STENSIÖ, 1963b, figs. 52–54; JARVIK, 1967b, figs. 12, 13, pl. 4) is situated in front of the hemisphere separated from that by a more or less long tractus olfactorius (*tr. olf*), but also from sharks, rays, holocephalians, dipnoans, actinopterygians and brachiopterygians (see e.g. JARVIK, 1942, figs. 3, 8, 11; STENSIÖ, 1963b).

Pineal and parapineal organs. – In porolepiforms both the pineal (*pin*) and parapineal (*pap*) organs were well developed (figs. 70A, 83A; JARVIK, 1967b, fig. 2C; see also *c.pap*, *c.pin*, figs. 16, 17, 72A, 80A). In urodeles, on the other hand, the pineal organ (epiphysis) and its innervation are said to be rudimentary and it is stated that the parapineal organ is lacking (ARIËNS KAPPERS, 1965, p. 104). In view of the strong development of these organs in porolepiforms and the close agreement with urodeles in so many other regards these statements seemed a little peculiar, and after looking through a number of microtomised series of *Hynobius retardatus* BJERRING made detailed wax-models of the epiphysial complex and the adjoining part of the brain in the 18.5 mm and 33 m series. The pineal body or epiphysis in urodeles (see e.g. HERRICK, 1948; KELLY, 1963, 1965; ARIËNS KAPPERS, 1965) is generally described as a simple vesicle and according to SUMI (1926, p. 254) this applies also to *Hynobius nebulosus*. However, in *H. retardatus* the "pineal body" has a more intricate structure. In the 18,5 mm stage (figs. 81, 82A,B) it consists of a posterior high portion (*div. p*), which dorsally reaches the membraneous roof (*membr*) of the cranial cavity, and an

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c.IV, *c.V*, canals for optic, oculomotor, trochlear and trigeminal nerves; *dien*, diencephalon; *div. bulb*, division of cranial cavity for bulbus olfactorius; *div. dien*, *div. fbr*, *div. mes*, diencephalon, forebrain and mesencephalon divisions of cranial cavity; *f. pin*, pineal foramen; *hab*, habenula; *hem*, forebrain hemisphere; *med*, medulla oblongata; *mes*, mesencephalon; *n. acust*, n. acusticus (dorsal branch of n. facialis); *n. olf*, n. olfactorius; *n. II*, *n. III*, *n. IV*, *n. V*, *n. VII*, *n. IX*, *X*, optic, oculomotor, trochlear, trigeminal, facial, glossopharyngeal and vagus nerves; *pap*, parapineal organ; *pin*, pineal organ; *pphy*, paraphysis; *p. tr. olf*, part of cranial cavity for tractus olfactorius; *re. bulb*, recess for bulbus olfactorius; *re. pap*, recess for parapineal organ; *tr. olf*, tractus olfactorius.

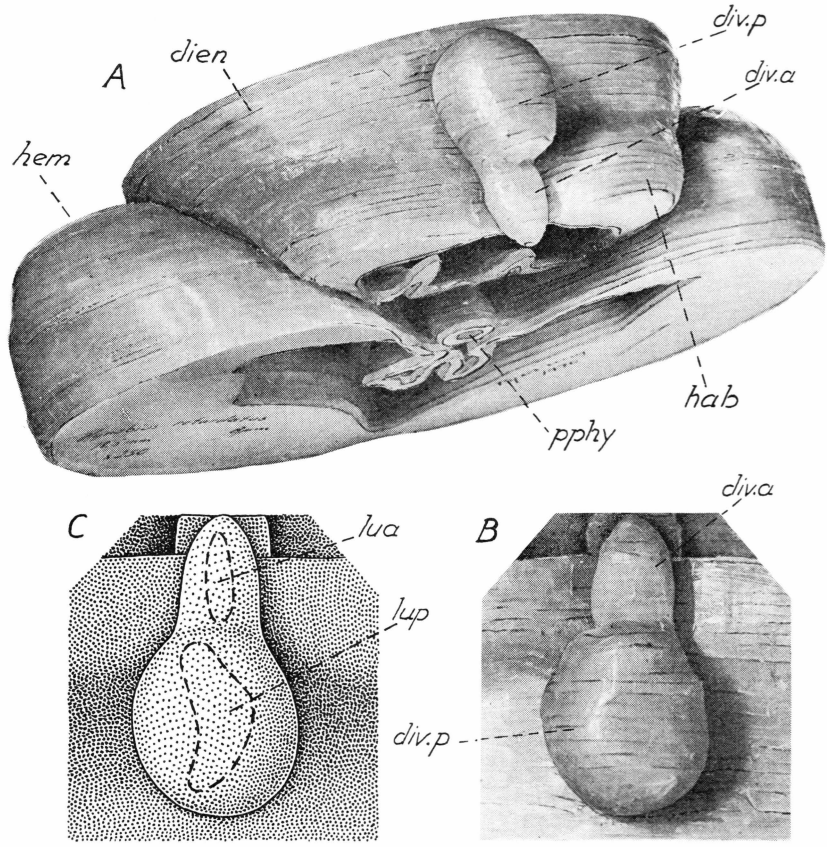


Fig. 81. *Hynobius retardatus*, larva 18.5 mm. *A*, photograph of model of part of brain in antero-dorso-lateral view to show epiphysial complex. Model made by H. C. BJERRING in magnification 250/1. *B*, photograph of part of same model in dorsal aspect. *C*, drawing of same to show position of separate lumina of anterior low and posterior high divisions. × 190/1 approx.

For explanation of index letters see fig. 82.

anterior ventral and lower portion (*div. a*) situated between the habenulae (*hab*). Each of these portions has a separate lumen (*lua*, *lup*). Not knowing the innervation (cf. HERRICK, 1948, p. 235; KELLY, 1965) it is of course difficult to interpret these structures quite safely and further investigations are necessary. However, in view of the conditions in porolepiforms it is tempting to assume that the posterior and high portion represents the pineal and the anterior and low one the parapineal organ.

This assumption is strongly supported by the fact that the 33 mm embryo of *Hynobius retardatus* (fig. 80 B) shows two organs, one posterior (*pin*) situated as the "pineal body" in urodeles as it is generally described, and a small vesicle (*pap*) situated farther forwards, between the habe-

nulae, and obviously corresponding to the anterior, low portion in the 18.5 mm stage. If it is added that the two organs in fishes and in lizards may arise in close connection with each other (Oksche, 1965, p. 7, fig. 4C) there seems to be little doubt that the anterior low portion (*div. a*, fig. 81) and the anterior vesicle (*pap*, fig. 80B) in *H. retardatus* really represent the parapineal organ. However, judging from the wax-models both organs in *Hynobius* are median structures, whereas these organs and the stalks connecting them with the brain in porolepiforms (see figs. 75B, 83A) were asymmetrical in position. This may appear to be a difference but an interesting fact is that the lumen (*lup*, fig. 81C) of the posterior portion in *Hynobius* is asymmetrical. Moreover, Braitenberg & Kemali (1970) have recently recorded asymmetry in the epithalamus and marked differences between the left and right habenular nuclei in *Triturus* and it seems likely that the pineal and parapineal organs in ancestral urodeles, as in porolepiforms, were asymmetrical in position.

Hypophysial area. – The fossa hypophyseos and associated canals and other structures in porolepiforms (see pp. 50–54) may, after comparisons in the first hand with urodeles, be interpreted in the following way.

In urodeles (figs. 83C, D, 84; for review see Wingstrand, 1966) the neurohypophysis, situated in the postero-ventral part of the infundibulum, includes the neural lobe (*ne. l*) and the median eminence (*em*), whereas the adenohypophysis is composed of three parts, the pars intermedia (*p. int*), the pars anterior or distalis (*ad. hy*), and the paired pars tuberalis (*p. tub*). According to observations made on very early stages (about 4 mm) of *Ambystoma* by Kingsley & Thyng (1904) the adenohypophysis arises from a paired primordium (*ad. pr*, fig. 84B). This observation has not been confirmed by later students (Atwell, 1921; Grenell, 1939; and others) but is nevertheless of great interest because the buccohypophysial canal in porolepiforms is paired and possibly we in this respect are concerned with primitive conditions (as regards paired primordia of the adenohypophysis in fishes see Kingsley & Thyng, 1904, p. 368; cf. also Stensiö, 1963a, pp. 93–97, figs. 37, 44; as regards the neurohypophysis see *ap. hyp*, fig. 108A and Bjerring, 1971, fig. 16, *pri. nhy*). The paired primordia soon fuse and a median body which for a short time is connected with the buccal cavity by an epithelial stalk (buccohypophysial duct) is formed. The median body in the first hand gives rise to the pars distalis and most posteriorly to the pars intermedia. According to Atwell (1921, pp. 374–378) the epithelial stalk is connected with the anterior end of the pars distalis and after the disappearance of the stalk that end becomes blunt and rounded. Somewhat later (*Ambystoma* 14mm) "a thin shelflike lateral extension" is formed on each side of the anterior part of the pars distalis. This lateral extension (*lhy*), the

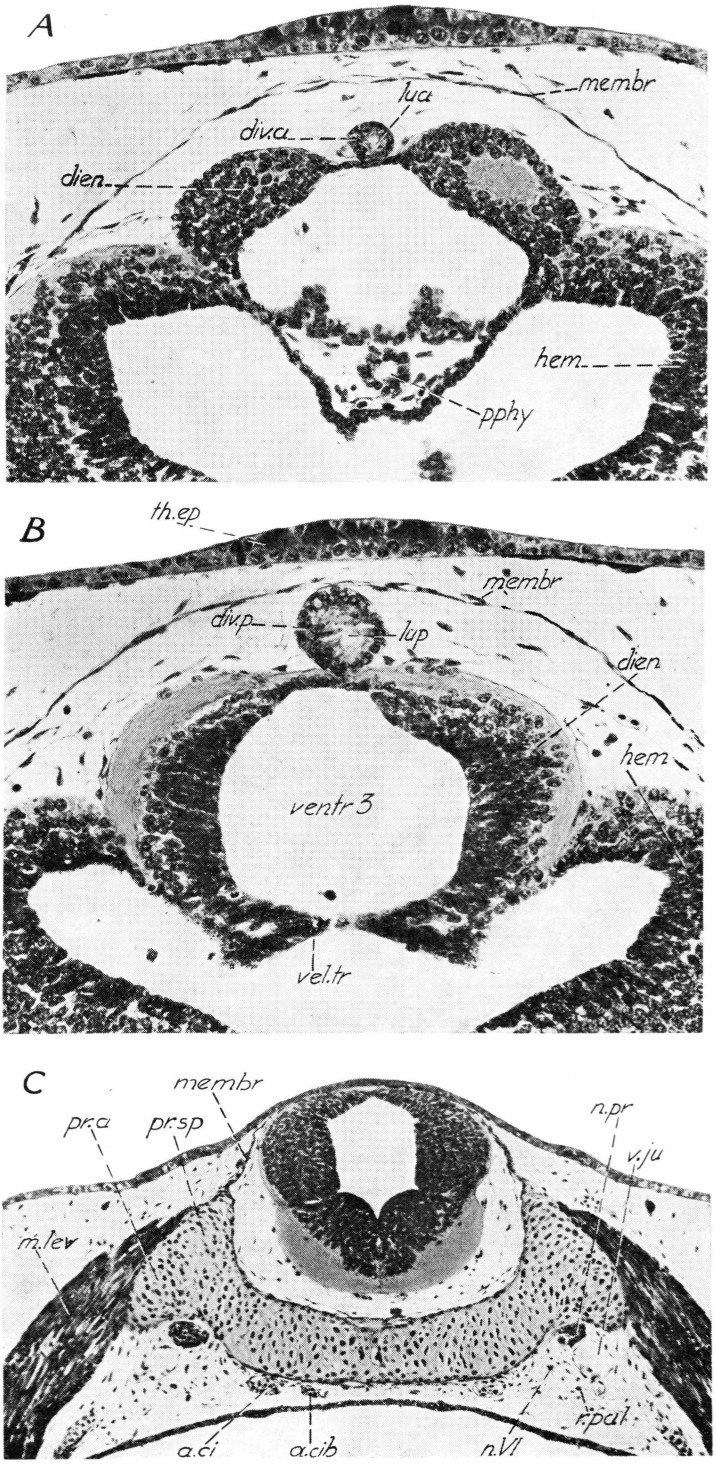

A
membr
luca
diva
dien
hem
pphy
B
th.ep
membr
div.p
lup
dien
hem
ventr 3
vel.tr
C
membr
pr.a
pr.sp
n.pr
v.ju
m.lev
r.pal
a.ci
a.cib
n.VI

Fig. 82.

lateral lobe (pars lateralis, GRENELL, 1939), is of interest because it is from this lobe that the pars tuberalis is formed. The paired pars tuberalis (*p. tub*), which in certain urodeles is a prominent structure, grows out in direction forwards and slightly upwards (see also ROOFE, 1937, figs. 2, 4) and is in the adult a long slender process situated close to the floor of the diencephalon behind the optic chiasma.

In porolepiforms (figs. 17–19, 72A, pp. 50–51) the ventral horizontal portion of the fossa hypophyseos (*fo. hyh*), which no doubt housed a part of the pars distalis of the adenohypophysis, anteriorly—laterally to the paired buccohypophysial canal (*c. bhd*, *c. bhs*)—broadens and forms a paired lateral recess (*re. lhy*). This recess is continued forwards and upwards by a wide canal (*c. p. tub*) which reaches the cranial cavity in the recess (*re. chi*) which probably lodged the optic chiasma and is continued backwards by a groove (*gr. p. tub*) in the floor of the cranial cavity. These conditions and the fact that canal *c. p. tub* is wider than the canal for the internal carotid artery (*c. a. ci*, cf. STENSIÖ, 1963b, fig. 48) can only mean that the paired canal lodged the pars tuberalis (*p. tub.* fig. 83A, B) and given this interpretation we may assume that the hypophysis in porolepiforms was developed somewhat as follows (fig. 83A, B).

In urodeles the brain as seen in lateral aspect generally forms a ventral swelling (*chi*) at the optic chiasma (fig. 84A; see also FRANCIS, 1934, pl. 9:50; HERRICK, 1948, fig. 1A) and behind that the ventral surface of the brain is concave (*con*). The presence of a fairly deep recess, the chiasma recess (*re. chi*, fig. 18), between the inner openings of the opticus canals in *Glyptolepis* and the fact that the floor of the cranial cavity behind that recess shows a median elevation (*m. el*) with a convex dorsal side suggests that the brain also in porolepiforms had a ventral swelling at the optic chiasma and that its ventral side behind that was concave as seen in lateral view. In this concave part (*con*) of the floor of

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Fig. 82. *Hynobius retardatus*, larva 18.5 mm. Photographs of transverse sections. *A*, through anterior low and, *B*, through posterior high portion of epiphysial complex. × 133/1 approx. *C*, through processus ascendens palatoquadrati to show transient artery medially to a. carotis interna. × 50/1.

a. ci, a. carotis interna; *a. cib*, transient vessel probably representing medial branch of a. carotis interna; *dien*, diencephalon; *div. a*, anterior low portion of epiphysial complex, probably representing parapineal organ; *div. p*, posterior high portion, probably representing pineal organ; *hab*, habenula; *hem*, hemisphere of forebrain; *lua*, *lup*, lumina of anterior low and posterior high portions of epiphysial complex; *membr*, membraneous roof of cranial cavity; *m. lev*, musculus levator mandibulae; *n. pr*, n. ophthalmicus profundus; *n. VI*, n. abducens; *pphy*, proximal portion (stalk) of paraphysis; *pr. a*, processus ascendens of palatoquadrate; *pr. sp*, suprapterygoid process of pila antotica; *r. pal*, r. palatinus VII; *th. ep*, median thickening of epidermis dorsal to epiphysial complex; *vel. tr*, velum transversum; *ventr3*, third ventricle; *v. ju*, jugular vein.

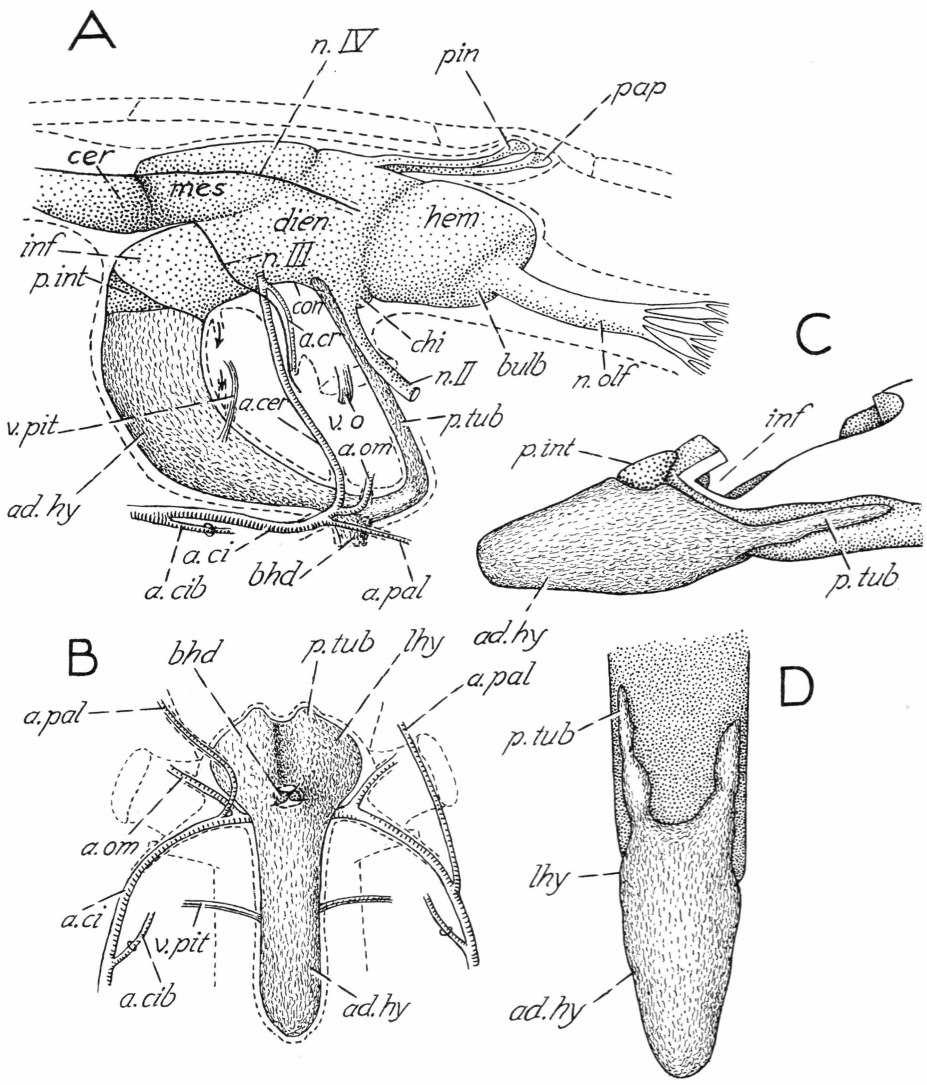


Fig. 83. *A*, *B*, *Glyptolepis groenlandica*. *A*, attempted restoration of anterior part of brain, hypophysis, and certain nerves and vessels in lateral aspect (cf. figs. 17, 18). Portal vessels indicated by arrows. *B*, attempted restoration of hypophysis and vessels in ventral aspect. *C*, *D*, *Ambystoma punctatum*, larva 40 mm. Hypophysis with adjoining parts of brain in lateral and ventral aspects. From ATWELL, 1921, figs. 8, 10.

a. cer, cerebral artery; *a. ci*, a. carotis interna; *a. cib*, medial branch of a. carotis interna; *a. cr*, a. centralis retinae; *ad. hy*, principal part (pars distalis) of adenohypophysis; *a. om*, a. ophthalmica magna; *a. pal*, a. palatina; *bhd*, buccohypophysial duct of right side; *bulb*, bulbus olfactorius; *cer*, cerebellum; *chi*, chiasma opticorum; *con*, concave ventral side of diencephalon in area of median eminence; *dien*, diencephalon; *hem*, hemisphere; *inf*, infundibulum; *lhy*, lateral lobe of adenohypophysis; *mes*, mesencephalon; *n. olf*, n. olfactorius; *n. II–n. IV*, optic, oculomotor and trochlear nerves; *pap*, parapineal organ; *pin*, pineal organ; *p. int*, pars intermedia of adenohypophysis; *p. tub*, pars tuberalis of adenohypophysis; *v. o*, optic vein; *v. pit*, pituitary vein.

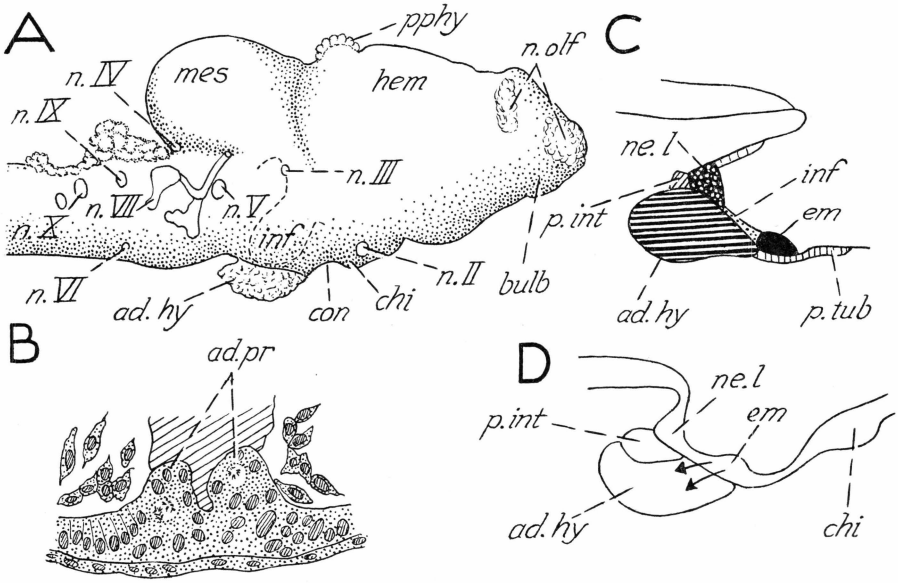


Fig. 84. *A*, *Diemyctylus viridescens*, adult. Brain in lateral aspect. From GAGE, 1893, pl. 2:5. ×13/1 approx. *B*, *Ambystoma*, early larval stage. Transverse section to show paired primordium of adenohypophysis. From KINGSLEY & THYNG, 1904, fig. 3. *C*, *Ambystoma*, diagram of hypophysis. From GREEN, 1947, fig. 4. *D*, diagram of hypophysis in typical urodele. Arrows indicate certain portal vessels. From GREEN, 1951, fig. 14.

ad. pr, paired primordium of adenohypophysis; *em*, median eminence; *ne. l*, neural lobe of neurohypophysis; *n. V–n. X*, trigeminal, abducens, facial, glossopharyngeal and vagus nerves; *pphy*, paraphysis.

For explanation of other index letters see fig. 83.

the diencephalon in urodeles lies the eminentia mediana (*em*, fig. 84C, D) of the neurohypophysis and because this structure is present also in other tetrapods and in fishes (see WINGSTRAND, 1966; MEURLING, 1967, p. 92) it seems likely that there was a median eminence in porolepiforms as well. At the posterior part of the median elevation of the floor of the cranial cavity in porolepiforms, close in front of the narrow dorsal opening of the fossa hypophyseos, lie the dorsal openings of the narrow paired canals (*c. port*) which connect this part of the cranial cavity with the fossa hypophyseos. Because these canals obviously run from that part of the brain that contained the median eminence to a part of the fossa hypophyseos that lodged the adenhyopophysis it seems likely that they transmitted vessels belonging to the portal system (see GREEN, 1947 1951; MEURLING, 1967, pp. 92, 95–97). Postero-dorsally to the dorsal openings of these canals lies the large division of the cranial cavity which has been described as the infundibular recess (*re. inf*) and which most likely housed the saccus infundibuli of the diencephalon with the neural

lobe of the neurohypophysis (*inf*, fig. 83 A). Nothing as to the development of the latter can be said on the basis of the fossil material and the same is true of the pars intermedia (*p. int*) of the adenohypophysis. The pars distalis of the adenohypophysis (*ad. hy*) seems to have been well developed and together with vessels it probably occupied the main division of the fossa hypophyseos. Judging from the shape of the fossa it consisted of a posterior vertical portion which ventrally bent gently forwards and was continued by an anterior almost horizontal portion. The latter anteriorly, where it was still in communication with the buccal cavity by a short paired buccohypophysial duct (*bhd*), widened and formed on each side a lateral lobe (*lhy*) which occupied at least the medial part of the lateral recess. The lateral lobe was continued forwards by the long and slender, paired pars tuberalis (*p. tub*). The latter curved upwards and slightly backwards and its dorsal end was probably applied to that part of the brain behind the chiasma (*chi*) that contained the median eminence of the neurohypophysis.

The fact that the pars distalis in urodeles lies close to but in porolepiforms far below the diencephalic floor is certainly a consequence of the flattening of the braincase and the skull as a whole that has occurred in the phylogeny of urodeles. As will be explained below (pp. 217–219) the basipterygoid process of the neural endocranium together with the basal process and the antero-medial articular lamina of the palatoquadrate have become reduced in urodeles and the fossa autopalatina has disappeared. These changes have led to a shift of the parasphenoid to a more dorsal position (cf. JARVIK, 1942, pp. 422–423, 508–509) and a compression from below of the adenohypophysis towards the floor of the brain.

The internal carotid artery (*a. ci*) in porolepiforms (figs. 83 A, B, 85 D, 92 A) no doubt entered the fossa hypophyseos through canal *c. a. i* (fig. 17). In that fossa it gave off a rather strong a. ophthalmica magna (*a. om*) which passed out from the fossa through the ascending canal (*c. a. om*) in the lateral part of the lateral recess. After giving off this branch the internal carotid artery, or as it now may be termed, the cerebral artery (*a. cer*), turned dorsally, passed laterally to the pars distalis of the adenohypophysis and entered the cranial cavity through the ascending carotid canal (*c. a. cer*). Within the cranial cavity it probably gave off a lateral branch (*a. cr*) which passed the groove connecting the inner openings of canals *c. a. cer* and *c. III* and emerged from the cranial cavity together with the n. oculomotorius. This artery probably is the centralis retinae.

The a. palatina (*a. pal*) probably had a different course on the right and left sides of the sectioned specimen of *Glyptolepis* (figs. 83 A, B 85 D). On the right side it branched off from the internal carotid within the fossa hypophyseos, probably a little behind the point where the a. ophthalmica magna was given off, thence it went forwards ventrally to that

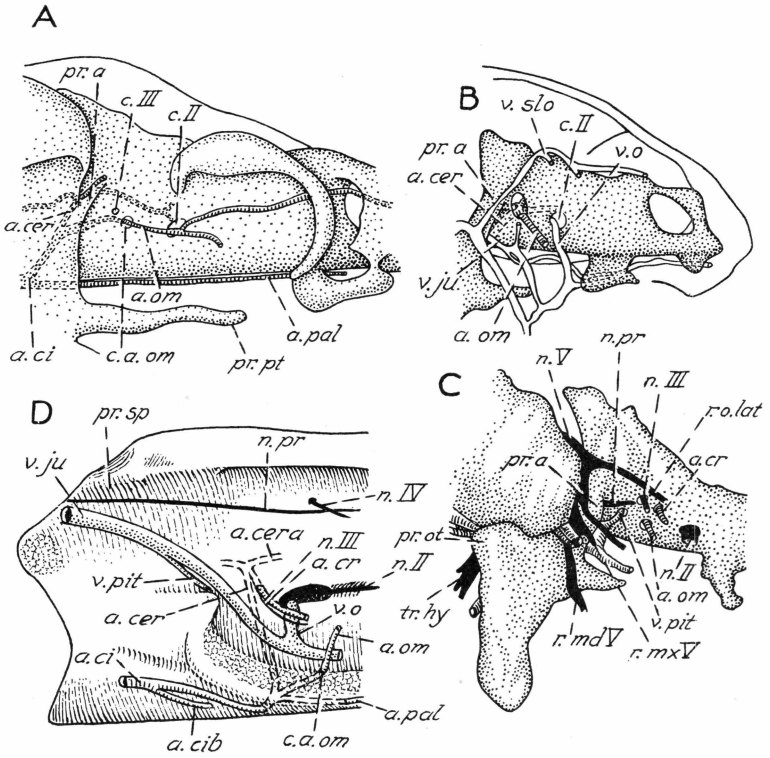


Fig. 85. Part of endocranium in lateral aspect to show course and mutual relations of certain nerves and vessels in orbitotemporal region of, *A–C*, urodeles and, *D*, porolepiforms. *A*, *B*, *Hynobius nebulosus*, larvae, 32 and 17 mm. From Fox, 1959, figs. 25 and 9 (cf. Jarvik, 1966, fig. 10). *C*, *Hynobius keyserlingii*, larva about 16 mm. From Regel, 1964a, fig. 13 (see also Schmalhausen, 1964, fig. 130, 1968, fig. 128). *D*, *Glyptolepis groenlandica* (cf. fig. 21A). Nerves and vessels tentatively restored.

a. cer, a. cerebralis; *a. cera*, a. cerebralis anterior; *a. ci*, a. carotis interna; *a. cib*, medial branch of a. carotis interna; *a. cr*, a. centralis retinae; *a. om*, a. ophthalmica magna; *a. pal*, a. palatina; *c. a. om*, canal or foramen for a. ophthalmica magna; *c. II*, *c. III*, canals or foramina for n. opticus and n. oculomotorius; *n. pr*, n. ophthalmicus profundus; *n. II*, *n. III*, *n. IV*, *n. V*, n. opticus, n. oculomotorius, n. trochlearis and n. trigeminus; *pr. a*, processus ascendens palatoquadrati; *pr. ot*, processus oticus; *pr. pt*, pterygoid process; *pr. sp*, suprapterygoid crest; *r. mdV*, *rmxV*, r. mandibularis and maxillaris trigemini; *r. o. lat*, ramus ophthalmicus lateralis; *tr. hy*, truncus hyomandibularis VII; *v. ju*, jugular vein; *v. o*, vena optica; *v. pit*, pituitary vein; *v. slo*, superior lateral orbital vein (Fox).

artery, passed canal *c. a. pal* (fig. 17) and continued forwards in the groove in the lateral side of the parasphenoid. But on the left side where canal *c. a. pal* is lacking the palatine artery obviously branched off from the internal carotid somewhat farther back, before the internal carotid artery entered the braincase, that is as in urodeles, and passed forwards ventrally to the basipterygoid process (cf. fig. 92A) to the groove (*gr. a. pal*, fig. 39) in the lateral side of the parasphenoid.

The pituitary vein (*v. pit*, figs. 83A, B, 85D, 92A) passed upwards from the postero-ventral lateral recess of the fossa hypophyseos which presumably lodged a vascular plexus situated on the lateral and postero-ventral sides of the adenophypophysis (cf. GREEN, 1947, fig. 3). The vein entered the orbit close dorsally to the basipterygoid process where it at least in the sectioned specimen turned backwards to join the jugular vein (*v. ju*).

As discussed elsewhere (1966, p. 64) the shape of the opticus canal (*c. II*) suggests that a large vessel (*v. o*, figs. 84A, 85D), probably a vein corresponding to the optic vein in urodeles (fig. 85B; see also FOX, 1954, fig. 13) went out from the cranial cavity in the posterior part of that canal, passed ventrally in groove *gr. v. o* (figs. 20B, 21A) presumably to empty in an infraorbital branch of the jugular vein.

The n. opticus (*n. II*) certainly emerged from the area of the optic chiasma and passed out to the orbit through the anterior part of the wide opticus canal. From that opening a more or less long groove (*gr. II*, fig. 21A) carried the nerve forwards to the eye. The n. oculomotorius (*n. III*, fig. 83A) probably emerged from the posterior ventral part of the mesencephalon (*mes*), crossed the lateral side of the diencephalon, turned forwards and continued in the groove on the lateral side of the median elevation of the floor of the cranial cavity to the oculomotor canal (*c. III*) in the lateral cranial wall. The n. trochlearis (*n. IV*) probably ran forwards across the lateral side of the mesencephalon to the groove (*gri. IV*, fig. 19D) on the inner side of the lateral cranial wall, passed out to the orbit through the trochlearis canal (*c. IV*) and continued in the groove (*gre. IV*, fig. 19B) on the external side of the interorbital wall.

The development of the fossa hypophyseos, the course and position of the canals associated with this fossa and the adjoining part of the cranial cavity, and the position of the openings of the canals on the lateral side of the internasal wall fit very well with the conditions in urodeles and no doubt the hypophyseos and the adjoining parts of the brain and cranial nerves were developed very much as in that group and the related main vessels ran and branched in the urodele fashion (fig. 85).

Because no comparative analysis has been made it is difficult to say to which extent the many common features of porolepiforms and urodeles in the hypophysial region are specific to these two groups or are shared with other groups. Nevertheless it is evident that the fact that porolepiforms agree well with urodeles also in the development of the hypophysis, etc. is in accord with and supports the view that these two groups are closely related.

But there remains one canal that could not be interpreted from the information in the literature on urodele anatomy. This canal (*c. a. cib*, figs. 20B, 21A, 31, 39, 73A) which certainly carried a vessel enters the

ventral side of the parasphenoid behind the groove (*gr. psp*) for the prespiracular gill-slit and runs forwards towards the fossa hypophyseos but disappears without reaching that cavity. Because of the constant occurrence of this paired canal in porolepiforms it seemed reasonable to search for a vessel in the corresponding position in the microtomised series of *Hynobius*. Again the search was successful. In almost exactly the place where it was to be expected BJERRING discovered a paired vessel (*a. cib*, fig. 82C) similar to, but narrower, than the internal carotid artery (*a. ci*) running forwards lateral to it. As also was to be expected, this vessel disappears forwards but unfortunately it disappears also backwards and is present only in a few sections. Its nature could therefore not be determined but most likely it is a medial branch (*a. cib*, figs. 83A, B, 85D, 92A–C) of the internal carotid artery.

Dorsal parts of prootic visceral arches

Turning next to the dorsal parts of the three foremost visceral arches (premandibular, mandibular and hyoid) and their relations to the neural endocranium (cf. JARVIK, 1954) it is most convenient to start from behind, with the hyoid arch and the problem of the columella auris.

Hyomandibula, columella, foot-plate. – Alleged similarities in the development of the columella auris, the cartilage in the fenestra ovalis known as the operculum, and the musculus opercularis have been one of the main arguments for the view that recent Amphibia are monophyletic (see JARVIK, 1965a, p. 125). However, according to the most recent studies of the m. opercularis (DUNN, 1941; MONATH, 1965) this muscle is not homologous in urodeles and anurans and most likely not even in the various urodeles. In view of this fact and because the operculum, which is situated in the posterior part of the fenestra ovalis (vestibuli), serves as the area of insertion of that muscle and occurs only when the muscle is present, it may be reasonable to assume (JARVIK, 1965a, p. 126) that the operculum is a secondary formation that has arisen independently as a fixing device for those different parts of the axial musculature from which the m. opercularis has developed. That this is so is also supported by the fact that both the m. opercularis and the operculum are lacking in hynobiids which are generally considered to be the most primitive urodeles and which according to SCHMALHAUSEN (1968) display the most primitive conditions among urodeles with regard to the development of the columella auris.

But before turning to the columella it is necessary to make a few remarks about the so-called foot-plate (*foot-pl*, fig. 89). According to current views (see e.g. BARRY, 1956) this plate which forms the proximal part of the columella and occupies the anterior part of the

fenestra ovalis (*fe. ov*) is a derivative of the lateral wall of the auditory capsule.

In both porolepiforms and osteolepiforms there is a large opening (*fe. ov*, figs. 86B, 92A, 93D,E) in the wall of the otic capsule which no doubt represents the fenestra ovalis (vestibular fontanelle, JARVIK, 1954). The antero-dorsal part of the margin of that opening, at any rate in osteolepiforms, projects backwards into a tongue-like lamella (*foot-pl*) which conceals the antero-dorsal part of the fenestra ovalis from the outside. On the external side of this projection lies part of the articular area (*hyv*) for the ventral articular head (*ahv*) of the hyomandibula. According to the views set forth in 1954 this articulation is the original articulation between the epiphyal (hyomandibula) and the infrapharyngohyal (see also *Eh*, *Ih*, fig. 88) and if this be true the tongue-like projection most likely is the posterior part of the infrapharyngohyal. The ventral articular head is continued distally by the shaft of the hyomandibula which in its middle part is provided with a process, the opercular process (*pr. Op*), received by a pit on the inner side of the opercular bone (*Op*) of the gill-cover. If we now assume (see fig. 86) that the opercular bone becomes reduced and replaced by a tympanic membrane (cf. JARVIK, 1965a, p. 125, 1967b, p. 197) sound waves from this membrane will be conducted to the inner ear via the processus opercularis, the proximal part of the shaft and the ventral articular head of the hyomandibula. If we further imagine (cf. fig. 92B) that the ventral articular head fuses with the projection (*foot-pl*) of the posterior part of the infrapharyngohyal in the antero-dorsal part of the fenestra ovalis, it is readily seen that a structure will arise suggestive of a columella auris of the type found in anurans, stegocephalians and reptiles, and like that provided with a foot-plate formed by the posterior part of the infrapharyngohyal and a dorsal process (processus ascendens partis externa plectri; see GOODRICH, 1930; SÄVE-SÖDERBERGH, 1936; STADTMÜLLER, 1936; WESTOLL, 1943b; BARRY, 1956; WESTHUIZEN, 1961, and others) derived from the dorsal articular head (*ahd*) of the hyomandibula in osteolepiforms.

In the sections of *Eusthenopteron* the part of the hyoid arch situated behind the articulation of the lower jaw is imperfectly preserved but there seems to be a stylohyal (*Sh*, fig. 86A; JARVIK, 1954, fig. 8) and below that the dorsal part of ceratohyal 2 (*Ch 2*) has a process (*pr. Sop*) which fits into a distinct pit on the inner side of the subopercular (*Sop*). This pit (JARVIK, 1954, fig. 14A, *p. Sop*) is situated behind a distinct crescent-shaped flange which projects inwards from the anterior margin of the subopercular and encircles the jaw joint from behind. Moreover ceratohyal 2 is provided with a tongue-like process (*pr. Rbr*) which abuts against the inner side of the submandibulobranchiostegal plate (*Sbm Rbr*) and farther forwards submandibular 7 is supported by a lateral crest (*lcr. Ch*) of the ceratohyal (see also JARVIK, 1963a, pp. 15, 17, 27, figs. 8C, 12A, 19C).

In anurans, reptiles and birds it is, as mentioned above, probably the opercular bone (*Op*, fig. 86) of their osteolepiform ancestors that has been replaced by a tym-

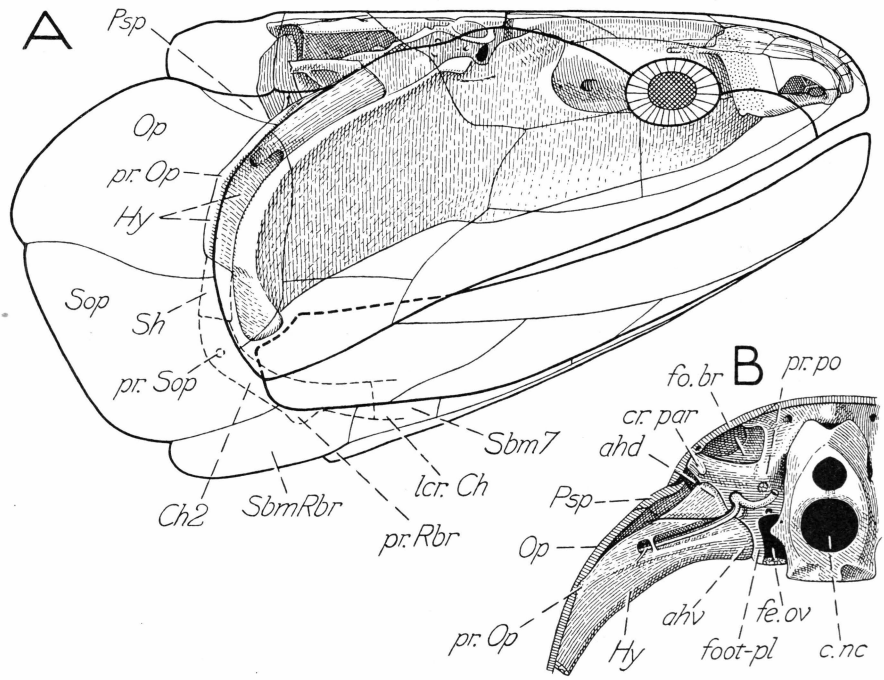


Fig. 86. *Eusthenopteron foordi*. Restorations to illustrate possible origin of auditory ossicles in Osteolepiform-Tetrapod stock. Nat. size. *A*, neural endocranium, palatoquadrate and dorsal part of hyoid arch with dermal bones of skull in lateral view. Cf. JARVIK, 1944a, fig. 18A, 1954, figs. 1A, 8A, 23A, 1963a, fig. 12A. *B*, left side of divisio cranialis posterior with hyomandibula, opercular and postspiracular plate in posterior aspect. Cf. JARVIK, 1954, fig. 47, 1964, fig. 6B.

Ch2, posterior ceratohyal; *Hy*, hyomandibula; *Op*, opercular; *Psp*, postspiracular plate; *Sbm*, submandibular 7; *SbmRbr*, submandibulobranchiostegal plate; *Sh*, stylohyal; *Sop*, subopercular.

ahd, *ahv*, dorsal and ventral articular heads of hyomandibula; *c. nc*, canal for notochord; *cr. par*, crista parotica; *fe. ov*, fenestra ovalis; *fo. br*, fossa bridgei; *foot-pl*, part of lateral wall of auditory capsule probably forming foot-plate of columella; *lcr. Ch*, lateral crest of ceratohyal articulating with submandibular 7; *pr. Op*, opercular process of hyomandibula; *pr. po*, postotical process; *pr. Rbr*, process of ceratohyal 2 probably articulating with submandibulobranchiostegal plate; *pr. Sop*, position of presumed subopercular process of ceratohyal 2.

panic membrane. However, if we now imagine that in other tetrapod descendants of osteolepiforms or osteolepiform-like ancestors (cf. JARVIK, 1960, p. 56, fig. 18; 1968b, fig. 3) it is instead the subopercular (or the submandibulobranchiostegal plate, or possibly submandibular 7) that is replaced by a tympanic membrane it is readily seen that conditions recalling those in mammals (and other theropsids) will arise. The tympanic membrane will be situated low down, behind the jaw joint, and from that membrane sound waves will be conducted to the inner ear via a chain of three bones, namely the dorsal part of the ceratohyal with process *pr. Sop* (or possibly with process *pr. Rbr*, or lateral crest *lcr. Ch*), the stylohyal and the hyomandibula. In view of

these facts it would be tempting to suggest a new solution to the old and much debated problem as to the origin of the auditory ossicles in mammals, a problem which, however, is much too intricate to be discussed in this connection (cf. GOODRICH, 1930, pp. 449–485; WESTOLL, 1943b; PARRINGTON, 1958, 1967b; DEVILLERS, 1961, pp. 371–407). It may only be mentioned that many writers, among them VERSLUYS (1898), favour the view that the mammalian ear ossicles are derivatives of the hyoid arch and that accordingly the incus and the malleus, in contrast to current views, cannot be homologous with the pars quadrata and the pars articularis of the mandibular arch.

As regards the development of the dorsal part of the operculo-gular series of bones porolepiforms (*Op*, *Sop*, *Rbr*, figs. 43–45, 63) differ considerably from osteolepiforms and also because the underlying part of the hyoid arch is still incompletely known it is difficult to say if the necessary prerequisites for the formation of a tympanic membrane were present in porolepiforms. It may very well happen that the absence of that membrane in urodeles is primitive (cf. JARVIK, 1965a, p. 126). The vestigial spiracular pouch (*gs. sp*, fig. 89A) found in urodele larvae is an inheritance from their piscine ancestors and solely the presence of this pouch cannot be used as an argument for the view (SCHMALHAUSEN, 1968, p. 191) that the ancestral urodeles had a tympanic cavity and a tympanic membrane.

In porolepiforms the relations between the proximal part of the hyomandibula and the neural endocranium seem to be about the same as in osteolepiforms and we may therefore assume that the ventral articular head of the hyomandibula also in them articulated with a projection (*foot-pl*, fig. 92A) from the anterior margin of the fenestra ovalis and that that projection formed the foot-plate (fig. 92B, D) of the urodele columella (*Hy*). Consequently the foot-plate also in urodeles must be the posterior part of the infrapharyngohyal which is in accordance with the results gained experimentally by TOERIEN (1963) that both the foot-plate and the stylus columellae share an origin with the visceral skeleton and most likely belong to the hyoid arch.

If we disregard the foot-plate which thus most likely is the posterior part of the infrapharyngohyal the comparison of the columella in hynobiid urodeles as described by SCHMALHAUSEN (1956a, 1956b, 1957b, 1964, 1968) with the hyomandibula in porolepiforms gives the following results (figs. 87, 92):

Quite as the hyomandibula in porolepiforms the columella in *Hynobius* has two proximal articular heads one ventral (*hyv*) which in *Hynobius* has fused with the foot-plate (*foot-pl*) and one dorsal which extends to the crista parotica and squamosal and lies lateral to the jugular vein (see SCHMALHAUSEN, 1923, fig. 6, 1968, figs. 106, 107). The ventral articular head in porolepiforms lies farther back than the dorsal one and the same seems to be true of *Hynobius* as well. Distal to the articular heads follows the shaft which in its proximal part lies close to the posterior margin (*Pq. dm*) of the palatoquadrate and in porolepiforms and sometimes in *Hynobius* (SCHMALHAUSEN, 1968, fig. 112) is pierced by a canal for the r. mandibularis VII. But the most important resemblance is no doubt

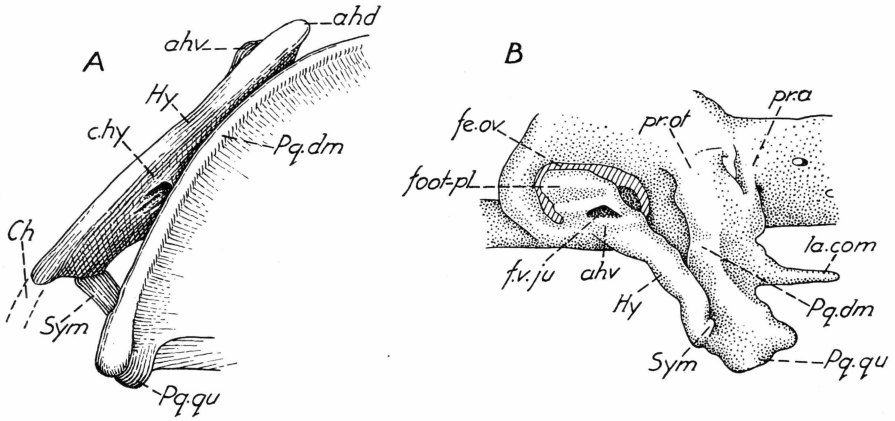


Fig. 87. Two drawings to illustrate similarities between, *A*, porolepiforms and, *B*, urodeles in relations between hyomandibula, symplectic and posterior part of palatoquadrate. *A*, *Glyptolepis groenlandica*. Attempted restoration mainly after specimen shown in pl. 19:2. *B*, *Hynobius keyserlingii*, larva 34 mm. From SCHMALHAUSEN, 1956b, fig. 5 (see also 1968, fig. 113).

Ch, ceratohyal or stylohyal; *Hy*, hyomandibula, in urodeles generally called stapes or columella; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate assumed to represent epimandibular; *Pq. qu*, pars quadrata; *Sym*, symplectic (processus hyoideus, SCHMALHAUSEN).

ahd, dorsal articular head of hyomandibula; *ahv*, ventral articular head of hyomandibula or its presumed equivalent in urodeles; *c. hy*, hyomandibular canal; *fe. ov*, fenestra ovalis; *foot-pl*, foot-plate, probably derived from posterior end of infrapharyngohyal; *f. v. ju*, foramen for jugular vein; *la. com*, commissural lamina (processus pterygoideus); *pr. a*, *pr. ot*, processus ascendens and oticus of palatoquadrate.

that the columella distally diverges from the palatoquadrate as does the hyomandibula in porolepiforms giving place for the symplectic ("interhyal"). This element (*Sym*) which according to SCHMALHAUSEN (1968, p. 184) arises "from a mesenchyme condensation lying between the palatoquadrate cartilage and the hyoid, i.e. between elements of two distinct visceral arches" is known in several other urodeles and it may be independent or fuse with the palatoquadrate forming the hyoid process (see WIEDERSHEIM, 1877, p. 376, HF; SCHMALHAUSEN, 1923; LITZELMAN, 1923; STADTMÜLLER, 1924, p. 188, 1936, p. 589; DE BEER, 1937; CLOETE, 1961, p. 136; SRINIVASACHAR, 1962, p. 278). This element may correspond to the symplectic in fishes (STADTMÜLLER, 1936, p. 589; cf. BERTMAR, 1959, 1961) but of great importance is that it is lacking in osteolepiforms, and as far as I can find in all tetrapods belonging to the osteolepiform-tetrapod stock. That the symplectic is lacking in osteolepiforms (fig. 86A) is, besides by the grinding series of *Eusthenopteron* (JARVIK, 1954), evidenced by the fact that there is no equivalent to the

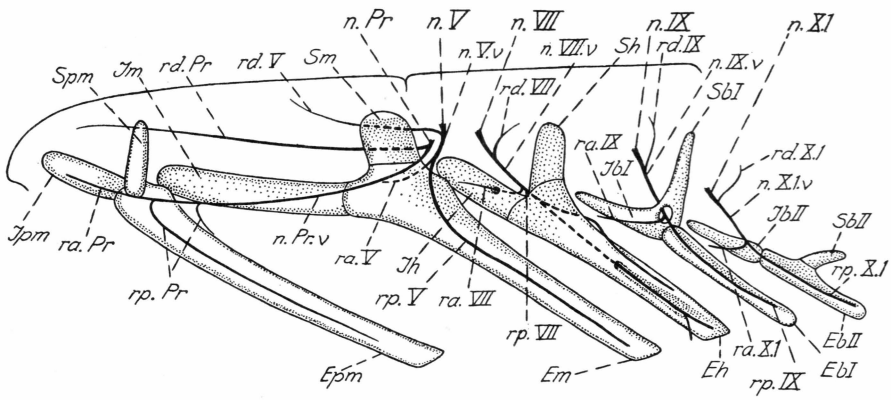


Fig. 88. Diagrammatic representation to show dorsal cranial nerves and dorsal parts of visceral arches of five foremost metameres in *Eusthenopteron*. Slightly modified from JARVIK, 1954, fig. 43.

Eb. I, *Eb. II*, epibranchials I and II; *Eh*, epihyal (= hyomandibula); *Em*, epimandibular (= postero-dorsal marginal portion of palatoquadrate); *Epm*, epipremandibular (= pars autopalatina palatoquadrati); *Ib. I*, *Ib. II*, infrapharyngobranchials I and II; *Ih*, infrapharyngohyal (= otical shelf); *Im*, infrapharyngomandibular (=part of trabecula); *Ipm*, infrapharyngopremandibular (= ventral part of ethmoidal region carrying vomer); *Sb. I*, *Sb. II*, suprapharyngobranchials I and II; *Sh*, suprapharyngohyal (= lateral commissure); *Sm*, suprapharyngomandibular (= processus ascendens palatoquadrati); *Spm*, suprapharyngopremandibular (= lateral part of postnasal wall).

n. Pr, nervus profundus, dorsal nerve of 1st or premandibular metamere ("trigeminus I"); *n. V*, nervus trigeminus, dorsal nerve of 2nd or mandibular metamere ("trigeminus II", "trigeminus proper"); *n. VII*, nervus facialis, dorsal nerve of 3rd or hyoid metamere (including n. acusticus); *n. IX*, nervus glossopharyngeus, dorsal nerve of 4th or first branchial metamere; *n. X. 1*, part of nervus vagus, dorsal nerve of 5th or second branchial metamere.

n. Pr. v–n. X. 1. v, visceral trunks of dorsal nerves of metameres 1–5 (*n. Pr. v* = r. maxillaris trigemini; *n. V. v* = r. mandibularis trigemini); *ra. Pr–ra. X. 1*, anterior (pharyngeal) rami of visceral trunks (*ra. V*, hypothetic; *ra. VII* = r. palatinus; pretrematic branches omitted); *rd. Pr–rd. X. 1*, dorsal somatic sensory branches of dorsal cranial nerves (*rd. Pr* = r. ophthalmicus profundus; *rd. V* = r. ophthalmicus superficialis V; *rd. VII* = n. acusticus; *rd. IX* = r. supratemporalis IX; *rd. X. 1* = r. auricularis X; cf. JARVIK, 1954, p. 86); *rp. Pr–rp. X. 1*, posterior (posttrematic) rami of visceral trunks.

porolepiform preoperculosubmandibular, a bone which occupies the space outside the symplectic and marks the position of that element.

As has now been demonstrated the columella in *Hynobius*, with allowance for its foot-plate, agrees closely with the hyomandibula in porolepiforms and is no doubt homologous with that bone. It is also clear that neither the development of the columella nor of the operculum and the m. opercularis can be used as arguments for a monophyletic origin of

the Amphibia. As a matter of fact *the development of the columella and in particular the presence of the symplectic furnishes us with another strong proof of the views that urodeles are closely related to porolepiforms and that the Amphibia are diphyletic.*

But is the columella homologous with the hyomandibula it must be the epal element (*Eh*, figs. 88, 96) of the hyoid arch (JARVIK, 1954) and we have now to look for the infra- and suprapharyngeal elements of that arch.

Infra- and suprapharyngohyals, otic process, paratemporal commissure. – In urodeles (figs. 89, 91, 92C) the ventral side of the otic capsule anteriorly, at the foramen (*c. pal*) for the r. palatinus VII (*r. pal*), is provided with a more or less distinct shelf (*sh. ot*) generally considered to be the basipterygoid (basitrabecular) process (STADTMÜLLER, 1936, p. 375; DE BEER, 1937; RYKE, 1950, fig. 5; CLOETE, 1961, fig. 8; and others). However, as shown by LITZELMAN (1923, p. 471) this shelf arises from a mesenchymatic band which posteriorly is continuous with the hyomandibula, and the cartilage formed in the anterior part of the band, that is the shelf, is situated between the wall of the otic capsule and the so-called processus basalis (*com. pt*) of the palatoquadrate. This indicates (see also *Ih*, fig. 96) that the shelf belongs to the hyoid arch and because of its position in relation to the jugular vein, the palatine nerve, etc. it is evident that this shelf together with the so-called postpalatine commissure (FOX, 1959, fig. 27, 1963, "otoquadrate) is a vestige of the otical shelf in porolepiforms and homologous also with the shelf in osteolepiforms (*sh. ot*, figs. 90B, 93E; *Ih*, fig. 99) which has been shown to be the infrapharyngohyal (JARVIK, 1954). This is supported also by the fact that the postpalatine part of the shelf ("otoquadrate") according to FOX (1963, 1965) is homologous with the so-called otoquadrate in dipnoans which has been shown to belong to the hyoid arch and represent the "pharyngohyal" (cf. BERTMAR, 1959, pp. 308–330). In anurans, too, this structure is present and is represented by the otic (auditory) ledge (JARVIK, 1954; WESTHUIZEN, 1961) and of interest is that that ledge (*sh. ot*, fig. 90A) according to WESTHUIZEN is continued backwards to the fenestra ovalis and includes the pars interna plectri, that is the footplate (*foot-pl*) of the columella which probably represents the posterior end of the infrapharyngohyal (*Ih*, fig. 96).

The suprapharyngohyal (*Sh*) is in osteolepiforms (figs. 90C, 93E, 99A) and porolepiforms (figs. 21B, 92A) probably represented by the lateral commissure (*lc*, JARVIK, 1954; cf. BERTMAR, 1959). In tetrapods there is no distinct lateral commissure but as first suggested by ALLIS and later maintained also by WESTHUIZEN (1961, pp. 59–63) it is probably represented by the processus oticus (*pr. ot*, fig. 85C) of the palatoquadrate (cf. BERTMAR, 1962). However, judging from the observations

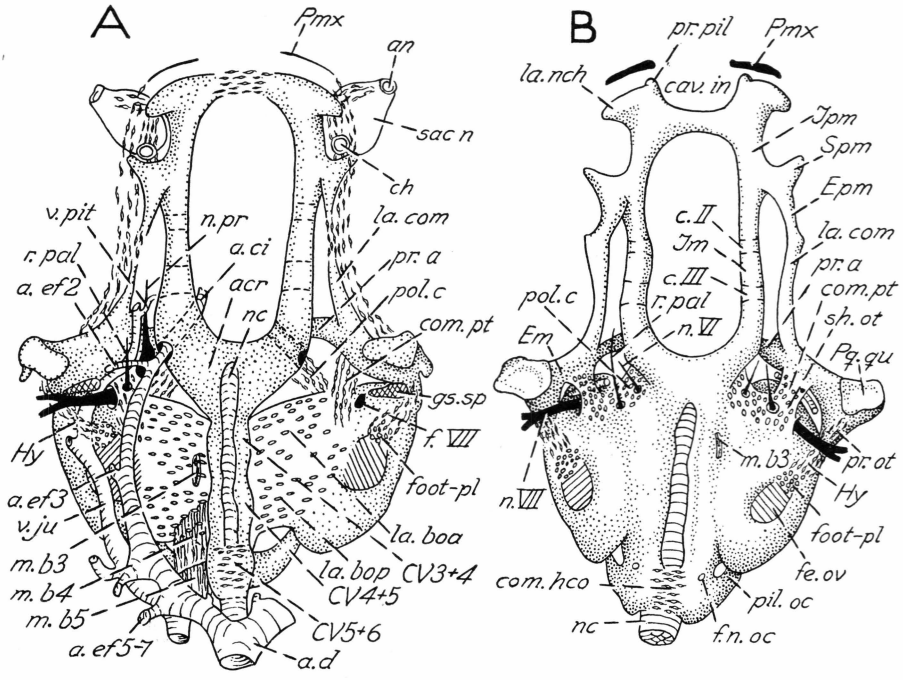


Fig. 89. *Ranodon sibiricus*, *A*, larva 21 mm, *B*, larva 25 mm. Neural endocranium with palatoquadrate and certain nerves and vessels in ventral aspects. From REGEL, 1968, figs. 16 B and 22. Interpretation of skeletal structures (or blastemas) in accordance with views expressed in text and in figs. 92, 96, 97. For orientation certain index letters used by REGEL and SCHMALHAUSEN are given in brackets in explanation below.

CV3 + 4, *CV4 + 5*, *CV5 + 6*, swellings probably representing ventral parts of cranial vertebrae 3 + 4, 4 + 5 and 5 + 6 (*ppocc1*, *pocc2*, *occ3*, REGEL); *Em*, epimandibular; *Epm*, epipremandibular (anterior pterygoid process, *ppta*, REGEL); *Hy*, hyomandibula (ventral extension of columella, *pv*, SCHMALHAUSEN); *Im*, infrapharyngomandibular (part of "trabecula"); *Ipm*, infrapharyngopremandibular (part of "trabecula"); *Pmx*, premaxillary; *Pq. qu*, pars quadrata of palatoquadrate; *Spm*, suprapharyngopremandibular (processus antorbitalis, *pao*, REGEL).

a. ci, a. carotis interna; *acr*, acrochordal cartilage; *a. d*, dorsal aorta; *a. ef2*, efferent branchial artery of 2nd metamere (a. quadrato-mandibularis, *amd*, REGEL); *a. ef3*, efferent branchial artery of 3rd metamere (hyoid artery, SCHMALHAUSEN); *a. ef5–7*, common stem of efferent branchial arteries of metameres 5–7; *an*, anterior nostril; *cav. in*, cavum internasale; *ch*, choana; *com. hco*, occipital hypochordal commissure; *com. pt*, paratemporal commissure (processus basalis palatoquadrati, *prb*, REGEL); *c. II*, *c. III*, canals for n. opticus and n. oculomotorius; *fe. ov*, fenestra ovalis; *f. n. oc*, foramen for occipital nerve; *foot-pl*, foot-plate of columella (probably formed by posterior end of infrapharyngohyal, stapes; *st*, SCHMALHAUSEN, REGEL); *f. VII*, foramen for truncus hyo mandibularis VII; *gs. sp*, spiracular pouch; *la. boa*, *la. bop*, anterior and posterior basiotic laminae formed from myotomes of 3rd and 4th somites (commissura basicapsularis anterior and posterior, *cbcan*, *cbcp*, REGEL); *la. com*, commissural lamina between epimandibular and epipremandibular (posterior part of processus pterygoideus, *pptp*, REGEL); *la. nch*, lamina nariochoanalis

by EEDEN (1951) in larval anurans and the conditions in *Eusthenopteron* it seems likely that the processus oticus as tentatively shown in fig. 90 is a double formation consisting of a medial part which is the lateral commissure (*lc*; processus dorsalis in anurans, EEDEN, 1951, p. 104, figs. 29, 32, 34B, 35) and a lateral part (*Pq. dm*) formed by the palatoquadrate. This condition will arise if we assume that the palatoquadrate in *Eusthenopteron*—after the reduction of the anterior part of the spiracular gill-slit—fuses with the adjoining lateral side of the lateral commissure. That this is what really has happened is supported also by the fact that the processus dorsalis in anurans may be separated from the palatoquadrate by a layer of connective tissue (EEDEN, 1951, p. 110, fig. 35) and is further evidenced by the fact that the squamosal (*Sq*) has retained its original position in relation to the palatoquadrate. Because the squamosal in urodeles, too, covers the external side of the processus oticus it is likely that this structure also in them is a double formation and this is supported by the fact that in larval stages of *Ranodon* (REGEL, 1964a, pp. 16, 19, figs. 7, 10) a strand of mesenchymatic cells connects the otic process with the hyomandibula. In this connection may be mentioned that the fact that the otic ledge (*sh. ot*) is received by a groove (*gr. pt*) on the inner side of the palatoquadrate is a character specific to osteolepiforms (fig. 90B) and anurans (fig. 90A).

However, is the so-called basipterygoid (basitrabecular) process (including the postpalatine commissure or "otoquadrate") in urodeles homologous with the subotical shelf (*sh. ot*) in porolepiforms it cannot be a true basipterygoid process (*pr. bp*). Nor can the articulation between that process and the palatoquadrate be a basal articulation and the so-called basal process (*com. pt*) is not a true basal process (*pr. b*). What has happened in the phylogeny of urodeles (fig. 92) is probably only that the palatoquadrate has developed an articulation with the adjoining lateral margin of the otical shelf or has fused with that shelf. If this secondary contact (*com. pt*) has occurred in front of the palatine canal (*c. pal*) as the paratemporal articulation (see *art. ptm*, fig. 93E) in osteolepiforms (JARVIK, 1954, pp. 27–29; cf. DE BEER, 1937, pp. 178, 419, "true palato-

(cornu trabeculae, *ctr*, REGEL); *m.b3*, *m.b4*, *m.b5*, basicranial muscles of 3rd, 4th and 5th metameres (*myI*, *myII*, *myIII*, REGEL); *nc*, notochord; *n.pr*, dorsal (ophthalmic) ramus of profundus nerve; *n.VI*, n. abducens; *n.VII*, n. facialis; *pil. oc*, pila occipitalis (arcus occipitalis, *aocc*, REGEL); *pol. c*, polar cartilage, probably homologous with subcranial muscle (com. basitrabecularis, *cbtr*, REGEL); *pr. a*, processus ascendens palatoquadrati (= suprapharyngomandibular); *pr. ot*, processus oticus palatoquadrati, probably including lateral commissure or suprapharyngohyal; *pr.pil*, processus prenasalis inferior lateralis; *r. pal*, r. palatinus VII; *sac n*, nasal sac; *sh. ot*, otical shelf or infrapharyngohyal (previously interpreted as basipterygoid or basitrabecular process); *v. ju*, jugular vein (vena capitis lateralis, *vcl*, REGEL); *v. pit*, pituitary vein.

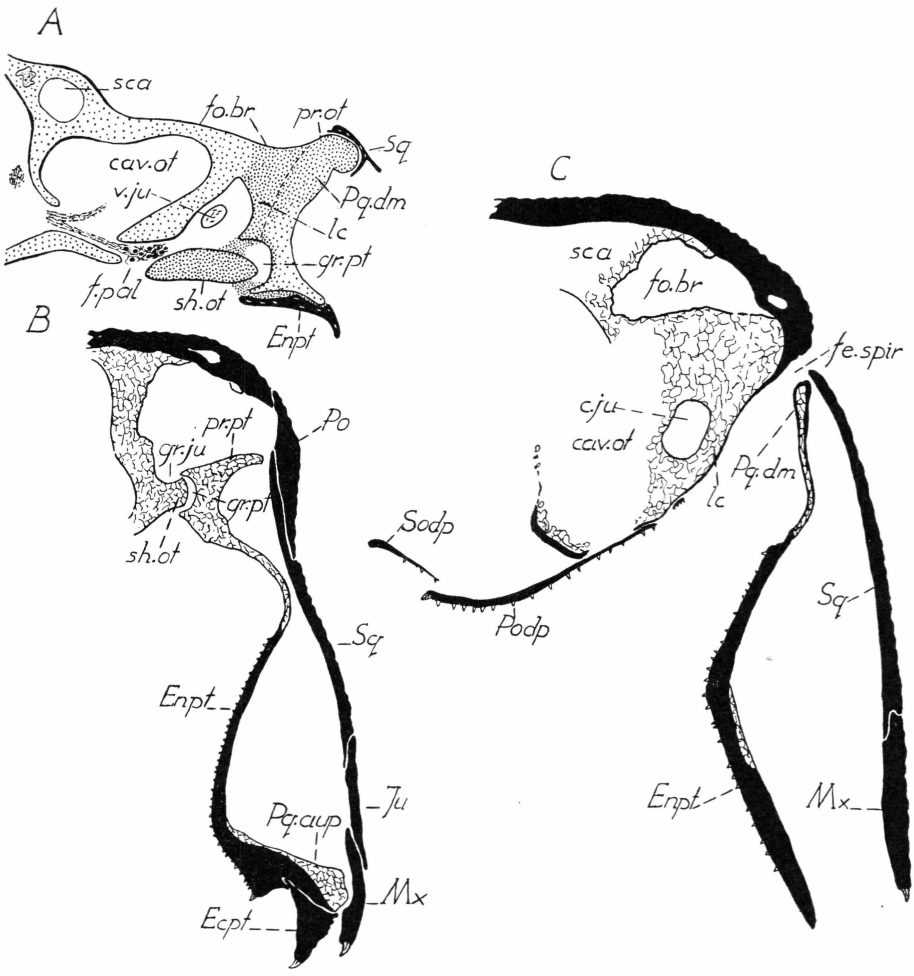


Fig. 90. Three almost transverse diagrammatic sections to explain presumed double origin of processus oticus. *A*, *Ascaphus truei*, stage 7. From EEDEN (1951, fig. 34C; see also JARVIK, 1954, fig. 13). Interrupted line marks where approximately presumed fusion between palatoquadrate and lateral commissure has taken place. *B*, *C*, *Eusthenopteron foordi*. Mainly after sections Nos. 240 (see JARVIK, 1954, fig. 12B) and 288 of grinding series 2.

Ecpt, ectopterygoid; *Enpt*, entopterygoid; *Ju*, jugal; *Mx* maxillary; *Po*, postorbital; *Podp*, paraotic dental plate; *Pq. aup*, pars autopalatina of palatoquadrate; *Pq. dm*, postero-dorsal marginal portion (epimandibular) of palatoquadrate; *Sodp*, subotic dental plate; *Sq*, squamosal.

cav. ot, cavity of otic capsule; *c. ju*, canal for jugular vein; *fe. spir*, spiracular fenestra; *fo. br*, fossa bridgei; *f. pal*, foramen for r. palatinus VII; *gr. ju*, groove for jugular vein; *gr. pt*, groove on medial side of paratemporal process for otical shelf (groove of processus basalis for articulation with auditory ledge, VAN EEDEN); *lc*, lateral commissure (processus dorsalis, VAN EEDEN, in anurans); *pr. ot*, processus oticus (adult processus oticus, VAN EEDEN) probably formed by fusion of palatoquadrate with lateral commissure; *pr. pt*, paratemporal process; *sca*, anterior semicircular canal; *sh. ot*, otical shelf (probably formed by anterior part of infrapharyngohyal; adult auditory ledge, VAN EEDEN); *v. ju*, jugular vein.

basal connexion"), behind that canal ("pseudobasal connexion", DE BEER; cf. also postpalatine commissure, FOX, 1959, fig. 27) or on both sides of it (see figs. 92B,C, 96) is of little importance. Irrespective of its position in relation to the palatine nerve the contact between the palatoquadrate and the otical shelf may be termed *the paratemporal articulation or commissure* (*com.pt*).

Mandibular and premandibular arches, basal and ethmoidal articulations. – The true basal articulation (cf. JARVIK, 1954, p. 27) is both in porolepiforms (fig. 92A) and osteolepiforms (figs. 88, 99) situated in front of the otical shelf, lateral to the fossa hypophyseos. This articulation, between the basipterygoid process (*pr. bp*) of the neural endocranium and the basal process (*pr. b*) of the palatoquadrate, or, in other words, between the infrapharyngomandibular (*Im*) and the epimandibular (*Em*), has no equivalent in urodeles. Following a general trend both the basipterygoid process and the basal process have been reduced as they have also in anurans and in advanced coelacanthiforms and actinopterygians (cf. JARVIK, 1954, p. 75). In connection with these reductions obviously also the antero-medial articular lamina (*la. am*) of the palatoquadrate in porolepiforms and with it the fossa autopalatina have disappeared and the parasphenoid has acquired a more dorsal position (cf. p. 206). The basipterygoid process probably represents the posterior articular head of the infrapharyngomandibular (JARVIK, 1954) and the latter element (*Im*) which forms part of the so-called trabecula (see p. 222) is therefore vestigial in urodeles (fig. 96; cf. fig. 99A).

The articular head (processus basalis) of the epimandibular has probably disappeared, too, but the main part of that element (*Em*, fig. 96) obviously persists together with the suprapharyngomandibular (*Sm*). The latter forms the processus ascendens (*pr. a*) which also in urodeles articulates with the suprapterygoid process of the neural endocranium (*pr. sp*, figs. 20, 21, 82C, 105; REGEL, 1964a, figs. 7, 10, 11, *prant*). The epimandibular in urodeles is continued forwards by a slender process, the processus pterygoideus (*pr. pt*, fig. 85A, *la. com*, figs. 89, 91), which usually ends freely. As illustrated in fig. 92A–C this process is most likely a vestige of the lamina (*la. com*) which in porolepiforms connects the pars autopalatina (*Pq. aup*, epipremandibular, *Epm*) with the postero-dorsal marginal portion (*Pq. dm*, epimandibular, *Em*) of the palatoquadrate and like that lamina it is covered ventrally by the entopterygoid (*Enpt*). However, in certain primitive urodeles (see also figs. 89, 91, 96) the processus pterygoideus is continued anteriorly by another element (*Epm*) which carries the dermopalatine (*Dpl*) and ectopterygoid (*Ecpt*) and obviously is a vestige of the pars autopalatina or epipremandibular. The latter is continued antero-medially by still another element (*Ipm*) which is situated in the floor of the nasal capsule and carries

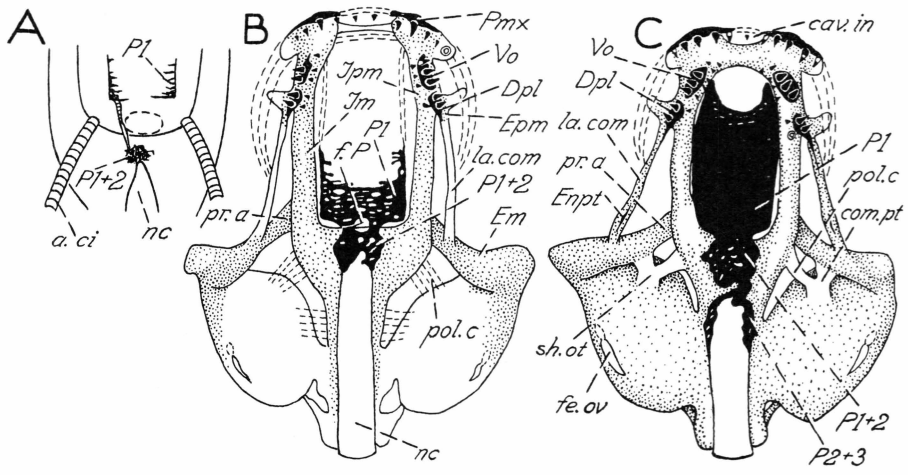


Fig. 91. *Ranodon sibiricus*, larval stages in ventral aspects to show development of dermal bones in roof of mouth cavity. *A*, stage III, 24 mm, *B*, stage IV, 22 mm, *C*, stage VI, 24.5 mm. From LEBEDKINA, 1964a, figs. 4B, 5, 6.

Dpl, dermopalatine; *Em*, epimandibular; *Enpt*, entopterygoid; *Epm*, epipremandibular; *Im*, *Ipm*, infrapharyngomandibular and infrapharyngopremandibular (visceral part of "trabecula"); *Pmx*, premaxillary; *P1*, prehypophysial parasphenoid primordium, probably developed in relation to cranial vertebra 1; *P1 + 2*, posthypophysial parasphenoid primordium, probably developed in relation to cranial vertebra 1 + 2; *P2 + 3*, subotical parasphenoid primordium, probably developed in relation to cranial vertebra 2 + 3; *Vo*, vomer.

a. ci, a. carotis interna; *cav. in*, cavum internasale; *com. pt*, paratemporal commissure; *fe. ov*, fenestra ovalis; *f. P*, foramen in parasphenoid; *la. com*, commissural lamina of palatoquadrate connecting epimandibular and epipremandibular; *nc*, notochord; *pol. c*, polar cartilage; *pr. a*, processus ascendens palatoquadrati; *sh. ot*, otical shelf.

the vomer. This element which hitherto has been regarded as a part of the "trabecula" is obviously the infrapharyngopremandibular (see JARVIK, 1954, pp. 76–79).

In the ontogeny of urodeles the choana migrates in a medial direction and because of this migration and other modifications the junction between the presumed epi- and infrapharyngopremandibulars appears to lie farther medially in urodeles (larval medial connection, JARVIK, 1942, pp. 296–300, 412) than in porolepiforms (see figs. 92, 96) and it was this condition that led me to the conclusion that the presumed articulation between the palatoquadrate and the neural endocranium in the anterior part of the fossa autopalatina (cf. pp. 70–71) corresponds to the larval medial connection in urodeles and to the antero-medial ethmoidal articulation in osteolepiforms (see also 1954, p. 27).

However, as is now clear from the relations to the vomer and dermopalatine it is the articulation (or fusion) close postero-medial to

the fenestra endochoanalis (*fe. ench*) in porolepiforms, between the ethmoidal articular process (*pr. e*) of the palatoquadrate and the articular fossa (*art. e*; figs. 9A,B, 32A1) of the postnasal wall, that corresponds to the larval medial connection in urodeles and to the antero-medial ethmoidal articulation in osteolepiforms (between the processus apicalis of the palatoquadrate and area art_1m of the postnasal wall; JARVIK, 1942, figs. 48–50, 54–55). This connection is the original articulation between the epal and infrapharyngeal elements of the premandibular arch and as demonstrated in 1954 (pp. 78–80) the corresponding connection in actinopterygians must be the rostro-palatine articulation (cf. STADTMÜLLER, 1936, p. 570; LEBEDKINA, 1963, p. 202). The articulations (or fusions) in the fossa autopalatina of porolepiforms between areas *art 1* and *art 2* (fig. 25B) on the ventral side of the antero-medial articular lamina (*la. am*) of the palatoquadrate and areas *art. am 1* and *art. am 2* (fig. 20) on the dorsal side of the suborbital ledge have no equivalents in urodeles. These articulations (or fusions) are interarcual in position and although differently developed they are nearest comparable to the orbital articulation in osteolepiforms (see p. 176).

The suprapharyngeal element (*Spm*, fig. 96) of the premandibular arch, finally, seems to be represented by the processus antorbitalis (preocular process) which according to REGEL (1964b, 1968) and SCHMALHAUSEN (1968, p. 220) "is developed at the expense of the anterior end of the pterygoid process, but then enters into the composition of the posterior wall of the olfactory capsule". The connection or articulation often found between the suprapharyngeal and epal (*Epm*) elements of the premandibular arch (the postero-lateral ethmoidal articulation in osteolepiforms, the corresponding lateral definitive connection in anurans, the ethmo-palatine connection in actinopterygians; see JARVIK, 1942, pp. 295–300, 1954, pp. 27, 79–80; cf. STADTMÜLLER, 1936, p. 569; LEBEDKINA, 1963) is in porolepiforms (p. 176) indistinct but is probably represented by a connection between the ventro-lateral process (*pr. vl*, figs. 74A,B, 92A) of the postnasal wall and the adjoining part of the pars autopalatina (epipremandibular). In urodeles the ventro-lateral process is obviously represented by the processus maxillaris posterior (*pr. mxp*, figs. 74E, 92B,D; LEBEDKINA, 1963, fig. 3; REGEL, 1968, figs. 36, 39, 43). This process extends backwards towards the antero-lateral process (*pr. al*) of the palatoquadrate. Most often these two processes are separate but sometimes (*Ranodon*, WIEDERSHEIM, 1877, pl. 23:69, 70; STADTMÜLLER, 1936, p. 571; *Batrachuperus*, STADTMÜLLER, 1936, pp. 569–570) they fuse forming a lateral definitive connection highly suggestive of that in anurans (JARVIK, 1942, pp. 296, 299).

Remarks on trabecula cranii

The nature of the so-called trabecula has been much debated (see e.g. DE BEER, 1937, pp. 375–379; BERTMAR, 1959, pp. 293–303). However, as is well established by experimental methods (see HÖRSTADIUS, 1950) and studies of the yolk content in the cells (DE BEER, 1947; REGEL, 1964a; and others) the "trabecula" in urodeles consists of two main divisions, one posterior endomesodermal in origin (*trp*, fig. 101C), and one anterior (*tra*) derived from the ectomesenchyme (neural crest). The posterior division is probably composed of arcual elements belonging to the cranial portion of the vertebral column (see figs. 96, 99A). In urodeles this division acccording to STONE (1926, figs. 12, 19) and HÖRSTADIUS & SELLMAN (HÖRSTADIUS, 1950, fig. 19A) extends forwards about to the opticus canal (*c. II*), where it is continued forwards by the anterior, ectomesenchymatic division. The latter consists of three parts: posterior, middle and anterior. The posterior part is the infrapharyngomandibular (*Im*, figs. 96, 99A) which in urodeles because of the reduction of the posterior articular head (basipterygoid process, *pr. bp*) is vestigial. This part extends forwards to about the transition between the orbitotemporal and ethmoidal regions of the neural endocranium where it is continued by the middle part. The latter which enters into the composition of the floor of the nasal capsule is the infrapharyngopremandibular (*Ipm*). As is shown in fig. 96 (see also figs. 89, 91, 92C) it forms a direct antero-medial continuation of the epipremandibular (*Epm*) and a characteristic feature is that the vomer (*Vo*) arises on its ventral side, whereas the dermopalatine (*Dpl*) and ectopterygoid (*Ecpt*) develop on the ventral side of the epal element of the premandibular arch (see JARVIK, 1954, p. 78, fig. 35B,C). The anterior part of the ectomesenchymatic division of the "trabecula", finally, the so-called trabecular horn (*la. nch*), has nothing to do with the visceral endoskeleton. It is simply a part of the wall of the nasal capsule (lamina nariochoanalis) and as explained in 1942 (p. 276, fig. 13; see also 1968a, p. 240) the "trabecular horn" in urodeles which lies ventral to the external nostril cannot be homologous with the "trabecular horn" in dipnoans which lies dorsal to that nostril and represents another part of the wall of the nasal capsule.

Parasphenoid and other palatal dermal bones

The tooth-bearing bone in larval urodeles (fig. 91B,C) situated on the ventral side of the epipremandibular (*Epm*) is generally considered to be the dermopalatine ("palatine"). However, as shown by LEBEDKINA (1964a) it extends backwards to the posterior end of what has been shown to be the epipremandibular and because it seems to arise from two primordia (LEBEDKINA, 1964a, figs. 28, 29) it very likely includes the

ectopterygoid as well (*Ecpt*, figs. 92C, 96). Later in ontogeny these bones disappear and in this respect urodeles differ from anurans in which the dermopalatine sometimes is retained in the adult as an almost transverse element which has a rather strange position, being situated on the ventral side of the postnasal wall (see JARVIK, 1942, p. 524).

These differences between urodeles and anurans and the peculiar position of the dermopalatine in anurans are easy to understand from the different conditions in porolepiforms and osteolepiforms. In the latter group (see p. 176; JARVIK, 1942, pp. 451–457, figs. 64, 65) the antero-lateral part of the pars autopalatina, postero-lateral to the antero-medial ethmoidal articulation (between the processus apicalis and area art_1m of the postnasal wall), lies underneath and abuts against the ventral side of the postnasal wall. If we now imagine that this part of the pars autopalatina, which corresponds to the commissura cranialis anterior in larval anurans, fuses with the postnasal wall the underlying dermopalatine will be situated on the ventral side of the structure that in adult anurans is called the postnasal wall but which as demonstrated by REINBACH (see JARVIK, 1942, pp. 321, 524, figs. 26, 64) is a composite structure. In porolepiforms (see p. 176), on the other hand, the pars autopalatina behind the ethmoidal articulation (between the ethmoidal articular process and area *art. e* of the postnasal wall) has no contact with the postnasal wall, except possibly at the inner side of the ventro-lateral process (*pr. vl*), and when this part (epipremandibular) of the palatoquadrate in late ontogenetic stages of urodeles is reduced it is natural that also the underlying dermal bones (dermopalatine and ectopterygoid) disappear.

As demonstrated above (p. 197) the vomer in urodeles is of the porolepiform type and another important resemblance is the presence of separate dental plates (*uodp*) underneath the parasphenoid. The latter bone, too, is very similar in the two groups and distinctly different from that in osteolepiforms, anurans and other eutetrapods.

Characteristic of the parasphenoid (*P*) in urodeles and porolepiforms (fig. 92) is certainly not only that it is broad and hardly goes forwards underneath the ethmoidal region (JARVIK, 1942, p. 419). The ontogenetic development of the bone as recently described in detail by LEBEDKINA (1960, 1964a) is interesting (see also fig. 91; WINTREBERT, 1922; JARVIK, 1966, fig. 3). In certain larval stages it is very similar to that in porolepiforms. It has the same posterior extent, ending just below the anterior tip of the notochord and the posterior portion (P1 + 2) of the bone has much the same shape. Moreover, the bone in front of that portion is pierced by a wide foramen (*f. p*) for the buccohypophysial duct and laterally to that foramen the internal carotid artery (*a. ci*) enters the braincase in much the same way and has within that a very similar

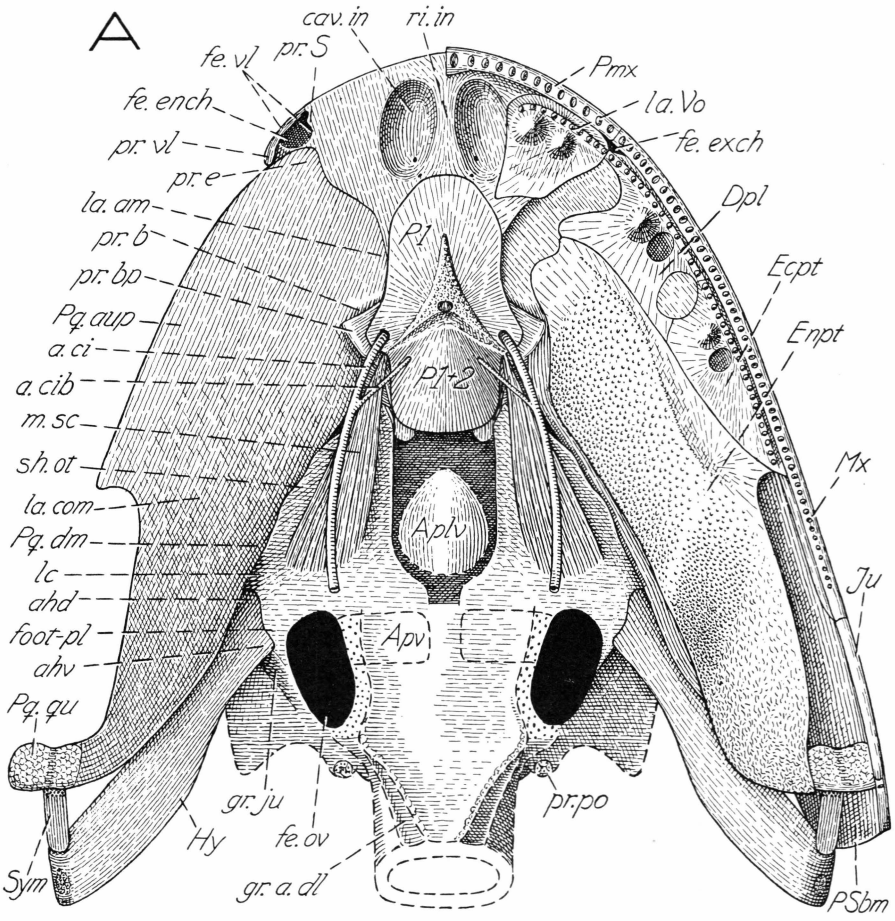


Fig. 92. Diagrammatic representations to demonstrate similarities between porolepiforms and urodeles in structure of palatal aspect of skull. *A*, *Glyptolepis groenlandica*. Posterior parts of otoccipital, hyomandibula, symplectic, subcranial muscle and a. carotis interna tentatively restored. Dermal bones of right side removed. In other respects as in fig. 31. *B*, Partly hypothetical intermediate stage. *C*, primitive urodele. Figure based mainly on data given by REGEL (1964a, 1968) and LEBEDKINA (1964a) in larvae, 20–25 mm, of *Ranodon sibiricus* (cf. figs. 89, 91). *D*, *Ranodon sibiricus*, larva 76 mm. Anterior part of palate in ventral aspect. From LEBEDKINA, 1964a, fig. 27. Postero-ventral part of nasal capsule slightly modified (cf. fig. 74C).

Aplv, subchordal arcual plate; *Apv*, paired posterior subchordal arcual plate (observed in specimen of *Holoptychius* in pl. 24:2); *CV4+5*, thickening (*pocc2*, REGEL) probably representing ventral part of cranial vertebra 4+5; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Em*, epimandibular; *Enpt*, entopterygoid; *Epm*, epipremandibular; *Hy*, hyomandibula (= columella without foot-plate in urodeles); *Ipm*, infrapharyngopremandibular (generally considered to be part of trabecula); *Ju*, quadratojugal; *Mx*, maxillary; *P*, parasphenoid; *Pmx*, premaxillary; *Pq. aup*, pars autopalatina of palatoquadrate (= epipremandibular); *Pq. dm*, postero-dorsal marginal portion of palatoquadrate (= epimandibular); *Pq. qu*, pars quadrata; *PSbm*, preoperculosubmandibular; *P1*, anterior, prehypophysial portion of parasphenoid, probably related to cranial vertebra 1; *P1+2*, posthypophysial portion of para-

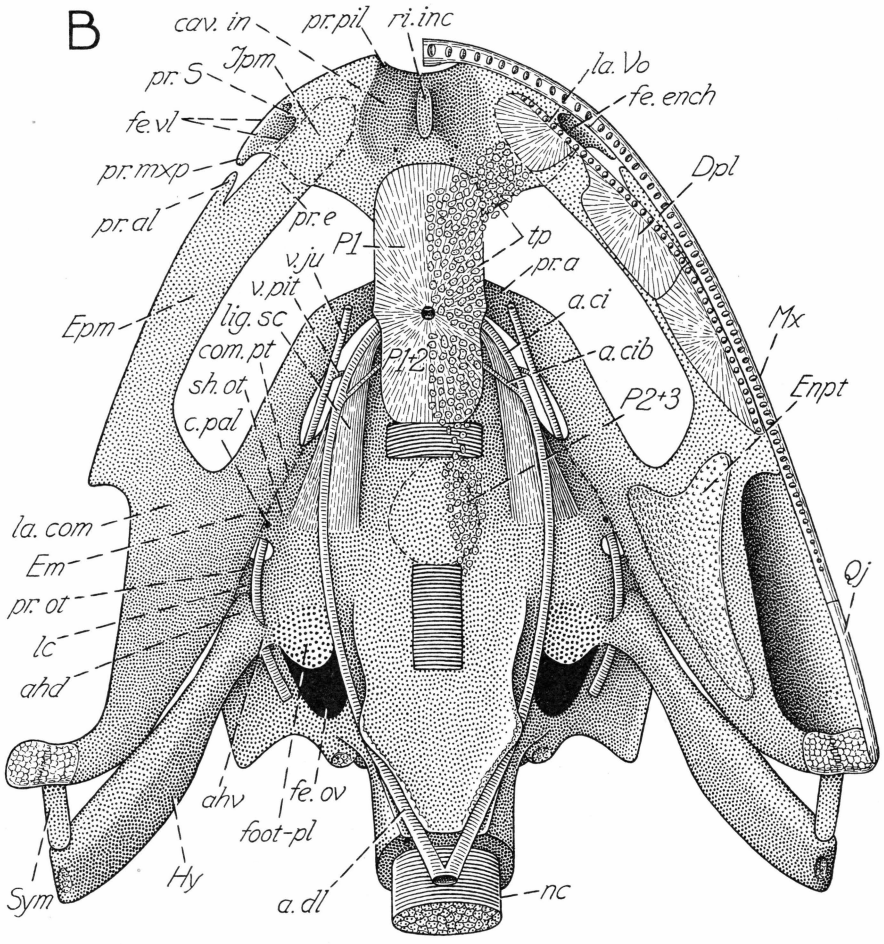


Fig. 92 B.

sphenoid, probably related to cranial vertebra 1 + 2; *P2 + 3*, subotic portion of parasphenoid, probably related to cranial vertebra 2 + 3 (corresponding to subotic dental plate in *Eusthenopteron*); *Oj*, quadratojugal; *Sym*, symplectic (= hyoid process, SCHMALHAUSEN, in urodeles); *Vo*, vomer.

a. ci, a. carotis interna; *a. cib*, medial branch of a. carotis interna; *a. d*, dorsal aorta; *a. dl*, lateral dorsal aorta; *a. ef4*, efferent branchial artery of 4th metamere; *ahd*, dorsal articular head of hyomandibula; *ahv*, ventral articular head of hyomandibula or its presumed equivalent in urodeles; *c. a. ci*, canal for a. carotis interna; *cav. in*, cavum internasale; *com. pt*, paratemporal commissure (in urodeles generally considered to represent basipterygoid or basitrabecular process); *c. pal*, canal for r. palatinus VII; *c. r. bo*, canal for r. basioticus of n. abducens; *c. II*, *c. III*, *c. VII*, canals for n. opticus, n. oculomotorius and n. facialis; *fe. ench*, fenestra endochoanalis; *fe. exch*, fenestra exochoanalis; *fe. ov*, fenestra ovalis; *fe. vl*, fenestra ventro-lateralis; *foot-pl*, foot-plate of columella, probably derived from posterior part of infrapharyngohyal; *gr. a. dl*, groove for lateral dorsal aorta; *gr. ju*, groove for jugular vein; *la. am*, antero-medial articular lamina of palatoquadrate (not represented in urodeles); *la. com*, commissural lamina connecting epimandibular and epipremandibular (pterygoid process in urodeles); *la. nch*, lamina nariochoanalis ("trabecular horn"); *la. Vo*, ventral tooth-bearing lamina of vomer; *lc*, lateral commissure (suprapharyngohyal;

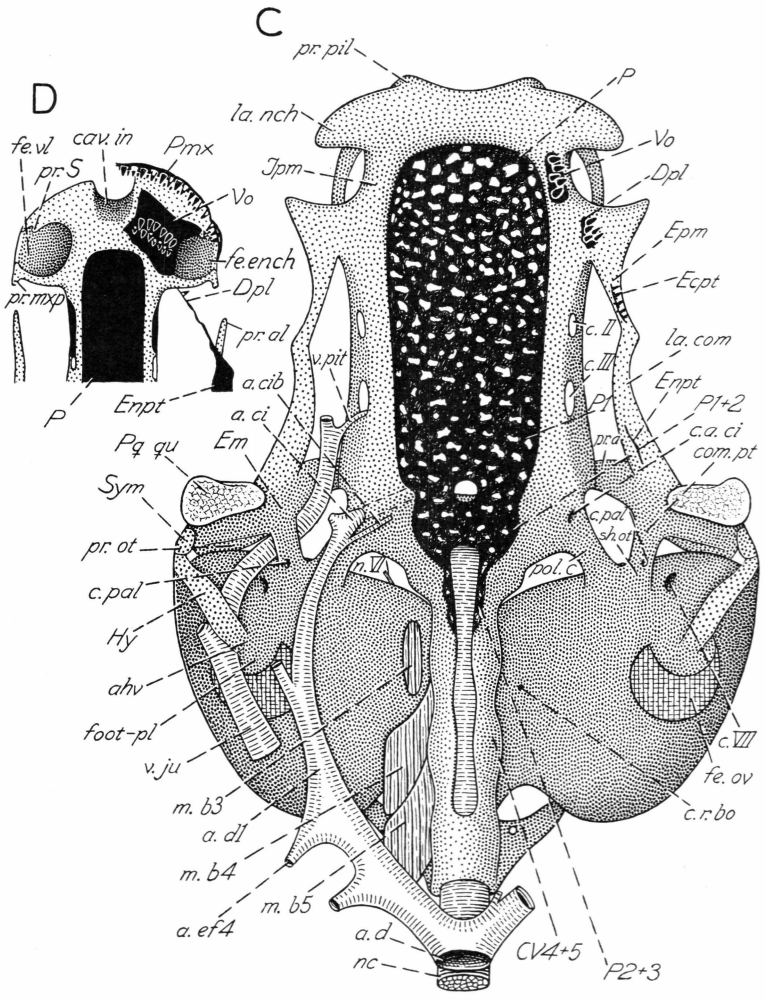


Fig. 92 C–D.

in urodeles probably incorporated in processus oticus); *lig. sc*, subcranial muscle transformed into ligament; *m.b3*, *m.b4*, *m.b5*, basicranial muscles of 3rd, 4th and 5th metameres; *m. sc*, subcranial muscle (in urodeles probably represented by polar cartilage; com. basitrabecularis, REGEL); *nc*, notochord; *n. VI*, n. abducens; *pol. c*, polar cartilage; *pr. a*, processus ascendens palatoquadrati (suprapharyngomandibular); *pr. al*, antero-lateral process of pars autopalatina (in urodeles, *Ranodon*, connected with processus maxillaris posterior by ligament); *pr. b*, processus basalis of palatoquadrate (not represented in urodeles); *pr. bp*, basipterygoid (basitrabecular) process (completely reduced in urodeles); *pr. e*, anterior ethmoidal articular process of pars autopalatina; *pr. mxp*, processus maxillaris posterior (in porolepiforms represented by ventro-lateral process of postnasal wall); *pr. ot*, processus oticus palatoquadrati (probably including lateral commissure); *pr. pil*, processus prenasalis inferior lateralis; *pr. po*, postotical process; *pr. S*, Seydel's palatal process; *pr. vl*, ventro-lateral process of postnasal wall; *ri. in*, internasal ridge; *ri. inc*, cartilaginous vestige of internasal ridge (cartilago infranasalis in urodeles); *sh. ot*, otical shelf (otoquadrate cartilage, post- and prepalatine commissures in urodeles); *tp*, upper oral dental plates forming tooth-bearing posterior process of vomer or patches of teeth below parasphenoid in urodeles; *v. ju*, jugular vein; *v. pit*, pituitary vein.

course. However, as explained above the basipterygoid process is reduced in urodeles and in connection with this reduction also the anterior ascending process (*pr. asc1*, figs. 20, 39) of the parasphenoid and the groove (*gr. psp*) for the prespiracular gill-slit disappeared. The small process which LEBEDKINA regards as the anterior ascending process is probably only a remainder of the small process in *Glyptolepis* situated in front of the opening for the internal carotid artery.

Nor is there a true processus ascendens posterior of the parasphenoid (see JARVIK, 1954, pp. 51–60) in urodeles. During late ontogenetic stages the parasphenoid in urodeles certainly grows backwards by incorporation of tooth-plates corresponding to those found underneath the otoccipital in porolepiforms (fig. 30, *P2 + 3*, fig. 92) but prerequisites for the formation of a processus ascendens posterior are lacking. In actinopterygians this process lies inside the tubular spiracular gill-pouch and as explained in 1954 it has arisen by fusion of dental plates corresponding to the spiracular dental plates in osteolepiforms. These plates, which are situated on the lateral side of the braincase, dorsally to the otical shelf and in front of the lateral commissure, have no equivalents in porolepiforms. According to the interpretation given above (p. 217) the lateral commissure in urodeles (and anurans) has become incorporated into the processus oticus of the palatoquadrate and such an incorporation was of course not possible as long as the spiracular gill-slit extended far forwards and separated the lateral commissure from the palatoquadrate as it did in osteolepiforms (1954, fig. 26). In porolepiforms the spiracular gill-slit most likely did not extend as far forwards as in osteolepiforms, and in urodeles this gill-slit has become further reduced and is represented only by a small pouch (*gs. sp*, fig. 89A) which as is to be expected is situated behind the processus oticus (see SCHMALHAUSEN, 1968, fig. 110). If we now look at the process of the parasphenoid in urodeles which LEBEDKINA (1964a, figs. 8, 10) named the processus ascendens posterior we will find that this process has no relations to the vestigial spiracular gill-pouch but is situated on the ventral side of the braincase, far medially to the shelf ("basipterygoid process") that has been shown to be homologous with the otical shelf (*sh. ot*) in porolepiforms. Accordingly this process cannot be a true processus ascendens posterior.

Basicranial muscles and cranial portion of vertebral column

Subcranial muscle and polar cartilage. – Like *Latimeria* and other coelacanthiforms also porolepiforms (fig. 92A) and osteolepiforms (fig. 99) certainly had a strong paired subcranial muscle (*m. sc*) spanning the intracranial joint and connecting the hypophysial and otic regions (see pp. 83, 237). The folding of the mucous membrane in the roof of the

mouth in *Glyptolepis* (figs. 24E–G, 30) informs as to the size and direction of that muscle in porolepiforms and no doubt the muscle originated in the large depression (*or.m.sc*) on the ventral side of the otoccipital, ran obliquely forwards and was inserted in the groove (*i.m.sc*) on the lateral side of the ethmosphenoid a little postero-dorsal to the opening of the canal for the a. carotis interna (*a. ci*). This artery must have passed ventral to the anterior tendon of the muscle and was farther back probably situated lateral and ventro-lateral to the muscle (cf. *Latimeria*, fig. 24A,B). Moreover, it is evident that the r. palatinus VII from the palatine foramen (*c. pal*, fig. 92B) ran forwards lateral to the muscle (cf. *Eusthenopteron*, BJERRING, 1968, fig. 4). No canal for the n. abducens has been found in the sections of *Glyptolepis* or other porolepiform material, but if that nerve emerged from the braincase through an opening situated somewhat as the abducens foramen in *Eusthenopteron* (*c. VI*, fig. 93D) it must in order to reach the orbit have passed medial and dorsal to the subcranial muscle.

If we now turn to larvae of primitive hynobiid urodeles as described by REGEL (1961, 1964a, 1968) we find in the place corresponding to that which in porolepiforms is occupied by the subcranial muscle a different structure, viz. a blastema which soon chondrifies and forms a commissure (*pol. c*, figs. 89, 91, 92C). Like the subcranial muscle this commissure (basitrabecular commissure, REGEL) connects the hypophysial region of the skull with the shelf (*sh. ot*) on the ventral side of the otic capsule that has been shown to be homologous with the otical shelf in porolepiforms. Moreover, the commissure has the same oblique position as the muscle, its anterior end is situated close behind the opening of the canal for the a. carotis interna and this artery runs postero-ventral to the commissure (see also REGEL, 1964a, figs. 17, 18; 1968, fig. 16A). Furthermore, the n. abducens runs medial and the r. palatinus lateral to the commissure. This very close agreement as to position, direction and extent and the identical relations to adjoining nerves and vessels cannot be a mere coincidence. In view of the very great similarities between porolepiforms and urodeles in the structure of the parasphenoid and the otical shelf, the course of the internal carotid artery and the close agreement in numerous other regards the only reasonable conclusion must be that the basitrabecular commissure of urodeles (*pol. c*) and the subcranial muscle (*m. sc*) of porolepiforms are homologous structures. However, as to its morphological relations the commissure agrees with the polar cartilage (see BJERRING, 1967, p. 249; 1971, fig. 10) and it no doubt represents that structure. By comparing urodeles and porolepiforms we thus arrive to the same conclusion as earlier BJERRING (1967), namely that *the subcranial muscle is homologous with the polar cartilage.*

This conclusion includes two statements which to many perhaps may appear to be a little too venturesome and therefore in need of further elucidation:

1) The homologisation of a muscle with a skeletal structure.

2) The view that a muscle innervated by a branch of the n. vagus belongs to the 2nd metamere. As shown by HOLMGREN (1940, pp. 245–246) the polar cartilage is a derivative of the 2nd somite (*mt2*, fig. 94) and it should therefore be expected that the subcranial muscle should be innervated by the ventral nerve of the 2nd metamere, that is the n. trochlearis. But the subcranial muscle in *Latimeria* is innervated by a nerve which appears to be a branch of the n. vagus which belongs to the 5th metamere and by MILLOT & ANTHONY (1965, p. 87) the muscle consequently is considered to be the somatic muscle of that metamere which is in agreement with my own suggestion in a previous paper (1963a, fig. 20; cf. NELSON, 1970).

However, ir order to be able to discuss these matters and create a basis for the subsequent discussion of the arcual plates and the basicranial muscles it is necessary to give a brief review of some of the more recent advances as to the metamerism and composition of the head (cf. GOODRICH, 1930, pp. 213–229; DE BEER, 1937, pp. 7–34; the use of the term segmentation as a synonym for metamerism has been avoided; see p. 235).

General remarks on cranial metamerism. – Is our skull a modified anterior part of the body or is it wholly or partly a new formation is a problem that has engaged scientists ever since the German poet GOETHE in 1790 got the idea that the skull was made up of a number of externally discernible rings which represented vertebrae. GOETHE's vertebral theory in its original form is since long abandoned but it is now generally admitted that at least the occipital region includes more or less modified vertebrae. As is well known the vertebrae develop from the sclerotomes of the metameric ("segmental") somites whereas the trunk musculature is derived from the myotomes. Embryological investigations have established that three paired mesodermal vesicles arise far forward in the head, in front of the otic capsules (*som1*, *som2*, *som3*, fig. 108A; see also *my1*, *my2*, *my3*, fig. 95A). These vesicles are generally regarded as cranial somites (cf. however STARCK, 1963) and according to the theory of metamerism of the head accepted by the vast majority of scientists (see GOODRICH, 1930; DE BEER, 1937; VANDEBROEK, 1969) there are three prootic metameres in the vertebrate head (premandibular, mandibular and hyoid) each with a pair of somites, a paired dorsal nerve (profundus or trigeminus I, trigeminus proper or trigeminus II, and facialis) and a paired ventral somatomotor nerve (oculomotorius,

trochlearis, abducens; fig. 99D) innervating the eye-muscles. The following somites in the head, the so-called metotic somites, are influenced by the otic vesicles and some of them are said to be completely suppressed. After a thorough review of the evidence DE BEER (1937, table 18, p. 25) came to the conclusion that "there is little evidence for the disappearance of more than two somites: the 1st and 2nd metotic, or 4th and 5th of the whole series". DE BEER (p. 13) also claims that the cartilaginous skull in the region of the first four segments of the body "never was (phylogenetically) composed of vertebrae" and according to him "evidence in favour of the formerly vertebral nature of the hinder part of the gnathostome chondrocranium begins in the 5th segment, and never farther forwards".

Quite naturally questions concerning the origin and composition of the vertebrate skull has attracted a considerable attention in connection with the studies of the early fossil vertebrates. In 1927 STENSIÖ demonstrated that early cyclostomes possess three prootic visceral arches corresponding to the three prootic metameres and that also the foremost of these arches, the premandibular arch, carried gills; and on the basis of serial sections, wax-models and other material of the osteolepiform *Eusthenopteron foordi* it has been shown (JARVIK, 1954) that there are three prootic visceral arches in the gnathostome skull as well (fig. 88). It was also shown that each of these arches includes three dorsal elements (epal, infrapharyngeal, suprapharyngeal) and that certain of these elements have become incorporated into and form essential parts of the braincase. These views have later been confirmed or accepted by a great number of workers (BERTMAR, BJERRING, PORTMAN, STENSIÖ, WESTHUIZEN, VANDEBROEK, and others; cf. JOLLIE, 1968, 1971) and as we have seen it has been possible to identify all these dorsal visceral elements in the urodele skull as well (fig. 96). Moreover, it was demonstrated in 1954 that the r. maxillaris V is the visceral trunk (*n. Pr. v*, fig. 88) of the n. profundus (*n. Pr*) which is the dorsal nerve in the 1st metamere. The n. ophthalmicus profundus is the dorsal branch (*rd. Pr*; cf. fig. 95A) of the n. profundus and as may be gathered from fig. 88 (see also fig. 99D) there is a complete series of dorsal nerves in the foremost five metameres, each with a dorsal branch (*rd. Pr*, *rd. V*, *rd. VII*, *rd. IX*, *rd. X.1*) and a visceral trunk (*n. Pr. v*, *n. V. v*, etc.).

Fig. 93. *Eusthenopteron foordi*. Drawings to demonstrate existence of cranial vertebrae, vestigial vertebral joints and impressions for basicranial muscles (cf. fig. 99). *A*, vertebra in posterior view. Ribs omitted. From JARVIK, 1952, fig. 13. *B*, posterior part of otoccipital and, *C*, posterior part of ethmosphenoid (with parasphenoid) in posterior aspects. *D*, *E*, posterior part of neural endocranium with parasphenoid in ventral aspects. *D*, from JARVIK, 1954, figs. 1C, 22, modified. *E*, after specimen (No.

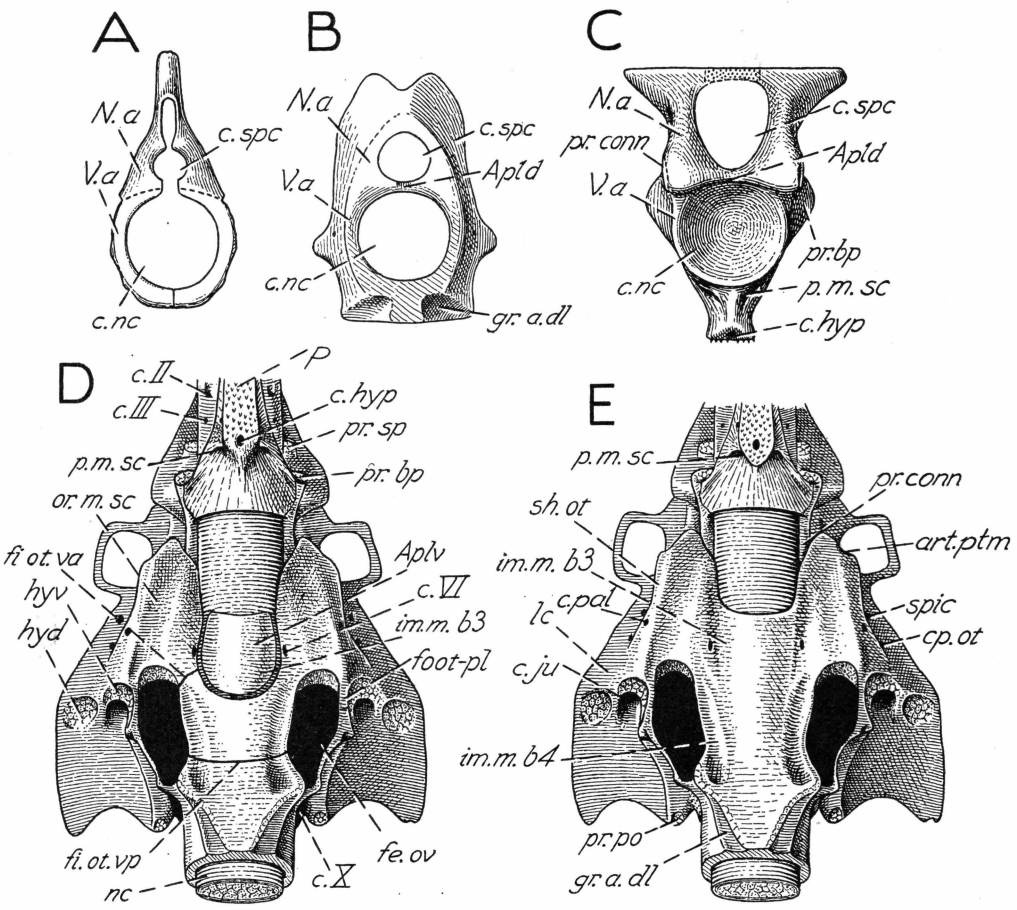


Fig. 93.

P. 342, Pal. Sect., Stockh.) shown in 1954, fig. 7, in which ventral arcual plate *Aplv* is incorporated in basis cranii. Muscle impressions after Nos. P. 342 and P. 2564 (see Bjerring, 1967, pl. 3:2; 1971, fig. 3).

Apld, dorsal (suprachordal) arcual plate; *Aplv*, ventral arcual plate; *N. a*, neural arch or its equivalent in neural endocranium; *P*, parasphenoid; *V. a*, ventral vertebral arch or its equivalent in neural endocranium.

art. ptm, area articulating with paratemporal process of palatoquadrate; *c. hyp*, canal for buccohypophysial duct; *c. ju*, jugular canal; *c. nc*, canal or pit for notochord; *c. pal*, canal for r. palatinus VII; *cp. ot*, posterior canal for r. oticus; *c. spc*, canal for spinal cord or brain; *c. II*, *c. III*, *c. VI*, *c. X*, canals for optic, oculomotor, abducens and vagus nerves; *fe. ov*, fenestra ovalis; *fi. ot. va*, *fi. ot. vp*, fissura oticalis ventralis anterior and posterior; *foot-pl*, lamina probably corresponding to foot-plate of columella; *gr. a. dl*, groove for lateral dorsal aorta; *hyd*, *hyv*, dorsal and ventral articular areas for hyomandibula; *im. m. b3*, *im. m. b4*, impressions of basicranial muscles 3 and 4; *lc*, lateral commissure; *nc*, notochord; *or. m. sc*, *p. m. sc*, areas of origin and insertion of subcranial muscle; *pr. bp*, basipterygoid (basitrabecular) process; *pr. conn*, processus connectens; *pr. po*, postotical process; *pr. sp*, suprapterygoid process; *sh. ot*, otical shelf; *spic*, spiracular canal.

The braincase in *Eusthenopteron* and other "crossopterygians" is divided into two divisions (ethmosphenoid, otoccipital) separated by an in tracranial joint and the notochord which is wide (like in recent embryos) extends forwards to the posterior end of the anterior division. The posterior part of the otoccipital (fig. 93B) is very suggestive of the vertebrae (fig. 93A) and as is quite evident this part is composed of vertebrae which have fused with each other. However, if we examine the posterior part of the ethmosphenoid (fig. 93C) it is easy to see that this part, too, is very suggestive of a vertebra. Like in the vertebrae of the trunk and in the posterior part of the otoccipital there is a wide canal (*c. nc*) for the notochord and this canal which is closed anteriorly and forms a pit is surrounded laterally and ventrally by a part of the ethmosphenoid which is similar to and probably serially homologous with the ventral vertebral arch (*V. a*) of the vertebrae; and dorsal to that lies the neural canal (*c. spc*) bounded laterally by the lateral walls of the cranial cavity in a way suggestive of the neural arch (*N. a*). Because of these conditions (see also pp. 247–250) I found it reasonable to assume (1959a, 1960) that the posterior part of the ethmosphenoid represents a vertebra and that the vertebral column accordingly extends forwards at least to the region of the hypophysis. I therefore concluded that the braincase is composed essentially of an axial part formed by the vertebrae of a fairly long *cranial portion of the vertebral column* to which has been added certain dorsal elements of the three prootic visceral arches (cf. fig. 99A). Moreover, I suggested that the various embryonic elements which according to HOLMGREN (1940, pp. 245–246) arise from the cephalic somites and which are found in association with the cranial portion of the notochord and the overlying part of the brain (the posterior endomesodermal part of the trabecula, the pila antotica, the acrochordal cartilage, the polar cartilage and the parachordal) represent arcual elements of cranial vertebrae. But is the posterior part of the ethmosphenoid a modified vertebra it follows that the intracranial joint very likely is a persisting vertebral joint and if so this joint must be a primitive feature. Accordingly the presence of such a joint cannot be used as an argument for a close relationship between the groups of fishes classified as crossopterygians (see also JARVIK, 1968a, p. 225).

Cephalic somites. – These partly new views as to the composition of the braincase gained by studies of the primitive fossil osteolepiforms were supported by the thorough embryological studies of the structure of the head in fish by HOLMGREN (1940, 1943). However, the excellent material of microtomised series of embryos of various elasmobranchs, brachiopterygians and actinopterygians used by HOLMGREN has later been utilised by BERTMAR (1959) and BJERRING (1967, 1968) and thanks also to these researches, the detailed descriptions of the anatomy of

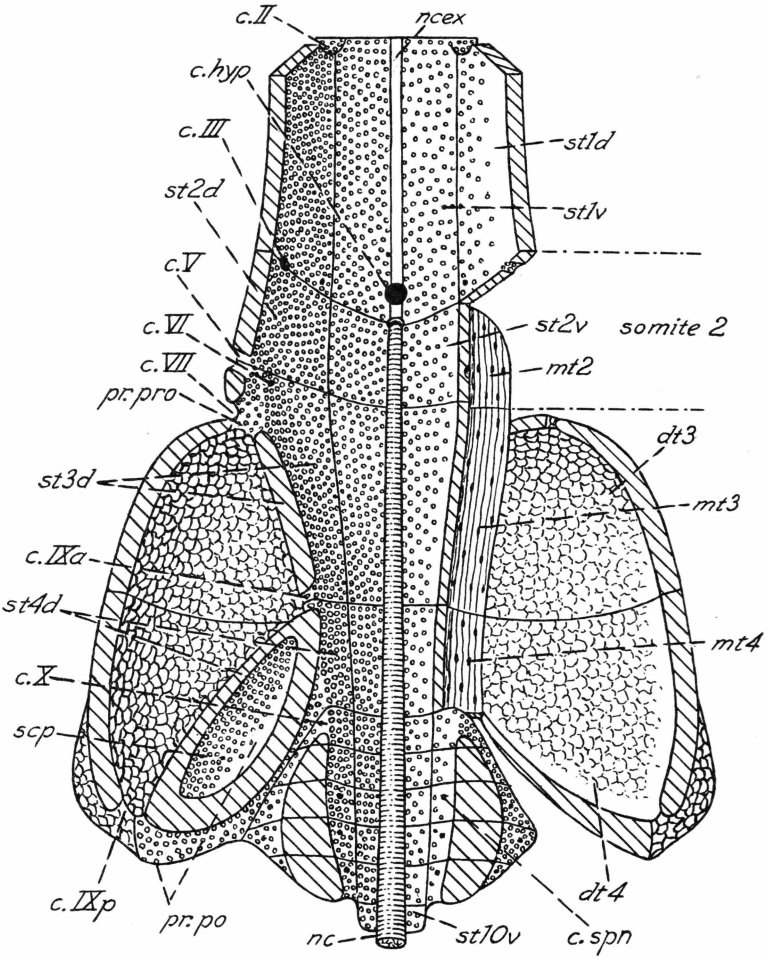


Fig. 94. *Squalus acanthias*. Diagram of skeletal derivatives of foremost ten somites. After BJERRING (1967, fig. 21). Modified.

c. hyp, opening for buccohypophysial duct; *c. spn*, canal for spinal nerve; *c. II*, *c. III*, *c. V*, *c. VI*, *c. VII*, canals for optic, oculomotor, trigeminal, abducens and facial nerves; *c. IXa*, *c. IXp*, anterior and posterior canals for n. glossopharyngeus; *c. X*, canal for n. vagus; *dt3*, *dt4*, skeletal derivatives of dermatomes of 3rd and 4th somites (= antero-lateral and postero-lateral otic cartilages); *mt2*, skeletal derivative of myotome of 2nd somite (= polar cartilage); *mt3*, *mt4*, skeletal derivatives of myotomes of 3rd and 4th somites (= anterior and posterior basiotic laminae); *nc*, notochord; *ncex*, exchordal; *pr. po*, posterior process of Källberg's cartilage (= post-otical process); *pr. pro*, anterior process of dorsal parachordal process of van Wijhe (= preotical process); *scp*, posterior semicircular canal; *st1d*, *st1v*, dorsal and ventral skeletal derivatives of sclerotome of 1st somite; *st2d*, *st2v*, dorsal and ventral skeletal derivatives of sclerotome of 2nd somite; *st3d*, dorsal skeletal derivative of sclerotome of 3rd somite (= dorsal parachordal process, VAN WIJHE); *st4d*, dorsal skeletal derivative of sclerotome of 4th somite (= Källberg's cartilage, HOLMGREN); *st10v*, ventral skeletal derivative of sclerotome of 10th somite.

Latimeria by MILLOT & ANTHONY (1958, 1965) and the important embryological studies of primitive urodeles (hynobiids) by SCHMALHAUSEN (1950–1968), FOX (1954, 1959, 1965), REGEL (1961, 1964a 1964b, 1968), LEBEDKINA (1960, 1964a) and BJERRING (1970) we have now got a much widened knowledge of the structure of the gnathostome skull and in particular of the basis cranii.

As is now well established (see DE BEER, 1937) and as is well shown in the illustrative wax-models of embryonic stages of *Squalus* (fig. 108A) made by BJERRING (1967, figs. 19, 20) there is a continuous series of somites which from the trunk extends forwards through the embryonic vertebrate head to the first or premandibular somite (*som1*, fig. 108A; as regards cyclostomes see DAMAS, 1944; VANDEBROEK, 1969, fig. 98; "*Amphioxus*", fig. 108B). Mainly because of the strong brain flexure in early embryos and the development of the otic vesicles the head somites may be more or less modified and some of them may be indistinct or in certain groups (e.g. urodeles) not discernible at all (see DE BEER, 1937). However, as now seems to be clear and as will be further elucidated below no somite disappears and exactly as in the trunk each of the head somites differentiates into a dermatome, a sclerotome and a myotome (see e.g. BERTMAR, 1959; BJERRING, 1968).

The *dermatomes* (see BJERRING, 1967, table, p. 262) form parts of the subcutaneous tissues and, in the 3rd and 4th metameres, parts of the lateral wall of the otic capsule (*dt3*, *dt4*, figs. 94, 97B, *otca*, *otcp*, figs. 96, 99A,C).

The *sclerotomes* as is well known (see e.g. HOLMGREN, 1940, pp. 245–246; BERTMAR, 1959, pp. 351–353, fig. 43; BJERRING, 1967, p. 262, fig. 21, 1968) also in the head produce skeletogenous material, which ventrally (*st1v*, etc., fig. 94) is next to the notochord and dorsally (*st1d*, etc.) extends along the spinal cord or brain. An important fact is that the notochord, as recently demonstrated by BJERRING (1971), originally extended forwards at least to the level of the opticus canals, that is about as far forwards as the basis cranii according to STONE (1926) and others (see p. 222) is endomesodermal in origin. The persisting mesenchyme of this anterior suppressed portion of the notochord, the *exchordal* (BJERRING; *ncex*, fig. 94, *ncex.mes*, fig. 108A), is posteriorly pierced by the buccohypophysial duct and along it the sclerotomic derivatives of the 1st somite (*st1d*, *st1v*) are found. Another important fact to be discussed below (pp. 241–255) is that the skeletal derivatives of the sclerotomes of the cephalic somites form arcual elements of vertebrae. Because the cranial vertebrae alternate with the myomeres associated with the basis cranii (see p. 241 and fig. 99B) it appears that they like the vertebrae in the trunk (see GOODRICH, 1930, pp. 7,15–18,57, figs. 56, 62), are intermetameric in position and are composed of material derived from half-sclerotomes of two adjoining somites.

For reasons given in a previous paper (JARVIK, 1965b, pp. 154–156, fig. 6) it is likely that the original supporting elements of the paired fins, the radials, are secondary formations arisen to form supports for the pre-existing radial muscles. It is reasonable to assume that also the metameric myomeres of the trunk are older, phylogenetically, than the supporting elements in the vertebral column (cf. "*Amphioxus*"). If it is true that a protognathostome was a swimming animal (see JARVIK, 1965b, fig. 5; cf. also the larva of "*Amphioxus*", fig. 108B) it is easy to understand that the vertebrae, in order not to prevent the effect of the alternate contractions of the metameric muscles, arose intermetamerically, the muscles spanning the intrametameric vertebral joints. It is then also easy to explain why the sclerotomes of two adjoining somites contribute to the formation of the vertebrae; and because we in each metamere may distinguish between paired dorsal and ventral sclerotomic skeletogenous material (*st1d*, *st1v*, etc., fig. 94; cf. GOODRICH, 1930, pp. 15–18) the consequence will be that four paired arcuals, two anterior (basidorsal, basiventral) derived from the posterior half of the sclerotome of one somite, and two posterior (interdorsal, interventral) derived from the anterior half of the sclerotome following next behind (see fig. 99B) develop in each vertebra. The formation of the vertebrae in this way implies a primary subdivision or segmentation of the metameric sclerotomic material and to call this process "resegmentation" (see SCHAEFFER, 1967, pp. 185–186; cf. LEHMAN, 1968) is most confusing. As may be gathered from a comparison of figure 94 which illustrates the metameric disposition of the somitic skeletal derivatives in the basis cranii (note that the transverse lines mark boundaries between metameres; not between vertebrae) with figure 99B which shows the cranial vertebrae and the intervertebral joints it is necessary to distinguish clearly between metamerism and vertebral segmentation and this is the main reason why I have avoided the term segmentation as a synonym for metamerism (cf. p. 229).

The *myotomes* in the occipital region produce myomeres, as in the trunk, and as is well known the eye-muscles (fig. 99B) are derivatives of the three most anterior myomeres (*my1*, *my2*, *my3*, fig. 95A). However, a most important fact first clearly recognised by BERTMAR (1959, pp. 268, 280, 352, fig. 43) is that the myomeres in the region of the otic capsules develop into skeletal tissue, namely the lamina basiotica. This structure (*mt3*, *mt4*, fig. 94; *la.boa*, *la.bop*, figs. 89A, 96, 97B, 99A, C) arises from the somites of the 3rd and 4th metameres, but as is well known the myotome of the 3rd somite produces also the external rectus eye-muscle (*m.r.e*, fig. 99B). As shown by BERTMAR this muscle arises from the anterior, and the front portion (*la. boa*) of the basiotic lamina from the posterior, part of the myotome of the 3rd somite.

However, as is well shown in the wax-models of an 8 mm embryo of *Amia* made by BJERRING (1967, fig. 18, 1968, fig. 5) the polar cartilage (*mt2*, fig. 94, *pol. c*, figs. 89, 91, 92C, 96), which BERTMAR considered to be a sclerotomic derivative of the 2nd somite, lies in the direct anterior continuation of the myotomic basiotic lamina and as shown by BJERRING the myotome in metamere 2, exactly as that in metamere 3, differentiates in an anterior part which forms an eye-muscle (the superior oblique, *m.o.s*, fig. 99B) and a posterior part which forms a skeletal element (the polar cartilage).

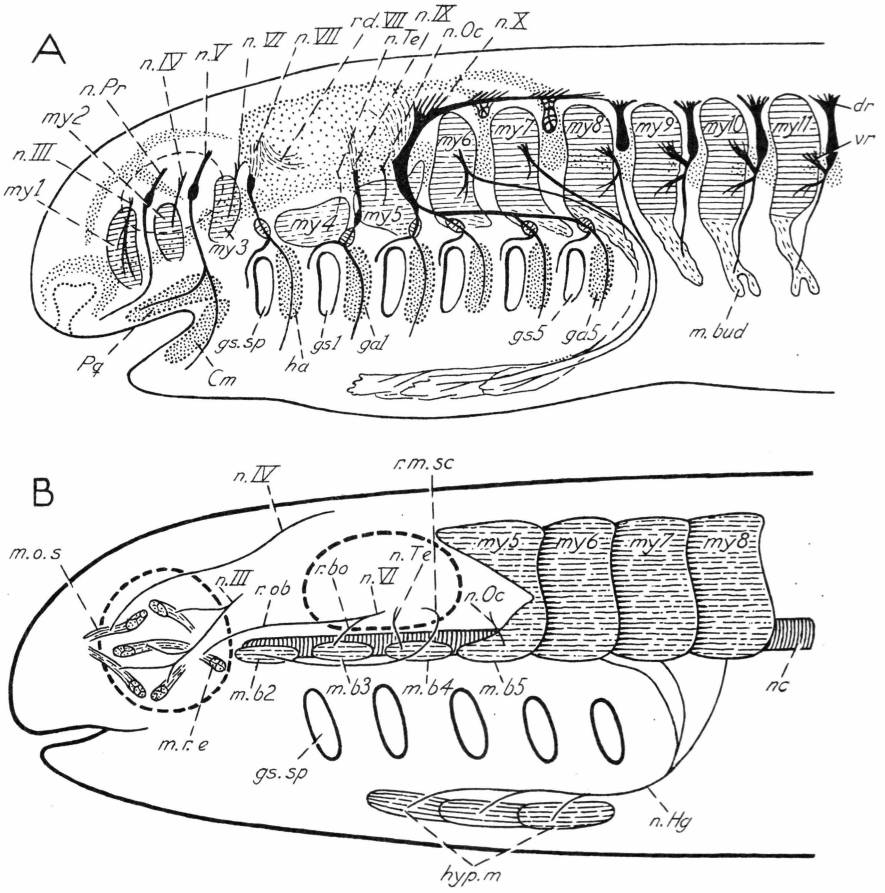


Fig. 95. *A*, diagram illustrating metamerism of head in selachian (cf. fig. 94). From GOODRICH (1930, fig. 240), simplified. *B*, diagram of somatic muscles and ventral cranial nerves of anterior eight metameres in gnathostomous vertebrate. From BJERRING (1970, fig. 3), simplified. As regards dorsal cranial nerves see *A* and fig. 88.

Cm, ceratomandibular (meckelian cartilage); *Pq*, palatoquadrate.

dr, dorsal root of spinal nerve; *ga1*, *ga5*, first and fifth post-hyoidean gill-arches; *gs. sp*, spiracular gill-slit; *gs1*, *gs5*, first and fifth post-spiracular gill-slits; *ha*, hyoid arch; *hyp. m*, hypobranchial musculature; *m. bud*, muscle bud of pectoral fin; *m.b2*, basicranial muscle of 2nd metamere (= subcranial muscle; probably homologous with polar cartilage); *m.b3*, *m.b4*, basicranial muscle of 3rd and 4th metameres; *m.b5*, basicranial muscle 5, represented by ventral portion of myomere of 5th metamere; *m. o. s*, m. obliquus superior; *m. r. e*, m. rectus externus (posterior); *my1–my11*, myomeres of metameres 1–11; *nc*, notochord; *n. Hg*, hypoglossal nerve; *n. Oc*, occipital nerve (ventral nerve in 5th metamere); *n. Pr*, profundus nerve (dorsal nerve in 1st or premandibular metamere); *n. Te*, tenuis nerve (ventral nerve in 4th metamere); *n. III*, *n. IV*, n. oculomotorius, n. trochlearis (ventral nerves in 1st and 2nd metameres); *n. V*, n. trigeminus (dorsal nerve in 2nd metamere); *n. VI*, n. abducens (ventral nerve in 3rd metamere); *n. VII*, *n. IX*, *n. X*, n. facialis inclusive n. acusticus, n. glossopharyngeus and n. vagus (dorsal nerves in 3rd, 4th and 5th–

Basicranial muscles and other myotomic derivatives. – Starting from the conditions in *Latimeria*, as described by MILLOT & ANTHONY (1958, 1965), BJERRING (1967) discussed the subcranial muscle (called basicranial muscle) in the three groups of fishes with a persisting intracranial joint and concluded: 1) that the muscle in coelacanthiforms has been secondarily lengthened, 2) that the muscle in porolepiforms and osteolepiforms retains more primitive conditions, being shorter and situated mainly in the 2nd metamere, and 3) that the muscle spans the intracranial joint which like the vertebral joints in the body is intrametameric ("intrasegmental") in position. Moreover, he demonstrated that the subcranial muscle in osteolepiforms (*Eusthenopteron*) has exactly the same position and morphological relations as the polar cartilage in *Amia*. On this evidence he suggested that the subcranial muscle and the polar cartilage are homologous structures, which is in agreement with the results gained above (p. 228) from the comparison between urodeles and porolepiforms.

Because the polar cartilage and the basiotic lamina are myotomic derivatives it is to be expected that the myotomes that produce these skeletal elements may also produce muscles which, if we disregard the eyə-muscle components in metameres 2 and 3, are serially homologous with the myomeres of the trunk. That this is so in mətameres 3 and 4 is evident from the descriptions of larval urodeles by REGEL (1961, 1964a, 1968) and BJERRING (1970).

According to GOODRICH (1911) and DE BEER (1937, p. 21) the first permanent myomere in urodeles arises from the 5th somite. This myomere (*my 5*, fig. 95) consists of a dorsal portion which later fuses with the next two posterior myomeres (the 6th and 7th) to form the temporal longitudinal muscle; and a ventral, basicranial, portion. The latter (*m. b 5*, figs. 89A, 95B, 96) soon disappears as does also the ventral nerve (*n. Oc*, fig. 95) of the metamere (this nerve in urodeles was not observed by GOODRICH; cf., however, sharks, GOODRICH, 1930, fig. 240). However, in front of the transient basicranial portion of the myomere of the 5th metamere REGEL, discovered no less than two transient basicranial muscles (*my I*, *my II*) which as shown by BJERRING must belong to the 3rd and 4th metameres (and not to the 4th and 5th as assumed by REGEL, 1968, table 2, pp. 58–59).

Basicranial muscle 4 (*m. b 4*, figs. 89A, 92C, 95B, 96–98; *my II*, REGEL) is sometimes situated in a more or less deep groove on the ventral side of the cartilaginous basal plate (see also REGEL, 1964a, figs. 16,

8th metameres); *r. bo*, r. basioticus of n. abducens; *rd. VII*, dorsal branch of n. facialis (= n. acusticus); *r. m. sc*, nerve-branch innervating subcranial muscle (probably posterior branch of ventral nerve of 2nd metamere); *r. ob*, r. orbitalis of n. abducens; *vr*, ventral root of spinal nerve.

24) but it may also be partly or wholly enclosed in the cartilage and when it disappears its place is obviously occupied by cartilage. As discovered by BJERRING (1970) this muscle is associated with a special ventral nerve, the *n. tenius*, (*n. Te*, fig. 95B) which may emerge from the brain separately or together with the n. abducens. The discovery of this nerve, which must be the ventral somatic motor nerve of the 4th metamere, is of particular importance because it makes the series of ventral nerves in the head complete (fig. 99D; this nerve is indicated by an interrupted line in GOODRICH's well-known diagram shown in fig. 95A).

The basicranial muscle of the 3rd metamere (*m.b3*, figs. 89, 92C, 95B, 96, 97A; *my I*, REGEL, 1964a, fig. 4, 1968, figs. 11, 16B, 22) is, compared with that of the 4th metamere, weakly developed and was not discernible in the material studied by BJERRING. This muscle is situated close below or within a part of the basis cranii which by comparison with fishes most probably represents the anterior part of the basiotic lamina (*la. boa*), whereas basicranial muscle 4 lies in the area of the posterior part of that lamina (*la. bop*) and, as mentioned above, also may be partly or wholly buried in the cartilage. These facts strongly support the views held by BERTMAR and BJERRING that the anterior and posterior parts of the basiotic lamina are derivatives of the myotomes of the 3rd and 4th metameres. As is thus likely these myotomes produce both basicranial muscles and skeletal tissue. And considering the fact that disintegrating embryonic musculature in other groups (JOHNELS, 1948, pp. 186–187; BERTMAR, 1959, p. 286) may be transformed into new muscles or into cartilage, it is reasonable to assume that the mesenchyme freed by dedifferentiation of the transient embryonic basicranial muscles —which, as again may be particularly stressed, may be buried in cartilage (figs. 97B, 98)—is used to form new cartilage in the area of the basiotic lamina. Be this as it may, however, it is quite clear that *no serious objection can be raised against the homologisation of a muscle with a skeletal element.* In other words the subcranial muscle in forms with an intracranial joint may very well be homologous with the polar cartilage.

But the myotome of the third somite also forms an eye-muscle (rectus externus) and very likely this muscle (*m.r.e*, figs. 95B, 99B) in urodeles (cf. DE BEER, 1937, p. 21), like in fishes, arises from the anterior part of the myotome whereas the posterior part produces basicranial muscle 3 (and the anterior part of the basiotic lamina). The fact that the myotome in the 3rd metamere thus very likely forms an eye-muscle in its anterior and a basicranial muscle in its posterior part is of great interest because this is exactly what BJERRING (1968, fig. 6) has suggested with regard to the 2nd metamere when he claims that the original myomere of that metamere has split into an eye-muscle (obliquus superior; *m.o.s*, fig. 99B) and a basicranial muscle (*m. b2*) which in forms

with an intracranial joint is represented by the subcranial muscle. Thus, what has happened in the 3rd metamere may very well have happened in the 2nd and it may be justified to conclude that the subcranial muscle (*m.sc*, *m.b2*) is serially homologous with basicranial muscle 3. If true this means that we have now identified myotomic muscles corresponding to the myomeres of the body in each metamere forwards to the 2nd. In the 1st or premandibular metamere, on the other hand, the myotome (see *m. b1*, fig. 99B), as far as may be judged at present, has formed only the four eye-muscles innervated by the n. oculomotorius.

Innervation of basicranial muscles. – Dorsally to the small basicranial muscle 3 REGEL (1964a, fig. 18, 1968, fig. 24) found a small foramen (*c. r. bo*, figs. 92C, 96) in the basis cranii pierced by a branch of the n. abducens. No contact with the muscle has been observed but both REGEL and BJERRING think that this branch which continues outside the cartilage to join the main branch of the n. abducens farther forwards, originally innervated the basicranial muscle. BJERRING (1970) calls this branch the r. basioticus (*r. bo*, fig. 95B) whereas the main abducens branch which innervates the rectus externus is referred to as the r. orbitalis (*r. ob*). In the 3rd metamere the ventral nerve (abducens) thus seems to divide into one branch for an eye-muscle and one branch for the basicranial muscle. Again this is what BJERRING (1968) has suggested for the ventral nerve of the 2nd metamere.

However, the ventral nerve of the 2nd metamere is the trochlearis (*n. IV*, fig. 95) and it should therefore be expected that this nerve, which innervates the obliquus superior, also gives off a branch to the subcranial muscle which has been interpreted as the basicranial muscle (*m. b2*) of that metamere. However, as is well known this is not the case. In *Latimeria*, the only form in which the innervation of the subcranial muscle is known (MILLOT & ANTHONY, 1965), the nerve to that muscle, which should be anterior to and serially homologous with the r. basioticus in metamere 3, emerges from the brain together with n. vagus in the 5th metamere.

This fact, one would imagine, ought to be fatal for the view that the subcranial muscle belongs to the 2nd metamere (cf. NELSON, 1970). But this is not so. As we now shall see the ventral nerves of the 2nd and 3rd metameres (trochlearis and abducens) show several pecularities which may shed some light on the innervation of the subcranial muscle (see also BJERRING, 1971, 1972a).

A most remarkable but still unexplained fact is that the n. trochlearis (*n. IV*), contrary to what is to be expected, generally does not run directly from the brain to its muscle. Instead the nerve of each side, or, as in *Latimeria* (MILLOT & ANTHONY, 1965, p. 47), part of it, crosses the dorsal side of the brain so that the nerve of the left side innervates the

muscle of the right side and vice versa. It may be suspected that this peculiar decussation has had some influence on the nerve to the subcranial muscle but of greater interest in this connection is no doubt the n. abducens.

This nerve (*n. VI*) which according to current views is the ventral nerve in the 3rd metamere (fig. 99D)—the nerve has usually two or more roots and has for this reason been considered to be a collector nerve (see REGEL, 1968, table 2)—emerges from the brain very far backwards, in certain forms, e.g. *Latimeria* (MILLOT & ANTHONY, 1965, p. 56, fig. 17) and *Salamandra* (FRANCIS, 1934, p. 138; cf. FOX, 1954, p. 266) on level with the glossopharyngeus and vagus roots which is strange in view of the fact that it innervates a muscle in the orbit. Remarkable is also that this nerve in *Latimeria* (MILLOT & ANTHONY, 1965, figs. 23–24) after emerging from the brain for a fairly long distance runs in a ventral direction to turn forwards and pass through the otic capsule. In fact the n. abducens is situated almost as far back and has much the same course as the nerve to the subcranial muscle which, however, passes outside the otic capsule (see op. cit. figs. 16, 31). Worth while to mention are also the peculiar migrations of the abducens nucleus which have been described in many forms (ARIËNS KAPPERS et al., 1960; as regards *Homo*, see also JACOBS, 1970), but of greater interest in this connection are no doubt the aberrant abducens branches. In early human embryos BOYD & HUGHES (1960, p. 121) found a transient branch in the area of the anterior tip of the notochord, the fibres of which "are caught up in the chondrification process and come to be included within the developing matrix of the basisphenoid cartilages". As pointed out by BJERRING (1970) this branch very likely corresponds to the r. basioticus (*r. bo*, fig. 95B) of the n. abducens in urodeles and if so a basibranchial muscle (*m. b3*) was probably present in the 3rd metamere in the ancestors of man. Moreover, the abducens gives off recurrent branches (BREMER, 1921) and of very great interest is that these branches in *Homo* can be "traced backwards beyond the IXth nerve to join the vagus and accessory trunks" (BOYD & HUGHES, 1960, p. 120).

Because the ventral nerve of the 3rd metamere (abducens) emerges from the brain far backwards, sometimes even behind the origin of the IX–X complex (FRANCIS, 1934, p. 138), because the nerve in just *Latimeria*, which has a strong subcranial muscle, in contrast to all other extant vertebrates passes through the otic capsule, because recurrent branches may join the vagus, and considering also the decussation of the trochlearis it is not so surprising if also branches of the latter has become associated with the vagus. What has happened with the ventral nerve in the 3rd metamere may very well have happened with that in the 2nd.

Although neurobiotaxis may have played a role (ARIËNS KAPPERS, et al., 1960, pp. 73–86; BJERRING, 1968, p. 355) we have to admit that we do not know the causes of the pecularities in the development of the trochlearis and the abducens, but whatever the explanation may be the fact that the nerve to the subcranial muscle in *Latimeria* is associated with the n. vagus does not exclude the possibility that this nerve belongs to the 2nd metamere and that the subcranial muscle is the basicranial muscle of that metamere. In this connection may be added that BJERRING (1971, 1972a) has recently demonstrated that the nerve to the subcranial muscle (n. rarus) in early coelacanthiforms probably accompanied the n. glossopharyngeus through the otic capsule and that this nerve also in osteolepiforms was situated farther forwards in the head than in *Latimeria*.

Cranial vertebrae in urodeles. – The new discoveries as to the basicranial muscles and their innervation by REGEL and BJERRING certainly imply a great advance, but of a great importance for the understanding of the origin and composition of the vertebrate skull are also the distinct traces of segmentation in the basis cranii, namely the swellings (*ppocc1*, *pocc2*, *occ3*) separated by constrictions, described by REGEL (1961, 1964a, 1968) in the parachordal region of larval hynobiid urodeles.

As evidenced by REGEL's figures the myosepta separating the basicranial muscles are attached to the tops of these swellings (*CV3+4*, *CV4+5*, *CV5+6*, figs. 89A, 92C, 96, 97A) and each muscle runs from one top to the next in front. The metameric basicranial muscles accordingly have much the same relations to these swellings and constrictions as have the myomeres in the trunk to the vertebrae and vertebral joints (see SCHAUINSLAND, 1905, figs. 281–283; GOODRICH, 1930, fig. 56; SCHMALHAUSEN, 1957c, fig. 20). Very likely therefore the swellings mark the position of the cranial vertebrae (cf. GOODRICH, 1930, fig. 267; FOX, 1959, figs. 3, 8), whereas the constrictions represent vestiges of the original vertebral joints. If so, the constriction between swellings *CV5+6* (*occ3*, REGEL) and *CV4+5* (*pocc2*) which lies medially to basicranial muscle 5 must be the vertebral joint within metamere 5; also the constriction between swellings *CV4+5* (*pocc2*) and *CV3+4* (*ppocc1*) which has the corresponding relations to basicranial muscle 4 represents the joint within metamere 4 (cf. fig. 99B). The basicranial muscle of metamere 3 (*m. b3*; *myI*, Regel) is much reduced but very likely it originally extended forwards from the top of swelling *CV3+4* to another swelling (*sw2*, *CV2+3*, figs. 96, 97A) shown in some of REGEL's figures (1968, figs. 11, 16A; see also REGEL, 1964a, figs. 4, 10). Accordingly, this muscle has the same relations to the said swellings and the interjacent

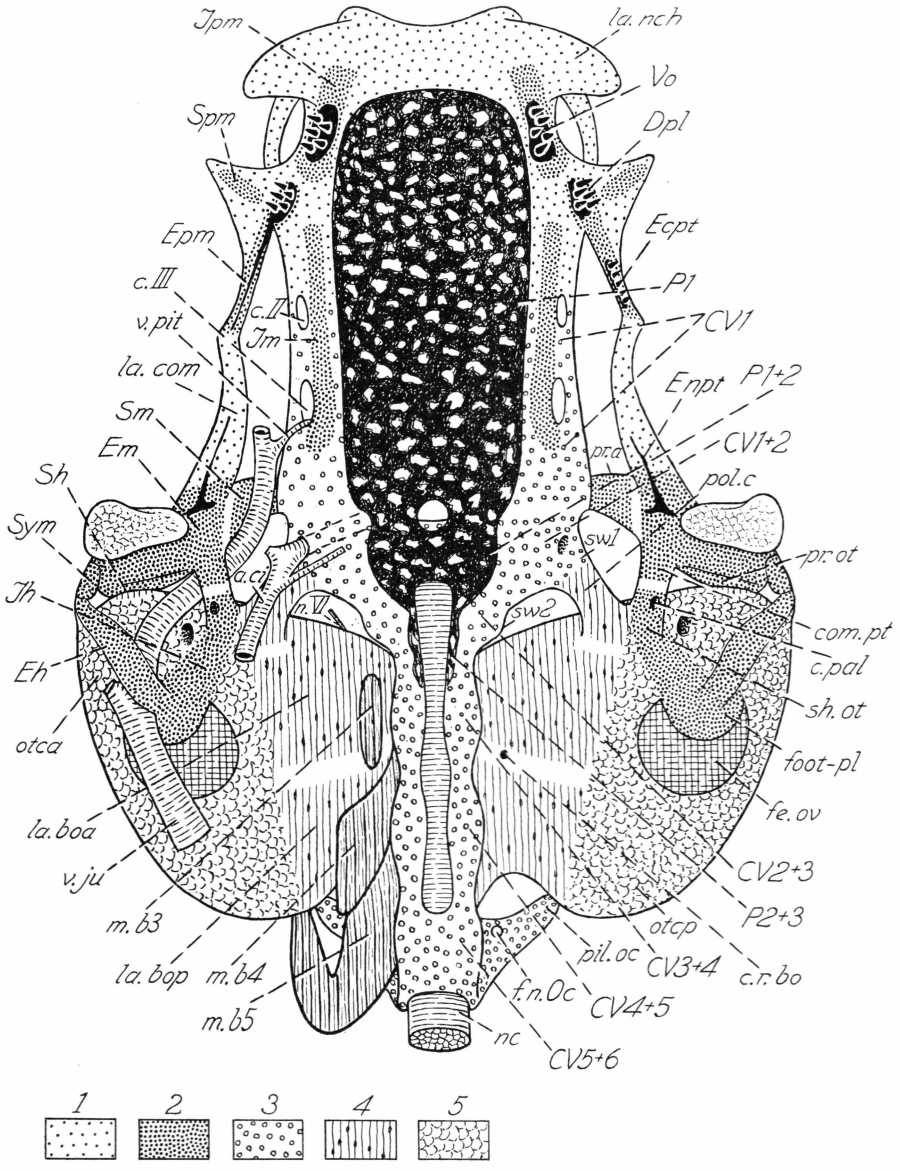


Fig. 96. Diagram of composition of endocranium and parasphenoid in primitive urodele (cf. figs. 89, 92).

CV1, cranial vertebra 1 (skeletal elements derived from anterior half of sclerotome of 1st metamere); *CV1 + 2*, cranial vertebra 1 + 2 (skeletal elements derived from posterior half of sclerotome of 1st metamere and anterior half of sclerotome of 2nd metamere); *CV2 + 3*, *CV3 + 4*, *CV4 + 5*, *CV5 + 6*, cranial vertebrae 2 + 3, 3 + 4, 4 + 5 and 5 + 6; *Dpl*, dermopalatine; *Ecpt*, ectopterygoid; *Eh*, epihyal (= hyomandibula); *Em*, epimandibular; *Enpt*, entopterygoid; *Epm*, epipremandibular; *Ih*, infrapharyngohyal (= otical shelf and foot-plate of columella); *Im*, *Ipm*, infrapharyngo-

constriction as have basicranial muscles 4 and 5 to the swellings and constrictions related to them and obviously the distinct constriction in front of swelling *CV 3 + 4* represents the vertebral joint within metamere 3. Farther forwards the conditions are obscure. However, in one of REGEL's figures (1968, fig. 16A) one more swelling is discernible. Of great interest is that this swelling (*sw1*, *CV 1 + 2*, fig. 96) is situated at the anterior end of the "basitrabecular commissure" (*pol. c*) which as discussed above very likely is the polar cartilage and homologous with the basicranial muscle of the 2nd metamere. It is therefore reasonable to assume that the original vertebral joint within metamere 2 is represented by the notch between the two last-mentioned swellings and has been situated somewhat as indicated in fig. 97A.

That these swellings really represent cranial vertebrae is evidenced also by the fact that they consist of a ventral part situated along the notochord and comparable to the ventral vertebral arches (*V. a*) of the vertebral column in *Eusthenopteron* (fig. 93A) and a paired dorsal process suggestive of the neural arch (*N. a*). On the basis of the facts now presented and on our present knowledge of the ontogeny of the basis cranii also in sharks and other fishes (HOLMGREN, 1940, 1943; BERTMAR, 1959; BJERRING, 1967, 1968, 1971) and of the vertebral column (see in particular SCHAUINSLAND, 1905) an attempt will now be made to unravel the cranial vertebrae in urodeles from swelling *occ3* (REGEL) forwards (cf. BERTMAR, 1959, pp. 263, 348).

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mandibular and infrapharyngopremandibular (parts of ectomesenchymatic portion of trabecula); *P1*, *P1 + 2*, *P2 + 3*, parts of parasphenoid developed in relation to cranial vertebrae 1, 1 + 2 and 2 + 3; *Sh*, suprapharyngohyal (= lateral commissure; forms part of processus oticus); *Sm*, suprapharyngomandibular (= processus ascendens palatoquadrati); *Spm*, suprapharyngopremandibular; *Sym*, symplectic (=processus hyoideus); *Vo*, vomer.

a. ci, a. carotis interna; *com. pt*, paratemporal commissure; *c. pal*, canal for r. palatinus VII; *c. r. bo*, canal for r. basioticus of n. abducens; *c. II*, *c. III*, canals for n. opticus and n. oculomotorius; *fe. ov*, fenestra ovalis; *f. n. Oc*, foramen for n. occipitalis; *foot-pl*, foot-plate (= posterior end of infrapharyngohyal); *la. boa*, *la. bop*, anterior and posterior basiotic laminae; *la. com*, commissural lamina connecting epimandibular with epipremandibular; *la. nch*, lamina nariochoanalis ("trabecular horn"); *m.b3*, *m.b4*, *m.b5*, basicranial muscles 3, 4, and 5; *nc*, notochord; *n. VI*, n. abducens; *otca*, *otcp*, anterior and posterior otic cartilages; *pil. oc*, pila occipitalis; *pol. c*, polar cartilage; *pr. a*, processus ascendens palatoquadrati; *pr. ot*, processus oticus palatoquadrati (probably including suprapharyngohyal); *sh. ot*, otical shelf (= anterior part of infrapharyngohyal); *sw1*, *sw2*, swellings 1 and 2; *v. ju*, jugular vein; *v. pit*, pituitary vein.

1, ectomesenchymatic skeletal parts; *2*, visceral elements; *3*, skeletal derivatives of sclerotomes of metameres forming cranial vertebrae; *4*, skeletal elements derived from myotomes of metameres 2–4; *5*, skeletal elements derived from dermatomes of 3rd and 4th metameres.

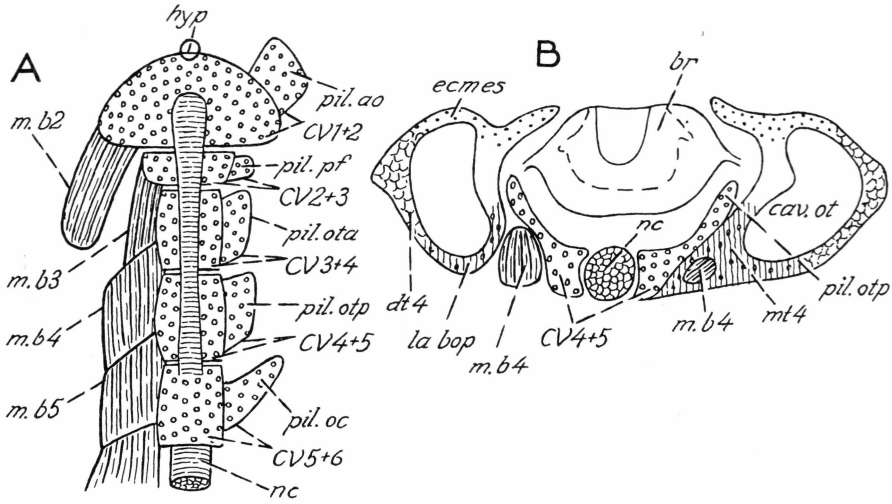


Fig. 97. Partly hypothetical diagrammatic representations to illustrate composition of cranial vertebrae and relations to basicranial muscles and (in *B*) otic capsules in urodeles. *A*, cranial vertebrae and basicranial muscles in ventral view (cf. figs. 89, 92C, 96). Cranial vertebra 1 omitted. *B*, *Hynobius keyserlingii*, larva, stage 8. Transverse section through cranial vertebra 4 + 5 (cf. figs. 96–98). From REGEL, 1964a, fig. 16, modified.

CV1 + 2–CV5 + 6, cranial vertebrae 1 + 2–5 + 6.

br, brain; *cav. ot*, cavity of otic capsule; *dt4*, skeletal derivative of dermatome of 4th metamere; *ecmes*, ectomesenchymatic portions of otic capsules and cranial roof; *hyp*, position of hypophysis; *la. bop*, posterior basiotic lamina (derived from myotome of somite of 4th metamere); *m. b2*, basicranial muscle of 2nd metamere (in urodeles represented by polar cartilage); *m. b3*, *m. b4*, *m. b5*, basicranial muscles 3, 4, and 5; *mt4*, skeletal derivative of myotome of 4th somite (= posterior basiotic lamina); *nc*, notochord; *pil. ao*, pila antotica; *pil. oc*, pila occipitalis; *pil. ota*, *pil. otp*, pila oticalis anterior and posterior; *pil. pf*, pila prefacialis.

For further explanations see symbols 1–5 in fig. 96.

The cranial vertebra represented by swelling *occ3* presumably includes material derived from the posterior part of the sclerotome of metamere 5 and the anterior part of the sclerotome of metamere 6 and may therefore most conveniently be referred to as *CV 5 + 6* (figs. 89A, 96, 97A). This vertebra consists of a ventral part (cf. *V. a 5 + 6*, fig. 99B) formed by portions of the parachordals derived from the adjoining half-sclerotomes of the 5th and 6th metameres, and a dorsal process, the occipital arch or pila occipitalis (*pil. oc*). The latter is suggestive of and probably serially homologous with the neural arches and it may therefore be assumed that it at least mainly represents the basidorsal (see *Bd 5*, fig. 99B) of metamere 5 formed by the posterior part of the sclerotome of that metamere (cf. Fox, 1957). The next vertebra, *CV 4 + 5* (*pocc 2*, REGEL), also consists of a ventral part derived from the parachordals and a dorsal process ("preoccipital arch", *pocc*, REGEL, 1964a,

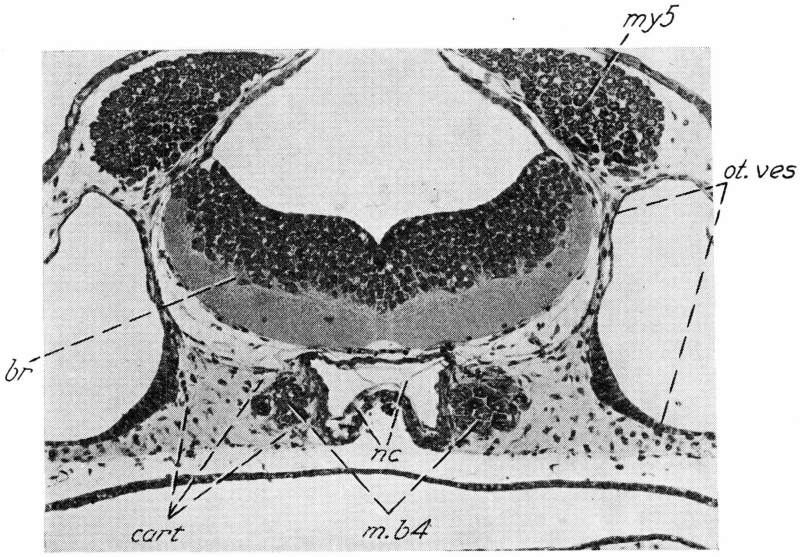


Fig. 98. *Hynobius retardatus*, larva 18.5 mm. Photograph of transverse section of stage in which basicranial muscle 4 is almost completely enclosed in cartilage (cf. fig. 97 B, right side). × 80/1.

br, brain (medulla oblongata); *cart*, cartilaginous basis cranii; *m. b4*, basicranial muscle of 4th metamere; *my5*, myomere of 5th metamere (occipital myomere); *nc*, notochord; *ot. ves*, otic vesicle.

fig. 16, 1968, fig. 25). This process (*pil. otp*, fig. 97), the pila oticalis posterior (Bjerring, 1970), which forms a posterior part of the medial wall of the otic capsule appears to have a greater rostro-caudal extent than the pila occipitalis and it is possible that it includes material not only from the posterior part (*Bd4*, fig. 99 B) of the sclerotome of metamere 4 but also from the anterior part (*Id5*) of the sclerotome of metamere 5. This implies that both the cranial and the caudal dorsal arcual elements (basidorsal and interdorsal) in this vertebra form neural arches, which as demonstrated by Schauinsland (1905, pp. 500–501, fig. 284) may be the case in the tail of urodeles.

The next vertebra, *CV 3 + 4* (*ppocc1*, Regel), may be supposed to have a similar composition. Its dorsal process, the pila oticalis anterior (*pil. ota*, fig. 97 A; *ppocc1*, Regel, 1964a, 1968, fig. 25) which forms an anterior part of the medial wall of the otic capsule (cf. fig. 94, *st3d*) is probably also a double formation derived from parts (*Bd3*, *Id4*) of the sclerotomes of the 3rd and 4th metameres (cf. Bertmar, 1959, pp. 276–277).

In the following vertebra, *CV 2 + 3*, the ventral arcual part (*sw2*) is probably formed posteriorly by parts of the parachordals belonging to the 3rd metamere and anteriorly by the posterior part of the acrochordal, a component part of the 2nd metamere. Its dorsal process is

probably represented by the prefacial commissure or pila prefacialis (*pil. pf*, see p. 254).

The next vertebra, *CV 1+2*, which probably is the foremost complete cranial vertebra, in its posterior part presumably includes material from the anterior part of the sclerotome of the 2nd metamere, that is the anterior part of the acrochordal ventrally (*sw1*) and the pila antotica (*pil. ao*) dorsally. The anterior part of this vertebra must be derived from the posterior part of the sclerotome of the 1st or premandibular somite and at least theoretically there should be a half vertebra, *CV 1*, in front of it formed by the anterior part of the sclerotome of that somite (see fig. 99B). Experimental and other investigations of urodeles have shown (see p. 222) that the lateral walls of the cranial cavity, forwards about to the canal for the n. opticus, are endomesodermal (somitic) in origin and as demonstrated by HOLMGREN (1940, p. 245; see also BERTMAR, 1959, fig. 43, *scl1*) the corresponding parts in sharks are derivatives of the 1st somite (*st1d*, fig. 94). Moreover, the notochord according to BJERRING (see p. 234) has an anterior modified portion, the exchordal (*ncex*, fig. 94, *ncex. mes*, fig. 108A), which represents the original premandibular portion of the notochord and in its posterior part is pierced by the buccohypophysial duct.

In view of these facts it may be justified to assume that the cranial portion of the vertebral column extends forwards in front of the hypophysis, and that the posterior part of the orbital wall in front of pila antotica, that is in the main the pila metoptica (DE BEER 1937, p. 388), represents dorsal, and the underlying lateral part of the ventral wall of the cranial cavity ventral arcual elements in the 1st metamere (see also the detailed analysis recently given by BJERRING, 1971). Speaking in terms of vertebrae it seems likely that the pila metoptica (cf. fig. 99B, *pil. met*), at least in its main anterior part is the interdorsal (*Id1*) of the presumed incomplete vertebra *CV 1*.

The ventral arcual elements of the anterior part of vertebra *CV 1+2* and of vertebra *CV 1* must be derived from the ventral arcual material of the 1st somite (*st1v*, fig. 94), which at least partly is situated in front of the hypophysis and inside that part of the "trabecula" that represents the vestigial infrapharyngomandibular (*Im*, fig. 96). Of some interest is that this material seems to be situated much as the "intertrabecular mesenchyma" described by HOLMGREN (1943, pp. 38–39; see also JARVIK, 1954, pp. 60, 65, 88–89) in *Amia* and which lies directly over "the first appearing rudiment of the prehypophysial portion of the parasphenoid bone". In the urodeles, too, there is in early stages a separate prehypophysial parasphenoid primordium (*P1*, fig. 91; LEBEDKINA, 1964a, figs. 4, 33) but in them there is also another primordium (*P1+2*) situated behind the hypophysial foramen. This latter primordium forms a part

of the parasphenoid which is very suggestive of, and no doubt corresponds to, the median posthypophysial portion (*P 1+2*, fig. 92A) of the parasphenoid in porolepiforms and as evidenced also by the conditions in that group (see p. 256) lies underneath *CV 1+2*. These conditions suggest that the prehypophysial portion of the parasphenoid (the primitive parasphenoid bone, JARVIK, 1954, pp. 64–65) arose on the ventral side of the most anterior part of the vertebral column formed by *CV 1* and as will be further elucidated below (p. 256) it is possible that the existence of the pre- and posthypophysial parasphenoid primordia in urodeles reflects the segmentation in the overlying part of the vertebral column. If true this would mean that the original vertebral joint between the presumed cranial vertebrae *CV 1+2* and *CV 1*, that is the joint within the 1st metamere, was situated in the area between the two parasphenoid primordia just mentioned, that is about at the hypophysial foramen (see also BJERRING, 1971).

Cranial vertebrae in porolepiforms and osteolepiforms. – The distinct traces of vertebrae and vertebral joints far forwards in the basis cranii and the presence of metameric basicranial muscles supplied by metameric ventral nerves in embryonic stages of urodeles are no doubt primitive features. The conditions in anurans are still imperfectly known but judging from the review given by SMIT (1953, pp. 108–119) and his own descriptions of transient basicranial muscles there are corresponding traces of metamerism in the basis cranii in this group as well. This primitiveness in urodeles and anurans is in agreement with the view expressed in a previous work, (JARVIK, 1968b), namely that the urodeles and anurans are closely related to, and possibly descendants of, two of the most primitive groups of vertebrates (porolepiforms and osteolepiforms). At that occasion (pp. 502, 509) I called attention to the fact that according to the unamnious results gained by specialists on brain anatomy the most primitive forebrain among recent vertebrates is found in modern Amphibia. It may be of interest to note that a corresponding primitiveness has recently been demonstrated with regard to the detailed structure of the amphibian cerebellum (LLINÁS & HILLMAN, 1969, pp. 43, 71; NICHOLSON et al., 1969, p. 240).

But in as much as metameric basicranial muscles are present in embryonic stages of urodeles and anurans and because there are traces of vertebrae and vertebral joints far forwards in the basis cranii it is to be expected to find still more primitive conditions in their piscine ancestors. The new facts as to the metamerism and vertebral segmentation in the head, therefore, strongly support the view advanced in 1959 (see also JARVIK, 1960) that the intracranial joint in "crossopterygians" is a persisting vertebral joint and it is now clear that this joint is situated in the 2nd metamere. But as indicated elsewhere (JARVIK, 1968b, p. 506)

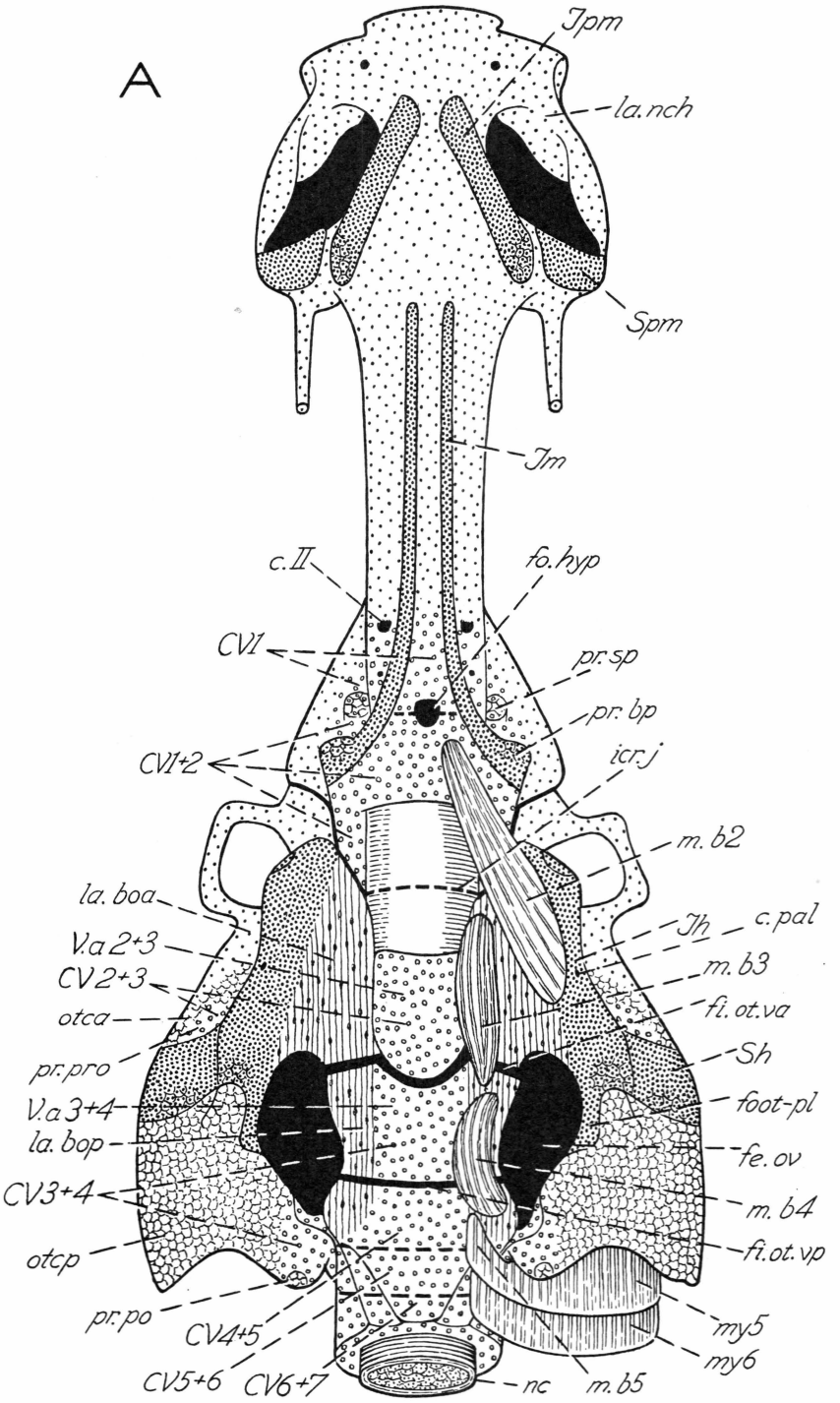
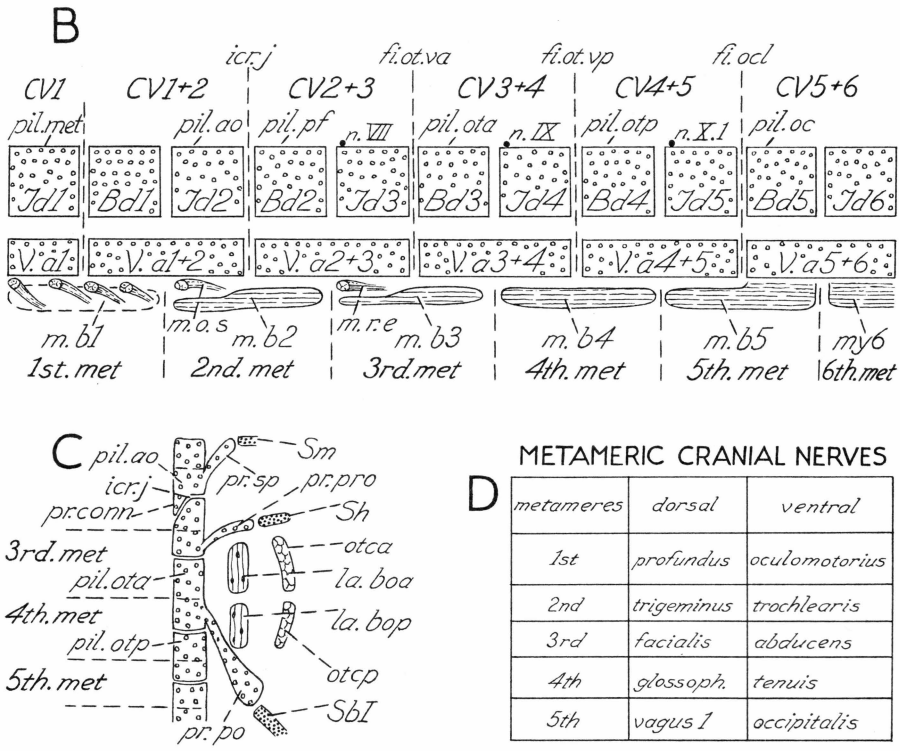

A
Jpm
la.nch
Spm
Jm
c.II
fo.hyp
CVI
pr.sp
pr.bp
CVI+2
icr.j
m.b2
la.boa
Jh
c.pal
V.a 2+3
m.b3
CV 2+3
fi.ot.va
otca
Sh
pr.pro
foot-pl
V.a 3+4
la.bop
fe.ov
CV3+4
m.b4
fi.ot.vp
otcp
pr.po
my5
CV4+5
my6
CV5+6
CV6+7
nc
m.b5

Fig. 99 A.



metameres	dorsal	ventral
1st	profundus	oculomotorius
2nd	trigeminus	trochlearis
3rd	facialis	abducens
4th	glossoph.	tenuis
5th	vagus 1	occipitalis

Fig. 99. *A*, *Eusthenopteron foordi*. Attempted interpretation of composition of neural endocranium. Ventral aspect (cf. fig. 93). Basicranial muscles tentatively restored. Interpretation of visceral elements after JARVIK, 1954. *B*, *C*, keys to interpretations of components derived from cranial somites. *B*, scheme of cranial vertebrae, metameric basicranial muscles and eye-muscles. Lateral aspect. *C*, scheme to show position of lateral processes of cranial vertebrae articulating with suprapharyngeal elements of visceral arches of metameres 2–4. *D*, scheme of dorsal and ventral cranial nerves of metameres 1–5 (cf. figs. 88, 95).

Bd1–Bd5, basidorsals of metameres 1–5; *CV1–CV6 + 7*, cranial vertebrae 1–6 +7; *Id1–Id6*, interdorsals of metameres 1–6; *Ih*, infrapharyngohyal; *Im*, infrapharyngomandibular; *Ipm*, infrapharyngopremandibular; *SbI*, suprapharyngobranchial of first (post-hyoidean) visceral arch; *Sh*, suprapharyngohyal; *Sm*, suprapharyngomandibular; *Spm*, suprapharyngopremandibular; *V. a1–V. a5 + 6*, ventral vertebral arches (subchordal arcual plates) of cranial vertebrae 1–5 + 6.

c. pal, canal for r. palatinus; *c. II*, canal for n. opticus; *fe. ov*, fenestra ovalis; *fi. ocl*, dorsal part of fissura occipitalis lateralis; *fi. ot. va*, *fi. ot. vp*, fissura oticalis ventralis anterior and posterior; *fo. hyp*, fossa hypophyseos; *foot-pl*, posterior part of infrapharyngohyal, probably forming foot-plate of columella in tetrapods; *icr. j*, intracranial joint (in 2nd metamere); *la. boa*, *la. bop*, lamina basiotica anterior and posterior; *la. nch*, lamina nariochoanalis (= "trabecular horn"); *m. b1*, basibranchial muscle of first metamere, probably completely used up to form eye-muscles innervated by n. oculomotorius; *m. b2*, basicranial muscle 2 (= subcranial muscle or polar cartilage); *m. b3*, *m. b4*, basicranial muscles 3 and 4; *m. b5*, basicranial muscle 5 (= ventral portion of myomere 5); *m. o. s*, m. obliquus superior; *m. r. e*, m. rectus

(cont. p. 250)

there are also traces of vertebral joints in the otoccipital. Unfortunately the postero-ventral parts of that element are still imperfectly known in porolepiforms and in the following attempt to make out the cranial vertebrae and the basicranial muscles in the piscine ancestors of the tetrapods we have therefore, as far as these parts are concerned, to keep mainly to osteolepiforms (fig. 99A).

As pointed out above (p. 232) the posterior end of the ethmosphenoid in *Eusthenopteron*, and, it may be added, also in other forms with a persisting intracranial joint, is very suggestive of a vertebra (fig. 93A, C). It appears now to be clear that this presumed vertebra in osteolepiforms as well as in porolepiforms corresponds to cranial vertebra *CV 1 + 2* in urodeles and very likely there is a half vertebra (*CV 1*, fig. 99A) in front of it. These two foremost vertebrae have fused with each other but for reasons given above (p. 247) it seems likely that the original joint between them, that is the vertebral joint within the 1st metamere, both in porolepiforms and osteolepiforms was situated at the hypophysial foramen as in urodeles.

The joint within the 2nd metamere, the intracranial joint (*icr. j*, fig. 99A–C), is well developed and on the whole very similar in osteolepiforms and porolepiforms (see also BJERRING, 1967).

Behind the intracranial joint which must be the persisting original joint between *CV 1 + 2* and *CV 2 + 3* there are in the otoccipital of osteolepiforms (*Eusthenopteron*) distinct traces of three further vertebral joints, all probably present also in porolepiforms (see also BJERRING, 1971).

In one specimen of *Eusthenopteron* (fig. 93E) the ventral wall of the notochordal canal extends farther forwards than in other specimens (fig. 93D), which as explained above (p. 69) certainly is due to the incorporation of a ventral arcual plate (*Aplv*) which is independent in other specimens. This separate plate which is present also in *Glyptolepis* (p. 69, fig. 24G, 31) and *Latimeria* (fig. 24B) extends backwards to an unossified area which as I have discussed elsewhere (1954, p. 7, figs. 1C, 30, *f. ot. v*) is situated as, and no doubt is homologous with, the fissura oticalis ventralis in palaeoniscids. Judging from its position, this fissura

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externus; *my5*, *my6*, myomeres 5 and 6; *nc*, notochord; *n. VII*, n. facialis; *n. IX*, n. glossopharyngeus; *n. X.1*, portion of n. vagus belonging to 5th metamere; *otca*, *otcp*, anterior and posterior otic cartilages; *pil. ao*, *pil. met*, *pil. oc*, *pil. ota*, *pil. otp*, *pil. pf*, antotic, metoptic, occipital, anterior otic, posterior otic and prefacial pilae; *pr. bp*, basipterygoid process (= posterior end of infrapharyngomandibular); *pr. conn*, processus connectens; *pr. po*, postotical process; *pr. pro*, preotical process; *pr. sp*, suprapterygoid process; *1st. met–6th. met*, first to sixth metameres.

For explanation of markings indicating origin of various endocranial components see symbols 1–5 in fig. 96.

which now may be termed the fissura oticalis ventralis anterior (*fi. ot. va*, figs. 93 D, 99 A, B) is a vestige of the vertebral joint within the third metamere, that is between *CV 2 + 3* and *CV 3 + 4*, and corresponds to the joint between these vertebrae in urodeles.

Behind the ventral arcual plate (*V. a 2 + 3*, fig. 99 A, B, *Apl v*, figs. 92 A, 93 D) belonging to the presumed vertebra *CV 2 + 3* there follows in *Latimeria* another ventral or subchordal arcual plate (see p. 65) which conceivably is the ventral vertebral arch (*V. a 3 + 4*) in vertebra *CV 3 + 4*. In *Eusthenopteron* the corresponding plate has been found independent in one specimen only (see BJERRING, 1971, fig. 3 A, *Cz 3p 4a*) but may in porolepiforms be represented by the paired plate (*Ap v*, fig. 92 A) observed in one specimen of *Holoptychius* (pl. 24:2). This plate (*V. a 3 + 4*, fig. 99 A) in *Eusthenopteron* extends backwards to a distinct transverse gap in the basis cranii, the fissura oticalis ventralis posterior (*fi. ot. vp*), which very likely is a vestige of the original vertebral joint within the 4th metamere. However, this joint is in *Eusthenopteron* discernible also in other specimens in which it is represented by the ventral part of the fissura occipitalis lateralis (JARVIK, 1954, p. 7, figs. 1, 30 E, *fi. occ. lat*) situated behind the glossopharyngeus canal and continuous ventrally with the lateral end of the fissura oticalis ventralis posterior (see also BJERRING, 1971, figs. 8 A, 9 B, *sy. iot. p*).

The third vertebral joint in the otoccipital of *Eusthenopteron* is discernible only on the lateral side and is formed by the dorsal part of the fissura occipitalis lateralis (see BJERRING, 1968, 1971, *sy. otoc. d*). This joint lies within the 5th metamere and separates *CV 4 + 5* and *CV 5 + 6*.

Behind the joint within the 5th metamere there are no traces of vertebral joints in the braincase of *Eusthenopteron* but because there are two canals for spinal nerves (see BJERRING, 1971, figs. 7, 8 A, *c. spo1*, *c. spo2*) and the spinal nerves generally are intrametameric in position it is to be assumed that there originally was a joint in the area between these canals, situated within the 6th metamere and separating *CV 5 + 6* and *CV 6 + 7*.

The latter is probably the hindmost complete vertebra incorporated in the braincase of *Eusthenopteron* which thus, as far as may be judged at present, includes $6^1/_2$ cranial vertebrae belonging to seven cranial metameres.

Each of these presumed cranial vertebrae is composed of a ventral part, which in each complete vertebral segment (as regards *CV 1*, see below) forms the ventral and lateral walls of the notochordal canal, and a paired dorsal process which shares in the formation of the lateral walls of the cranial cavity. These parts are very distinct in the occipital region (fig. 93 B) and in the posterior part of the ethmosphenoid (fig. 93 C) and

as its quite obvious the ventral parts (*V. a1–V. a5 + 6*, fig. 99B) are serially homologous with the composite ventral vertebral arches (*V. a*, fig. 93A) of the vertebral column (see JARVIK, 1952, p. 28, fig. 13), whereas the dorsal processes represent neural arches (*N. a*). However, because the spinal cord in the head has become much expanded forming the brain the neural arches of both sides (fig. 93A–C) only most posteriorly meet dorsally as they do in the vertebral column. In the main part of the braincase the dorsal parts of the neural arches in each vertebral segment lie far apart and are connected by the endoskeletal cranial roof which probably is a secondary formation of ectomesenchymatic origin (HOLMGREN, 1940, p. 246; cf. fig. 97B, *ecmes*). Moreover, there is a horizontal wall (*Apld*, fig. 93B,C) which separates the cranial cavity (*c. spc*) from the notochordal canal (*c. nc*) and obviously corresponds to the epichordal cartilaginous commissure in the basis cranii and to the suprachordal cartilages (*bl. sup*, *cart. sup*, fig. 24C, D) in the trunk vertebrae of anurans (see p. 65). An interesting fact is that parts of this horizontal wall in osteolepiforms, porolepiforms and coelacanthiforms may be separate forming dorsal or suprachordal arcual plates (anazygals, BJERRING, 1971; according to him present also in palaeoniscids). In *Glyptolepis* (p. 68) there is one dorsal arcual plate (*Apld*, fig. 24E, G) which judging from its position is homologous with the single dorsal plate in *Latimeria* (p. 65, fig. 24B) and belongs to cranial vertebra *CV 2 + 3*. In *Eusthenopteron* BJERRING (1971, figs. 2B, 5B, *Az2p*, *Az3a*) distinguished two such plates, one anterior homologous with that in *Latimeria* (and *Glyptolepis*) and one posterior, and conceivably there was originally one such plate in each vertebral segment.

The ventral vertebral arches of the three posterior cranial vertebrae in *Eusthenopteron* (fig. 99A) have fused into the ventral and lateral walls of the posterior part of the notochordal canal, but farther forwards, in *CV 2 + 3* and *CV 3 + 4*, they may be independent forming the ventral arcual plates mentioned above (*V. a2 + 3*, *V. a3 + 4*); these arcual plates were present also in porolepiforms (*Aplv*, *Apv*, fig. 92A). The ventral vertebral arch of *CV 2 + 3* is both in porolepiforms and osteolepiforms separated from that of *CV 1 + 2* by a gap and very likely it is the persistence of the intracranial joint that has prevented skeleton formation in the anterior part of *V. a2 + 3* and in the posterior part of *V. a1 + 2*. Most probably these parts were in the living animal represented by connective tissue filling the gap (see BJERRING, 1967, 1971).

With regard to the ventral vertebral arch (*V. a1*) in the foremost incomplete vertebra (*CV 1*) the conditions are more intricate (see also p. 293). This arcual element must be situated inside the infrapharyngomandibular (*Im*, fig. 99A) which in porolepiforms and osteolepiforms, in

contrast to urodeles (fig. 96) and anurans, is complete posteriorly and forms the hasipterygoid process (*pr. bp*). Another problem concerns the absence of the notochord and the notochordal canal in the area of *CV 1*. However, as recently shown by BJERRING (1971) the partly prehypophysial portion of the notochord belonging to the 1st or premandibular metamere persists as the exchordal (*ncex*, fig. 94). Of a great interest is that the exchordal mesenchyme instead of forming notochordal tissue may develop into endoskeleton and for good reasons BJERRING claims that the median hypophysial crest in porolepiforms (p. 51, *cr. m*, figs. 18, 19, 31) belongs to this category. But in this connection we have also to consider the intertrabecular mesenchyma described by HOLMGREN (see p. 246) in *Amia*. Because of the intimate relations between this mesenchyma and the underlying prehypophysial parasphenoid primordium (see *P 1*, figs. 91, 92) and because the posthypophysial parts of the parasphenoid lie close to the ventral sides of the cranial vertebrae (cf. p. 257) it is tempting to assume that this mesenchyma has been present in gnathostomes in general (cf. "medial area" in sharks, HOLMGREN, 1940, pp. 41, 95, 129; 1943, p. 38) and that it in porolepiforms and osteolepiforms—ventrally (and laterally?) to the median parts of the basis cranii derived from the exchordal—formed the ventral vertebral arch in *CV 1*.

The dorsal process of *CV 1* is probably also in porolepiforms and osteolepiforms the pila metoptica (*pil. met*, fig. 99B) which, since it is a derivative of the anterior half-sclerotome in the 1st metamere, is to be regarded as an interdorsal (*Id 1*). In the second cranial vertebra (*CV 1 + 2*) the dorsal process or neural arch is the pila antotica (*pil. ao*). Because this pila, which forms the lateral wall of the posterior part of the ethmosphenoid portion of the cranial cavity (see *N. a*, fig. 93C), belongs to the 2nd metamere (HOLMGREN, 1940, pp. 245–246) and lies in front of the intracranial joint, it must, as may be gathered from the diagram in fig. 99B, be the interdorsal (*Id 2*) in that metamere (because the pila antotica anteriorly has fused with the pila metoptica it is possible that it in the adult also includes material from the 1st metamere).

A remarkable fact is that the pila antotica or interdorsal 2 both in porolepiforms and osteolepiforms is provided with two distinct processes (fig. 99C), one posterior and one lateral. The posterior process, the processus connectens (*pr. conn*, see also figs. 20, 21, 31, 93, 105) articulates with the neural arch of the vertebra following next behind (*CV 2 + 3*) and is suggestive of a postzygapophysis. The lateral process, the suprapterygoid process (*pr. sp*), articulates with the processus ascendens of the palatoquadrate which is the suprapharyngeal element (*Sm*) of the mandibular arch. Accordingly in the 2nd metamere the suprapharyngeal ele-

ment of the 2nd visceral arch articulates with the interdorsal of this metamere. As we now shall see the conditions seem to be similar also in metameres 3 and 4.

In *CV 2+3* the dorsal process also in porolepiforms and osteolepiforms is probably represented by the pila prefacialis (*pil. pf*, fig. 99B), that is the lateral wall of the otoccipital portion of the cranial cavity in front of the facialis foramen. The dorsal processes in *CV 3+4* and *CV 4+5* are presumably represented by equivalents to the pila oticalis anterior (*pil. ota*) and the pila oticalis posterior (*pil. otp*) in urodeles. Besides in urodeles, these latter two pilae have been observed also in embryonic stages of other vertebrates and are in sharks known as the dorsal parachordal process (WIHJE, 1922; the dorsal process of de Beer, HOLMGREN, 1940, p. 118) and the cartilage of Källberg (HOLMGREN, 1940, p. 122) or the preoccipital arch (see also DE BEER, 1937; BERTMAR, 1959; BJERRING, 1967, table, 1971).

For reasons given recently by BJERRING (1971) the pila prefacialis very likely belongs to the 2nd metamere, which must mean that it is basidorsal 2 (*Bd 2*, fig. 99B), but theoretically *CV 2+3* should also include dorsal material derived from the anterior part of the sclerotome of the 3rd metamere, that is interdorsal 3 (*Id 3*). Turning to sharks it is of interest that HOLMGREN (1940, p. 121) in *Etmopterus* described a lateral lamella (*pr. pro*, fig. 94) which is situated between the anterior semicircular canal and the ganglionic complex of the facial nerve, forms part of the inner wall of the auditory capsule and posteriorly reaches an anterior extension of the dorsal parachordal process of van Wihje. However, the latter process, as demonstrated by HOLMGREN, is a derivative of the sclerotome of the 3rd somite (*st3d*, fig. 94). Accordingly, its "anterior extension" probably is a product of the anterior part of that sclerotome, that is it may be the interdorsal of the metamere (*Id 3*) whereas the principal part of the process probably in the main is the basidorsal (*Bd 3*). The lateral lamella (*pr. pro*) which thus appears to be a lateral process of interdorsal 3 laterally reaches the dorsal part of the lateral commissure, that is the suprapharyngeal element (*Sh*) in the third (hyoid) visceral arch. As indicated in fig. 99A, C this process, the processus oticalis anterior (*pr. pro*), might also be present in osteolepiforms and porolepiforms. Be this as it may the conditions in embryonic sharks strongly suggest that the suprapharyngeal element of the 3rd visceral arch articlates with a lateral process of the interdorsal of the 3rd metamere.

The cartilage of Källberg in sharks probably belongs to the fourth metamere (HOLMGREN, 1940) and because it arises independently it very likely is the dorsal sclerotomic derivative (*st4d*, fig. 94) in that metamere. The cartilage anteriorly reaches the anterior glossopharyngeus canal (*c. IXa*) and very likely the anterior part represents interdorsal 4, which

speaking in terms of vertebrae (fig. 99B, C) must form the postero-dorsal part of *CV 3 + 4*. Of great interest is now that the cartilage of Källberg, judging from the descriptions given by HOLMGREN (1940, pp. 122, 156, 1943, pp. 142–147), includes a lamella (*pr. po*, fig. 94) which from the anterior part of the cartilage, that is its interdorsal portion, extends in a postero-lateral direction and posteriorly forms part of the posterior wall of the auditory capsule. The corresponding part of the posterior wall of the auditory capsule in osteolepiforms is that part of the otoccipital which forms the postotical process (*pr. po*, fig. 99A), a process present also in porolepiforms (fig. 92A). Because the suprapharyngeal element (*Sb I*) of the first branchial arch, that is the 4th visceral arch, at any rate in *Eusthenopteron* (JARVIK, 1954), articulates with the postotical process it is tempting to assume (see fig. 99C) that the said lamella, which may be regarded as a lateral process (*pr. po*) of interdorsal 4, is serially homologous with the suprapterygid process (*pr. sp*), a probably lateral process of interdorsal 2, and with the processus oticalis anterior (*pr. pro*) interpreted above as a lateral process of interdorsal 3.

The fact that each of these three metameric lateral processes (*pr. sp*, *pr. pro*, *pr. po*) articulates with a suprapharyngeal element (*Sm*, *Sh*, *Sb I*, fig. 99C) is certainly not accidential. This fact, the presence of metameric muscular processes connecting each of the foremost somites with a branchial arch (BERTMAR, 1959, pp. 211, 260, fig. 43, *s1m–s5m*), the fact that each metameric dorsal nerve in the five foremost metameres has a visceral trunk (see fig. 88), the fact that there are three prootic visceral arches, etc. can only mean that there, at any rate as far the foremost five metameres are concerned, is a strict correspondance between branchiomerism and metamerism (cf. GOODRICH, 1930, p. 489).

This attempt to interpret the basis cranii in osteolepiforms (*Eusthenopteron*) and porolepiforms in terms of cranial vertebrae is supported also by the following conditions.

Basicranial muscles in porolepiforms and osteolepiforms. – As described above (p. 69) the ventral side of the otoccipital in *Eusthenopteron* shows three paired depressions (fig. 93D, E). The foremost of these depressions (*or. m. sc*), found also in porolepiforms (fig. 31), is no doubt the area of origin of the subcranial muscle (*m. sc*, figs. 24E, G, 92A). As we have seen (p. 228) this muscle occupies the same position as the polar cartilage, a derivative of the myotome of the 2nd somite, and, as claimed also by BJERRING, it very likely is homologous with that cartilage. Accordingly the muscle—in spite of its peculiar innervation—very likely belongs to the 2nd metamere and it is to be assumed that the joint spanned by the muscle, that is the intracranial joint, represents the intrametameric vertebral joint within the 2nd metamere. Consequently the subcranial muscle must represent basicranial muscle 2 (*m. b 2*, fig.

99A, B) and be serially homologous with basicranial muscle 3 in urodeles (*m. b3*, figs. 96, 97A). The middle of the three impressions (*im. m. b3*), also discernible in porolepiforms, crosses the presumed intervertebral joint (*fi. ot. va*) within the third metamere and on account of its position and extent it may be justified to assume that it was occupied by a muscle (*m. b3*, figs. 24G, 99A, B) homologous with basicranial muscle 3 in urodeles. The muscle is situated ventro-medially to the canal that has been identified as the abducens canal (*c. VI*) and very likely the muscle like in urodeles was innervated by a branch (r. basioticus) of that nerve (*r. bo*, fig. 95B). The third impression (*im. m. b4*, fig. 93D, E) finally, has such a position that it most likely was caused by a muscle corresponding to basicranial muscle 4 in urodeles, a condition which supports the view that the joint (*fi. ot. vp*) between *CV 3+4* and *CV 4+5* has been correctly identified. As indicated in the tentative restoration (fig. 99A) the myomere (*my5*) in metamere 5 probably had a basicranial portion (*m. b5*) as in urodeles (as regards the possible retention of a basicranial muscle in palaeoniscids see BJERRING, 1971).

Composition of median part of parasphenoid. – The vertebral segmentation in the basis cranii seems also to be reflected in the subdivisions of the median parts of the parasphenoid. As discussed above (p. 247) the prehypophysial portion of the median part of the parasphenoid (the primitive parasphenoid, JARVIK, 1954) in urodeles arises from a separate primordium (*P 1*, figs. 91, 96) situated underneath a part of the basis cranii that presumably is formed by cranial vertebra *CV 1*. Another parasphenoid primordium (*P 1+2*) arises in urodeles underneath the presumed cranial vertebra *CV 1+2*. This primordium in later ontogenetic stages forms a part of the parasphenoid which is very suggestive of the posthypophysial median part of the parasphenoid in porolepiforms (fig. 92A). This part is situated underneath the presumed cranial vertebra *CV 1+2* and extends backwards to the intracranial joint, that is the intrametameric vertebral joint in metamere 2. In view of these facts it is of interest that *Eusthenopteron* behind the corresponding part of the parasphenoid presents a paired dental plate, the subotic dental plate (JARVIK, 1954, p. 42, *Sodp*, figs. 22, 30) which extends backwards to the fissura oticalis ventralis anterior (*fi. ot. va*, fig. 99A), that is the presumed intrametameric vertebral joint in metamere 3. This plate (see *P 2+3*, figs. 92B, C, 96) is accordingly situated on the ventral side of cranial vertebra *CV 2+3* and it is tempting to assume that it is serially homologous with the pre- and posthypophysial parasphenoid primordia in urodeles. Behind the subotic plates in *Eusthenopteron* there are small dental plates (the suboccipital dental plates, JARVIK, 1954, p. 42, fig. 22, *Socdp*) on the ventral side of the posterior presumed cranial vertebrae but if their disposition reflects the supposed vertebral

segmentation is impossible to say. As explained in 1954 (pp. 68–69, figs. 38, 35) it is probably equivalents to these dental plates that form the posterior part of the parasphenoid in advanced actinopterygians and in other forms (e.g. in urodeles, see LEBEDKINA, 1964a) in which the parasphenoid "grows" backwards underneath the posterior part of the ventral side of the neural endocranium. A remarkable fact is that the parasphenoid in *Acipenser* extends backwards even underneath the vertebrae that have secondarily been plastered on to the hind end of the neural endocranium (DE BEER, 1937, pp. 94–95). This condition demonstrates the intimate relations between the median parts of the parasphenoid and the overlying vertebral column and supports the view advanced above that those ventro-median parts of the neural endocranium that are covered ventrally by the median part of the parasphenoid really represent cranial vertebrae.

Intermandibular division

The intermandibular division which includes the hyobranchial skeleton (the ventral parts of the visceral arches, the basibranchial series), the subbranchial series, exoskeletal elements in the mucous membranes and associated soft parts, has been subject of a thorough comparative analysis (JARVIK, 1963a; see also 1962 and 1963b). It was demonstrated that porolepiforms in this part of the head, exactly as in the snout, in a most remarkable way agree with urodeles and only with that group, and it was shown that the necessary prerequisites for the formation of a tongue of the type characteristic of urodeles were present in porolepiforms.

The most important characters common to porolepiforms and urodeles may be summarised as follows:

1. The fact that the basibranchial series consists of one basibranchial only (*Bb*, figs. 100, 101).

2. The fact that the posterior branchial arches, due to reduction in their distal (ventral) parts, do not reach the basibranchial but have developed secondary articulations with each other (figs. 100, 101).

In *Glyptolepis* (fig. 100 D) there are four (possibly five) branchial arches (*I–V*) behind the hyoid arch. The three anterior of these arches are complete ventrally and articulate with the basibranchial. But hypobranchial IV (*HbIV.v*) has become reduced in its ventral part and articulates with the middle part of hypobranchial III (*HbIII*) and an articulation has developed between hypobranchials III and II. In most larval urodeles (fig. 100 A, B) there are four branchial arches behind the hyoid but only two (*I, II*) articulate with the basibranchial. Hypobranchial IV has disappeared and ceratobranchial IV articulates with ceratobranchial III. In the most primitive urodeles (hynobiids, fig. 100 A) hypobranchial III (*HbIII.v*) is retained but in a little more advanced form such as *Salamandra* (fig. 100 B) it may be lacking

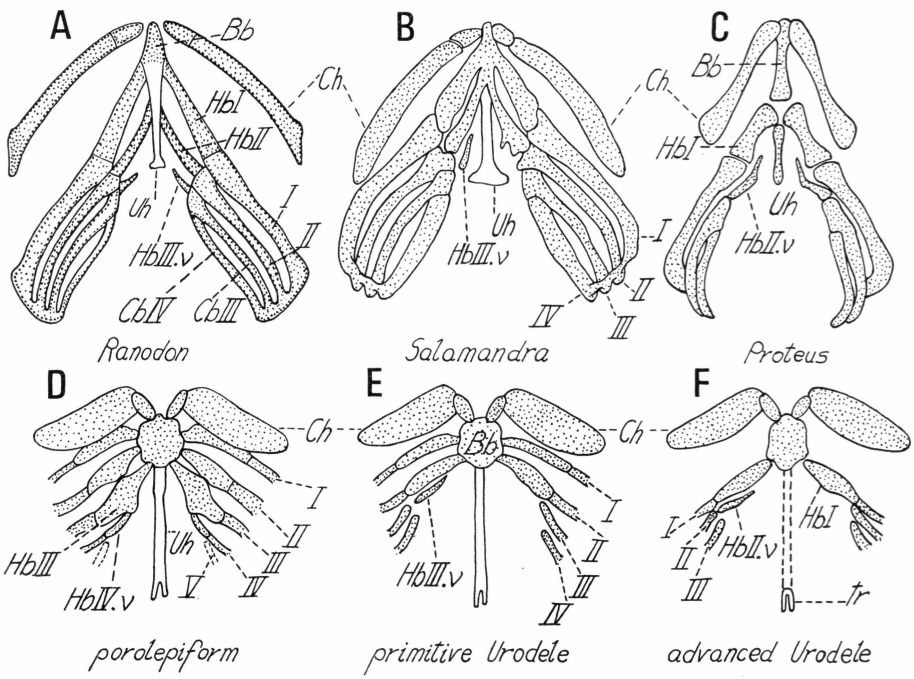


Fig. 100. *A–C*, hyobranchial skeleton and subbranchial series in three urodeles. *A*, *Ranodon sibiricus*, larva. Ventral aspect. From SEWERTZOFF, 1968, fig. 2A. *B*, *Salamandra maculosa*, larva ca 35 mm. Dorsal aspect. Compilation after KALLIUS, STADTMÜLLER and others, from JARVIK, 1962, fig. 5. *C*, *Proteus anguineus*, adult. Ventral aspect. After DOLIVO-DOBROVOLSKY, from STADTMÜLLER, 1936, fig. 504. *D–F*, diagrams illustrating changes in hyobranchial skeleton from a porolepiform to a primitive and an advanced urodele. From JARVIK, 1962, fig. 5.

Bb, basibranchial; *CbIII*, *CbIV*, ceratobranchials III and IV; *Ch*, ceratohyal; *HbI*, *HbII*, *HbIII*, hypobranchials of first, second, and third branchial arches; *HbII.v*, *HbIII.v*, *HbIV.v*, vestigial hypobrahcnials II, III, and IV; *Tr*, os triangulare; *Uh*, urohyal; *I–V*, ventral parts of post-hyoidean visceral arches *I–V*.

completely or may be represented either by a process of hypobranchial II or by a rod which in its distal part is associated with the middle part of hypobranchial II and is suggestive of hypobranchial IV in *Glyptolepis*. In those urodeles (*Necturus*, *Proteus*) which in these regards are most advanced there are only three branchial arches behind the hyoid and of them only one (*I*) reaches the basibranchial. Hypobranchial II (*HbII.v*) is vestigial and resembles hypobranchial IV (*HbIV.v*) in *Glyptolepis* and hypobranchial III (*HbIII.v*) in hynobiids and *Salamandra*.

As is thus evident the phylogeny of urodeles is distinguished by a gradual reduction of the branchial arches from behind, a process that has started already in their porolepiform ancestors, and as may be gathered also from figure 100 D–E the differences in the development of the hyobranchial skeleton between a primitive and an advanced urodele are of the same kind and not greater than between a primitive urodele and a porolepiform.

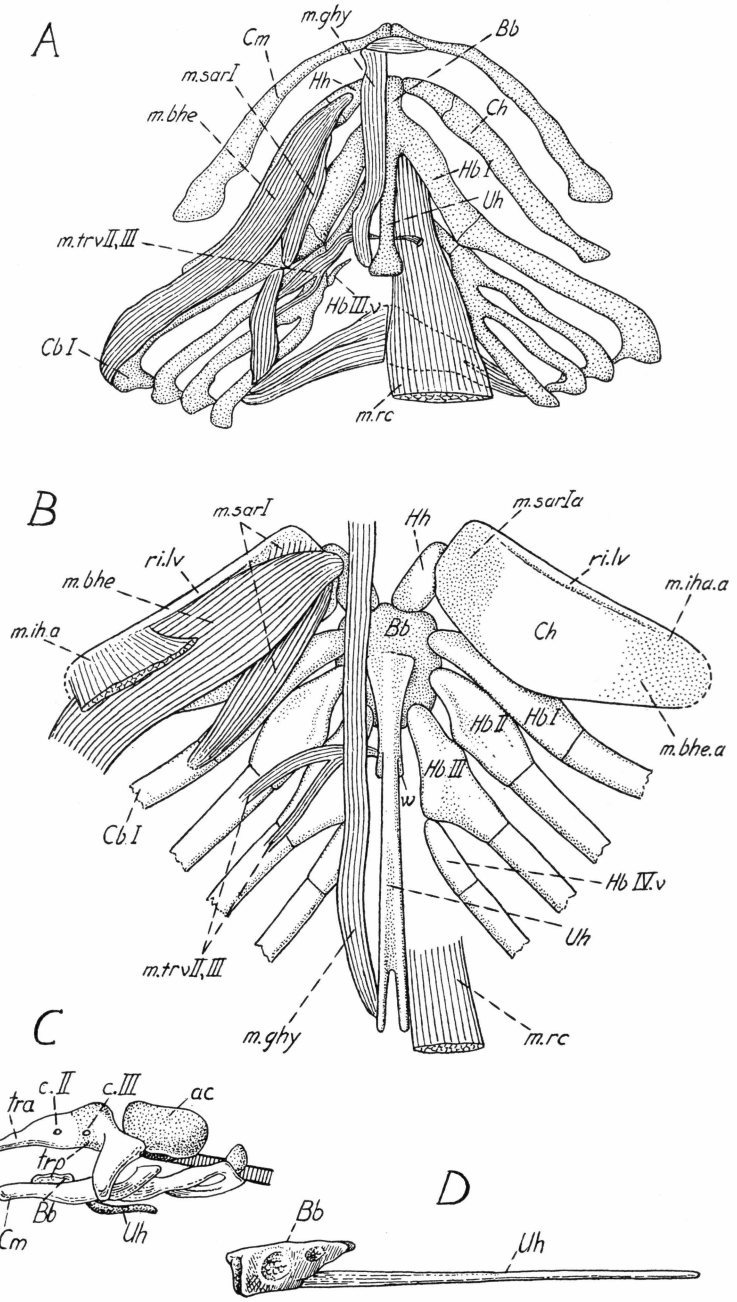


Fig. 101. *A*, *Hynobius nebulosus*, larva 22 mm. Lower jaws, hyobranchial skeleton and urohyal with certain muscles in ventral aspect. From Fox, 1959, fig. 32. *B*, *Glyptolepis groenlandica.* Hyobranchial skeleton and urohyal in ventral aspect with attempted restorations of certain muscles. From Jarvik, 1963a, fig. 18. *C*, *Ambystoma mexicanum.* Chondrocranium in lateral aspect. Basibranchial and urohyal partly con-

(cont. p. 260)

3. The fact that the external side of the ceratohyal in porolepiforms (in sharp contrast to osteolepiforms, fig. 29C) lacks teeth and shows impressions for the attachment of muscles clearly corresponding to those in urodele larvae (figs. 29A, 101A, B).

One such impression (*m. sarIa*) is situated exactly as the area of attachment of the m. subarcualis rectus (*m. sarI*) in urodeles and there are strong indications that there was also a large muscle corresponding to the m. branchiohyoideus externus (*m. bhe*), a muscle with among recent vertebrates has been encountered with certainty only in larvae of urodeles (1963a, pp. 20–21).

4. The fact that the subbranchial series consists of a single element, the urohyal (*Uh*, fig. 101).

5. The fact that the urohyal is a long narrow rod which also in porolepiforms may fuse anteriorly with the ventral side of the basibranchial. The posterior end (os terminale, *Tr*, in adult urodeles) is in certain urodeles bifurcate as in *Glyptolepis* (figs. 100, 101).

6. The fact that there in porolepiforms is a crescent-shaped field of lacunous, irregular dental plates, the prolingual field (*plf*), in the most anterior part of the floor of the mouth cavity situated exactly as, and no doubt homologous with, the glandular field of Kallius (*glf*) in larval urodeles (figs. 102, 103).

The structure and shape of the prolingual dental plates suggest that glands were present in this field already in porolepiforms. This peculiar glandular field, which has no equivalent in the osteolepiform-tetrapod stock, plays an important part in the formation of the tongue in urodeles (fig. 102C, D; JARVIK, 1963a, pp. 31–35; see also YAMASAKI, 1956).

7. The fact that the lower jaw in porolepiforms anteriorly shows a field of solid dental plates, the medial mandibular field (*mmf*), situated as, and no doubt homologous with, the so-called operculare ("*Op*"), a tooth-bearing dermal bone which among recent vertebrates has been found only in larvae of urodeles (figs. 102, 103).

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cealed by meckelian cartilage. Cartilage of endomesodermal origin dotted. After HÖRSTADIUS & SELLMAN, from JARVIK, 1954, fig. 11C. *D*, *Glyptolepis groenlandica*. Basibranchial and subbranchial series in lateral aspect. From JARVIK, 1963a, fig. 16B.

Bb, basibranchial; *CbI*, ceratobranchial I; *Ch*, ceratohyal; *Cm*, ceratomandibular (meckelian cartilage); *HbI–HbIII*, hypobranchials I–III; *HbIII.v*, *HbIV.v*, vestigial hypobranchials III and IV; *Hh*, hypohyal; *Uh*, urohyal.

ac, auditory capsule; *c. II*, *c. III*, canals for optic and oculomotor nerves; *m. bh.e*, musculus branchiohyoideus externus; *m. bhe.a*, area of attachment of ditto; *m. ghy*, m. geniohyoideus; *m. iha*, m. interhyoideus anterior; *m. iha. a*, area of attachment of ditto; *m. rc*, m. rectus cervicis; *m. sarI*, m. subarcualis rectus; *m. sarIa*, area of attachment of ditto; *m. trvII*, *III*, m. transversalis ventralis II and III; *ri. lv*, ventral lateral ridge of ceratohyal; *tra*, *trp*, anterior ectomesenchymatic and posterior endomesodermal portions of "trabecula"; *w*, wing-like projection of urohyal.

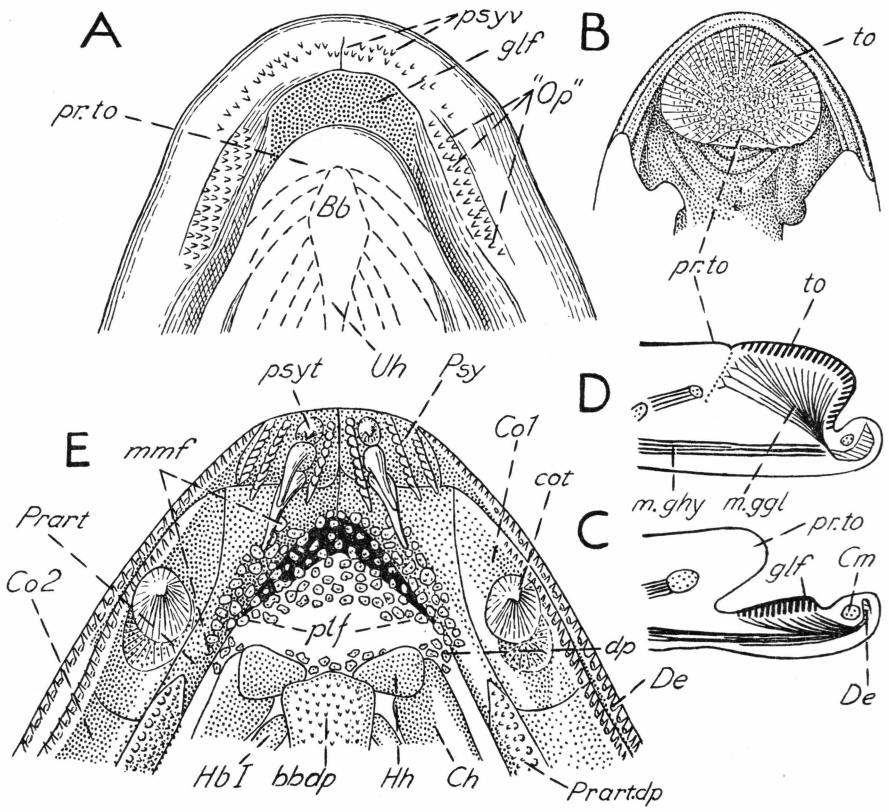


Fig. 102. *A–D*, evolution of tongue in urodeles. *A*, *Triturus punctatus*, 19 mm. Anterior parts of lower jaws and floor of mouth cavity in dorsal aspect. Mainly after specimen in fig. 103A. From JARVIK, 1963a, fig. 15C. *B*, *Salamandra maculosa*, adult. Tongue in dorsal aspect. After KALLIUS, from JARVIK, 1963a, fig. 26. *C*, *D*, diagrammatic longitudinal sections through floor of mouth cavity of urodele to illustrate two stages in development of tongue. *C*, about same stage as in *A*; *D*, nearly adult. After KALLIUS, from JARVIK, 1963a, fig. 15D. *E*, holoptychiid porolepiform. Restoration of anterior parts of lower jaws and skeleton of intermandibular division in dorsal aspect. From JARVIK, 1963a, fig. 15A. Slightly modified.

Bb, basibranchial; *Ch*, ceratohyal; *Cm*, ceratomandibular (meckelian cartilage); *Co1*, *Co2*, coronoids 1 and 2; *De*, dentary; *HbI*, hypobranchial I; *Hh*, hypohyal; "*Op*", so-called operculare or goniale of urodele larvae, probably homologous with medial mandibular field of dental plates in porolepiforms; *Prart*, prearticular; *Prart. dp*, prearticular dental plate; *Psy*, parasymphysial dental plate; *Uh*, urohyal.

bbdp, dental plates of dorsal side of basibranchial; *cot*, coronoid tusk; *dp*, dental plates; *glf*, glandular field, probably corresponding to prolingual field in porolepiforms; *m. ggl*, musculus genioglossus; *m. ghy*, m. geniohyoideus; *mmf*, medial mandibular field of dental plates; *plf*, prolingual field of dental plates; *pr. to*, primitive tongue; *psyt*, row of sigmoid tusks of parasymphysial dental plate; *psyv*, area with teeth, possibly representing vestige of parasymphysial dental plate of porolepiforms; *to*, part of tongue of adult formed from glandular field.

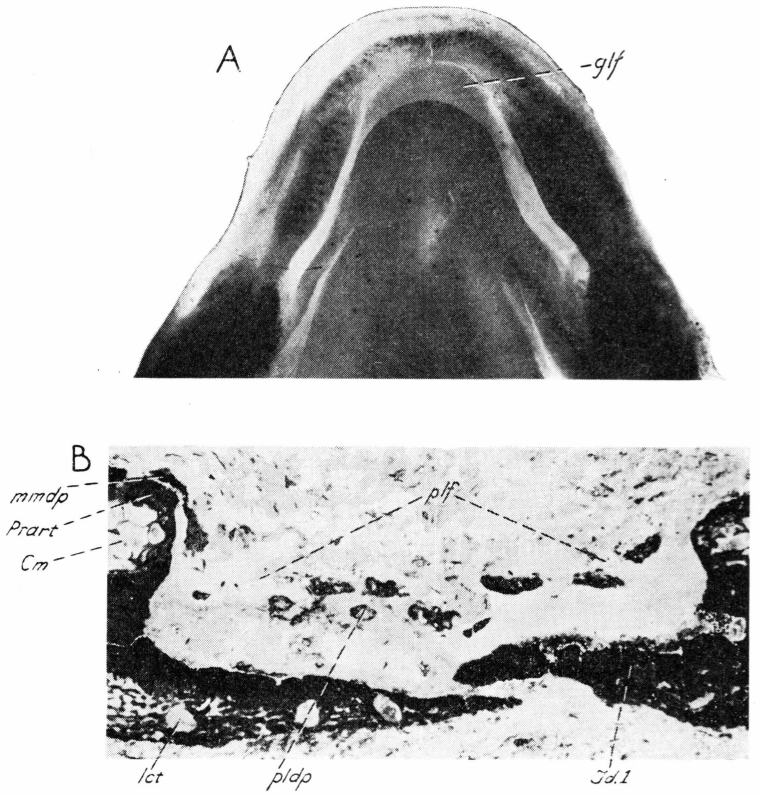


Fig. 103. *A*, *Triturus punctatus*, 19 mm. Photograph of anterior part of lower jaws and intermandibular division to illustrate glandular field and other structural details shown in fig. 102A. In glycerin. *B*, *Glyptolepis groenlandica*. Transverse section through prolingual field. Section No. 67 of grinding series. From JARVIK, 1963a, fig. 13.

Cm, ceratomandibular; *Id. 1*, infradentary 1; *Prart*, prearticular. *glf*, glandular field; *lct*, tube of sensory canal; *mmdp*, medial mandibular dental plate; *pldp*, prolingual dental plate with cavity, probably for gland; *plf*, prolingual field of dental plates.

All these facts (1–7) taken together and the fact that porolepiforms in most of these respects show specialisations encountered elsewhere only in larvae of urodeles strongly support the view that urodeles are more closely related to porolepiforms than to any other vertebrates. As a matter of fact in the structure of the intermandibular division as a whole, larval urodeles (fig. 102A) agree more closely with porolepiforms (fig. 102E) than with adult urodeles (fig. 102B).

External dermal bones of head

The external dermal bones of the skull in urodeles and anurans are fewer in number than in their piscine ancestors and in each of these groups they form a pattern that is subject to but small variations and accordingly is characteristic of the group. However, embryological investigations have revealed that many of the dermal bones are composite (see also pp. 147–150) and by combining evidence provided by several students I have recently demonstrated (1967b, 1968b) that the dermal bones of the cranial roof in anurans are more numerous than has generally been believed and that they are arranged in a pattern that in all fundamental respects agrees with that characteristic of osteolepiforms (fig. 104A, B). This fact and other similarities between anurans and osteolepiforms show that the osteolepiform frontal (*Fr*) is a true frontal homologous with that in anurans and other eutetrapods (not a parietal as claimed by WESTOLL, ROMER and PARRINGTON), and that the osteolepiform parietal (*Pa*) is a true parietal (not a postparietal).

In urodeles (see WIEDERSHEIM, 1877; STADTMÜLLER, 1936; and others) the main posterior part of the dermal cranial roof is formed by two large paired bones generally referred to as frontal and parietal (fig. 105C). In contrast to anurans these bones are always separate and other characteristic features are that the parietal (*Pa. u*) extends forwards about to the middle of the orbitotemporal region and that also the frontal (*Fr. u*) has become prolonged forwards. A considerable anterior part of the latter lies dorsally to the ethmoidal region and the bone often meets, or is overlapped by, the processus facialis of the premaxillary (as to the remarkable differences between urodeles and anurans in the growth of the dermal bones of the cranial roof see LEBEDKINA, 1968a, b).

As far as I know no subdivisions of the frontal or the parietal have been observed in adult urodeles. It is therefore interesting that LEBEDKINA (according to SCHMALHAUSEN, 1964, 1968, pp. 221–222) recently has established that these bones arise from several primordia (see also p. 149). Referring to LEBEDKINA, SCHMALHAUSEN says that "the frontal in *Ranodon* shows traces of complex origin of from three to four components". Moreover, behind the primordium of the parietal (*Pa. u*, fig. 104D) arises a separate bone (*StExt*) which as suggested by SCHMALHAUSEN probably is a supratemporal to which extrascapulars ("postparietals") have fused. This larval supratemporoextrascapular later fuses with the parietal primordium forming the so-called parietal of the adult. The conditions are still too imperfectly known to permit a safe comparison with porolepiforms (fig. 104C) but one likely possibility is that the parietal primordium corresponds to the porolepiform parietointertemporal (*PaIt*) and that primordium *StExt* includes equivalents of

the supratemporal (*St*), the lateral extrascapular (*Ext. l*) and possibly the extratemporal (*Et*). This assumption is to some extent supported by the following conditions (as regards the pit-lines of the skull-roof see p. 271).

In *Porolepis* (figs. 20A, 43), in which the parietal shield is comparatively short, this shield and the underlying part of the otoccipital end anteriorly behind the connection between the ascending process of the palatoquadrate and the suprapterygoid process (*pr. sp*) of the ethmosphenoid. This means that the frontal-parietal boundary, or we may also say the dorsal part of the intracranial joint, is situated about as in *Eusthenopteron* (figs. 104A, 105A). But in *Glyptolepis* (fig. 104C) and in particular in *Holoptychius* (figs. 20B, 61B, 105B) the dorsal part of the intracranial joint has moved forwards so that the frontal-parietal boundary is found far in front of the connection between the ascending and suprapterygoid processes, dorsally to the opticus canal (*c. II*). In other words the "parietal" in advanced porolepiforms extends about as far forwards as the parietal (*Pa. u*, fig. 105C) in urodeles, and as stressed elsewhere (1962, p. 91) also in this respect there is a remarkable agreement between porolepiforms and urodeles.

The frontal in urodeles arises above the middle part of the orbitotemporal region (ERDMANN, 1933; SRINIVASACHAR, 1962; LEBEDKINA, 1968a, 1968b) as does the frontal also in other extant tetrapods, and as it, judging from the position of the centre of radiation, did in porolepiforms and osteolepiforms (fig. 104A, C). It thus arises as a typical frontal (see JARVIK, 1967b) but later in ontogeny (see LEBEDKINA, 1968b) it "grows" forwards above the ethmoidal region (*Fr. u*, fig. 104D) and in the adult the anterior part of the bone occupies an area of the cranial roof that in porolepiforms is formed by the pineal plate, postrostrals and

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Fig. 104. *A*, *B*, representations to demonstrate similarities in number and relations to neural endocranium of dermal bones of skull-roof between, *A*, Devonian osteolepiforms (*Eusthenopteron foordi*) and, *B*, recent anurans. Place of origin of dermal bones marked with x. From JARVIK, 1968b, fig. 2. *C*, *Glyptolepis groenlandica*. Combination of figures 27 and 38 to show position of dermal bones of skull-roof in relation to neural endocranium. *D*, *Ranodon sibiricus*, larva 26 mm. Skull in dorsal view to show primordia of dermal bones of skull-roof. After LEBEDKINA, from SCHMALHAUSEN, 1964, fig. 133 (1968, fig. 131).

Et, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapular; *Fr*, frontal; *FrD*, frontodermosphenotic; *Fr. u*, larval urodele frontal; *It*, intertemporal; *Na*, nasal; *Pa*, parietal, *PaIt*, parietointertemporal; *Pa. u*, larval urodele parietalt *Pi. pl*, pineal plate; *Ptrp*, posterior median postrostral; *Rl*, lateral rostral (equivalen, to septomaxillary in Osteolepiform-Tetrapod stock); *Smx*, septomaxillary; *Sq*-squamosal; *St*, supratemporal; *StExt*, presumed supratemporoextrascapular.

a. occ, occipital artery; *c. a. occ*, canal for occipital artery; *cr. par*, crista parotica; *fo. br*, fossa bridgei; *f. pin*, pineal foramen; *gr. a. occ*, groove for occipital artery; *my5*, myomere 5.

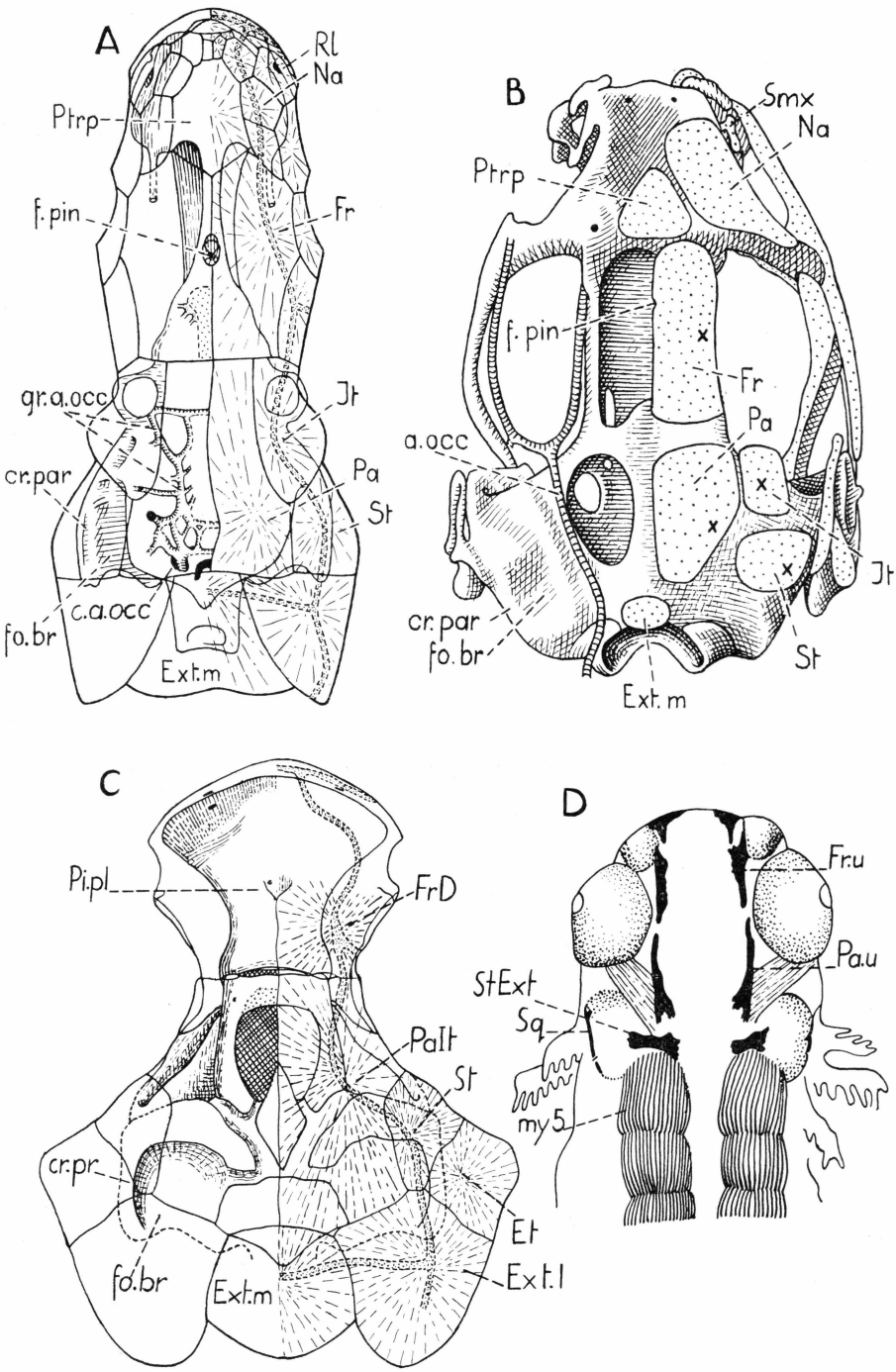

A
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Fig. 104.

nasals. This origin and mode of growth of the so-called frontal in urodeles shows that it cannot be a nasal that has migrated in a posterior direction from the ethmoidal to the orbitotemporal region as claimed by WESTOLL and ROMER (see JARVIK, 1967b, p. 184). But if it has become gradually prolonged forwards (as has possibly the parietointertemporal within the porolepiforms; see, however, JARVIK, 1967b, fig. 7), or if the incorporation of postrostrals and nasals is reflected in the ontogeny is at present impossible to say.

The nasal in urodeles arises from two separate primordia (LEBEDKINA, 1964b; SCHMALHAUSEN, 1968, p. 222) but to which extent equivalents to the porolepiform postrostrals, nasal and tectals enter into the formation of the bone is also difficult to decide. The composition of the prefrontal (*Pfr*, fig. 105C), too, is difficult to make out and if a prenasal (ERDMANN, 1933) really exists remains uncertain (see DE BEER, 1937, p. 185; JARVIK, 1942, p. 415). The premaxillary of urodeles is, like the porolepiform rostropremaxillary, composed morphologically of three parts, pars dentalis (*Pmxd*, fig. 77), pars facialis (*Pmxf*), and pars palatina (*Pmxp*), and the nariodal (*Nd*) is very similar in the two groups (see pp. 190–192).

The lachrymal (*La*) in porolepiforms (and osteolepiforms, fig. 79A, D) belongs to the palatoquadrate-cheek complex. However, as described above (p. 104) the anterior part of the bone in *Glyptolepis* rests on the lateral side of the neural endocranium and as explained elsewhere (JARVIK, 1942, pp. 407–408) it is mainly this anterior part of the bone that has been retained in certain primitive urodeles and forms the lachrymal (fig. 79F,G). The posterior part has become reduced as have apparently also the jugal, the postorbital and the prespiracular plate. The quadratojugal (*Qj*) is retained in urodeles (see STADTMÜLLER, 1936). The maxillary (*Mx*) also in porolepiforms has a palatal lamina (p. 109; cf. JARVIK, 1942, p. 414). The squamosal (*Sq*) in urodeles (fig. 105C,E; see STADTMÜLLER, 1936; according to HOLMGREN, 1949, this bone is homologous with the opercular in dipnoans) arises outside the posterior part of the palatoquadrate and judging from its position it corresponds either to the preopercular (*Pop*) or to the upper squamosal (*Sq. u*) in porolepiforms (figs. 43–45), but may also include equivalents of both these bones. The fact that the bone extends upwards to the auditory capsule is easily accounted for if it is true that the processus oticus of the palatoquadrate in urodeles is a double formation (see pp. 215–217).

In the lower jaw of urodeles (see STADTMÜLLER, 1936) the dermal bones have also become much reduced and generally there are only two bones, the dentary and the prearticular ("gonial", STADTMÜLLER, 1936, "angular", HERTWIG, 1874; WIEDERSHEIM, 1877; GAUPP, 1905). However, if we turn to the hynobiids, and in particular to their larvae we will find a considerable agreement with porolepiforms.

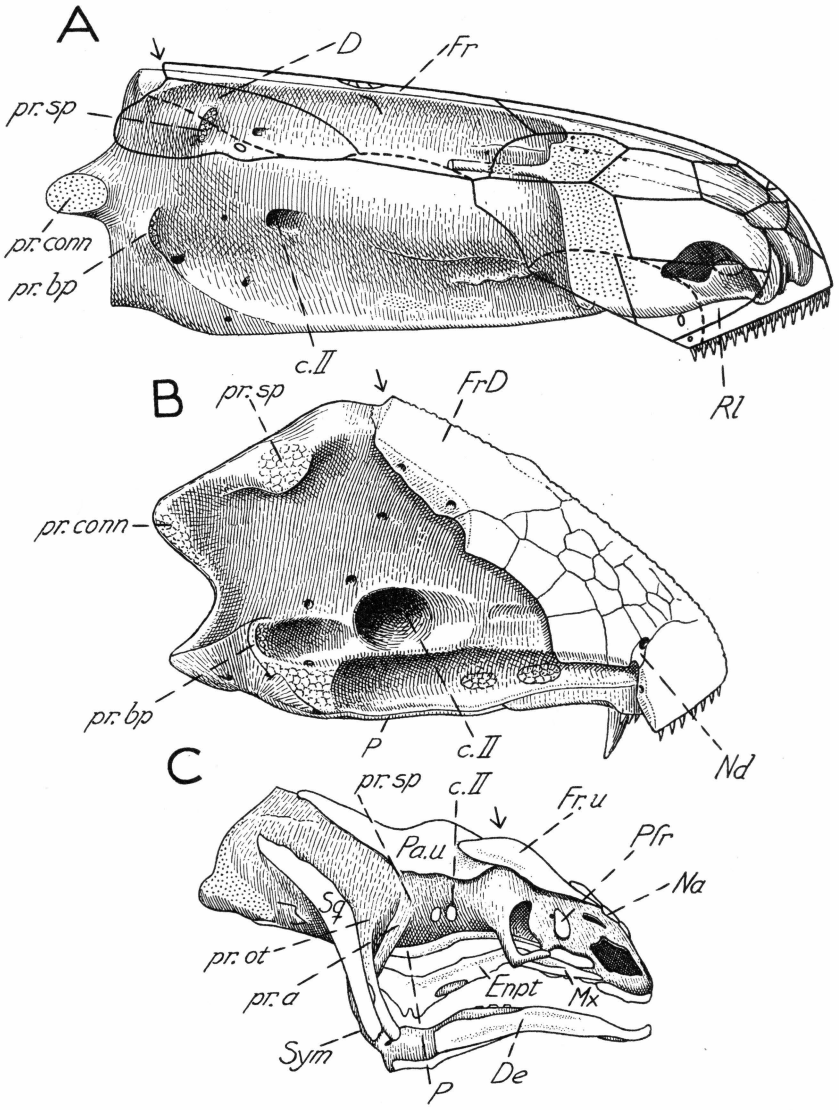


Fig. 105. Three drawings to illustrate variations in position of parietal-frontal boundary (indicated with an arrow). In early porolepiforms (*Porolepis*, fig. 20 A) as in, *A*, osteolepiforms (*Eusthenopteron foordi*) this boundary lies behind suprapterygoid process and far behind level of opticus canal, whereas it in, *B*, advanced porolepiforms (*Holoptychius* sp. cf. fig. 20 B) and, *C*, urodeles lies in front of suprapterygoid process and above or in front of level of opticus canal. *C*, *Salamandra maculosa*, larva 35 mm. Skull in lateral aspect. From STADTMÜLLER, 1924, fig. 5.

D, dermosphenotic; *De*, dentary; *Enpt*, entopterygoid; *Fr*, frontal; *FrD*, frontodermosphenotic; *Fr. u*, urodele frontal; *Mx*, maxillary; *Na*, nasal; *Nd*, nariodal; *P*, parasphenoid; *Pa. u*, urodele parietal; *Pfr*, prefrontal; *Rl*, lateral rostral; *Sq*, squamosal; *Sym*, symplectic (processus hyoideus).

c. II, opticus canal; *pr. a*, processus ascendens palatoquadrati; *pr. bp*, basipterygoid process (not represented in urodeles); *pr. conn*, processus connectens; *pr. ot*, processus oticus; *pr. sp*, suprapterygoid process or its equivalent in urodeles.

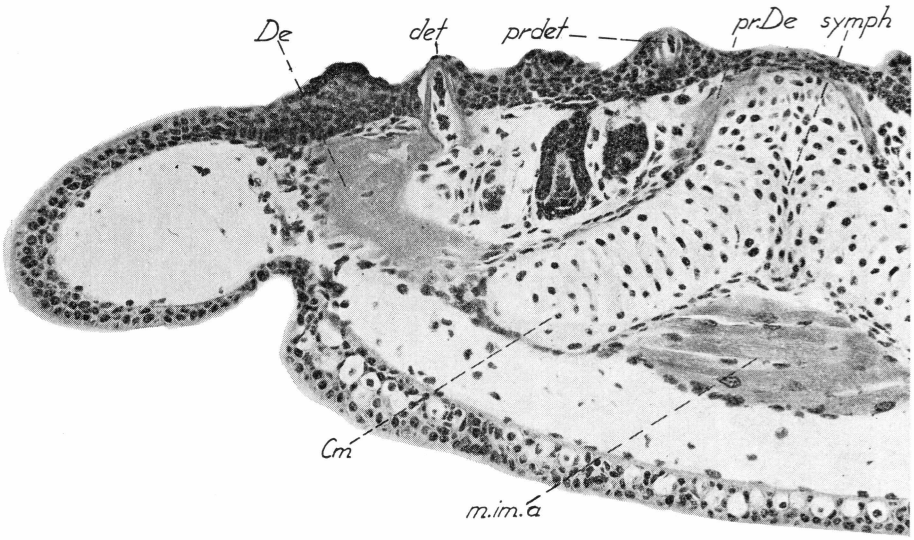


Fig. 106. *Hynobius retardatus*, larva 33 mm. Photograph of transverse section through lower jaw symphysis to show parasymphysial process of dentary. From BJERRING (unpublished). × 100/1.

Cm, ceratomandibular (meckelian cartilage); *De*, dentary.

det, dentary tooth; *m. im. a*, musculus intermandibularis anterior; *pr. De*, parasymphysial process of dentary; *prdet*, tooth of parasymphysial process; *symph*, symphysis.

The dentary (*De*) in urodeles (figs. 105, 106) arises on the anterior part of the lateral side of the meckelian cartilage (*Cm*) and grows mainly backwards (ERDMANN, 1933; see also HERTWIG, 1874, pl. 4:29) which is in agreement with the fact that the centre of radiation of the dentary in porolepiforms (and osteolepiforms) lies very far forwards in the bone (figs. 44, 45, JARVIK, 1944a). As recently discovered by BJERRING (unpublished) the dentary in larvae of *Hynobius retardatus* most anteriorly (fig. 106), close to the symphysis (*symph*), has a fairly strong posterior process (*pr. De*) situated much as the antero-medial lamina (*la. De*) of the dentary in porolepiforms (fig. 47), which carries the parasymphysial dental plate (*Psy*). In larvae of *Hynobius* BJERRING found only one tooth primordium (*prdet*) dorsally to that process, but in *Triturus* (figs. 102A, 103A) there seems to be several teeth (*psyo*) in the corresponding area; and because these teeth show a tendency to be arranged in longitudinal rows I have tentatively suggested (1962, pp. 93–94, 1963a, fig. 15C) that they may be vestiges of the teeth of the parasymphysial dental plate in porolepiforms. Behind the symphysis, on the medial side of the meckelian cartilage, lies in larvae of urodeles the so-called operculare ("Op") which as mentioned above (p. 85) in porolepiforms is represented by the medial mandibular field (*mmf*) of dental plates. The area between this

field and the dentary (*De*) is in porolepiforms occupied by the coronoid series (*Co 1*, *Co 2*, figs. 76B, 102C). In urodeles there are no coronoids but in the corresponding area in larvae of *H. retardatus* (fig. 76A), that is between the "operculare" and the dentary, BJERRING found dense connective tissue (*ti. Co*) of the same type as that in which the dermal bones are formed, and it seems likely that this dense tissue represents a vestige of the coronoids although no ossification occurs. Another surprising discovery made by BJERRING is that the "angular" (STADTMÜLLER, 1936, p. 654), which among urodeles seems to be represented only in hynobiids, in *H. retardatus* arises from three separate primordia. These primordia, which in the 33 mm stage have fused into a single bone, form a row along the ventral side of the meckelian cartilage, and judging from their position and forward extent they most likely correspond to infradentaries 2, 3 and 4 in porolepiforms (and osteolepiforms).

The dermal bones of the lower jaw in urodeles are obviously more numerous than hitherto has been known. Besides the dentary laterally and the prearticular medially, there may also be three infradentaries ventrally, and vestiges of the coronoid series dorsally, to the meckelian cartilage. All these elements are represented in both porolepiforms and osteolepiforms which in this respect are similar. But in porolepiforms there is, in addition, a medial mandibular field of dental plates (*mmf*) which corresponds to the urodelan "operculare", an element which has no equivalent in osteolepiforms or anurans, and moreover the parasymphysial dental plates are possibly represented by vestiges in larvae of certain urodeles. These facts, too, are in accordance with and support the view that urodeles and porolepiforms are closely related.

Sensory lines

The urodeles have no sensory canals but scattered neuromasts in the skin. In early larval stages when the neuromasts still are comparatively few they often form distinct simple rows or are arranged in linear fields. It is therefore possible to make out the sensory line system with a reasonable degree of certainty and it is fairly easy to see which lines that correspond to sensory canals in osteolepiforms and porolepiforms and which represent pit-lines. The restorations of the sensory lines in urodeles recently published by SCHMALHAUSEN (1968, figs. 93, 94) are based on the conditions in early larval stages of *Ranodon* (SCHMALHAUSEN, 1955b). In the slightly modified version of one of these restorations shown in figure 107B certain observations by SCHMALHAUSEN (1957a) as to the supposed equivalents of pit-lines in the skull-roof in *Hynobius* have been included, and the course of the pit-lines of the cheek have been changed a little in accordance with the conditions in some of

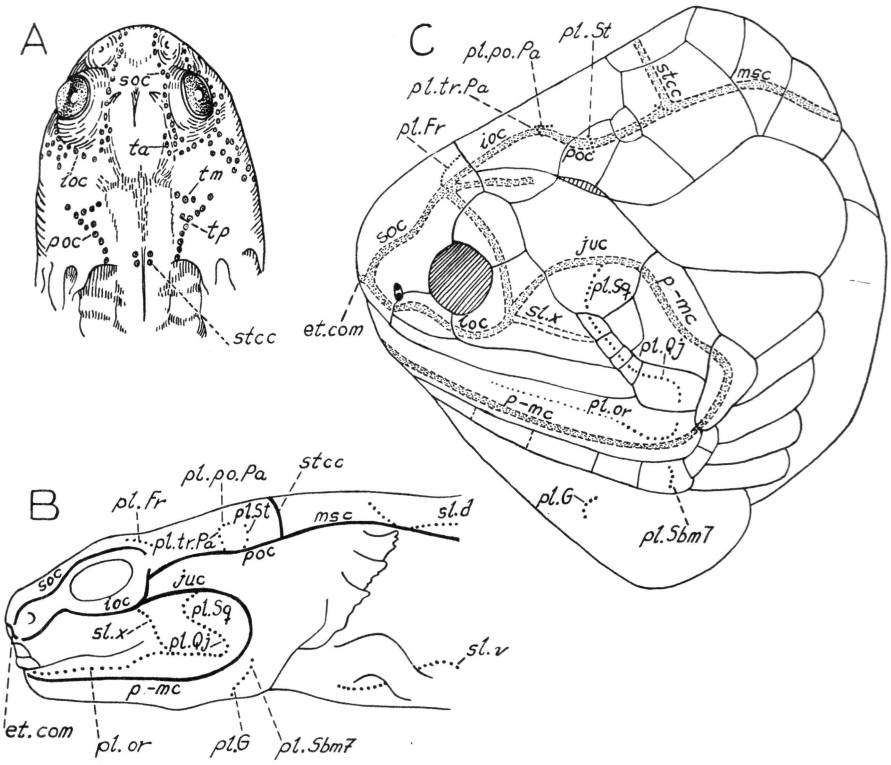


Fig. 107. Drawings to demonstrate similar arrangement of sensory lines of head between, *A*, *B*, urodeles and, *C*, porolepiforms. *A*, *Hynobius keyserlingii*, larva 16 mm. Head in dorsal aspect. From SCHMALHAUSEN, 1957a, fig. 4. *B*, arrangement of sensory lines of head in hynobiid urodele in lateral aspect. From SCHMALHAUSEN, 1955b, fig. 20 (1968, fig. 94). Slightly modified. *C*, *Holoptychius* sp. Head in lateral aspect. From JARVIK, 1948a, fig. 33B. Modified.

et. com, ethmoidal commissural canal; *ioc*, *juc*, *msc*, infraorbital, jugal, and main sensory canals; *pl. Fr*, frontal pit-line; *pl. G*, pit-line of principal gular; *pl. or*, oral pit-line; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. Qj*, quadratojugal pit-line; *pl. Sbm7*, pit-line of submandibular 7; *pl.Sq*, *pl. St*, squamosal and supratemporal pit-lines; *pl. tr. Pa*, transverse parietal pit-line; *p-mc*, *poc*, *soc*, preoperculomandibular, postotic, and supraorbital sensory canals; *sl. d*, *sl. v*, dorsal and ventral sensory lines of body; *sl. x*, anterior jugal line (SCHMALHAUSEN); *stcc*, supratemporal commissural canal; *ta*, *tm*, *tp*, anterior, middle and posterior pit-lines (SCHMALHAUSEN = frontal, parietal and supratemporal pit-lines).

the specimens figured by SCHMALHAUSEN (1955b, 1957a). With these small changes we will find that the sensory line system of the head (and the anterior part of the body) on the whole is very similar to that in porolepiforms and osteolepiforms. However, there are certain differences between these two groups of fishes (see pp. 132–137, 158) and again we find that it is with porolepiforms but not with osteolepiforms that the urode-

les agree. The following similarities supporting the view of relationship between porolepiforms and urodeles may be mentioned (fig. 107).

1. The neuromasts of the anterior part of the infraorbital sensory line, that is in the main the ethmoidal commissure (*et. com*), are innervated by buccalis branches that pass forwards medially to the choana (see p. 183).

2. The infraorbital line bends distinctly downwards antero-ventrally to the eye (see pp. 153, 195).

3. The similar position of the pit-lines of the cranial roof. Of particular importance is that that pit-line *tm* of SCHMALHAUSEN which probably includes the equivalents of the parietal pit-lines (*pl. tr. Pa*, *pl. po. Pa*) in porolepiforms is situated in front of pit-line *tp* which corresponds to the supratemporal pit-line (*pl. St*) in porolepiforms.

4. In one specimen of *Holoptychius* in which the squamosal and quadratojugal pit-lines are represented by a canal there seems to be a connection between this canal and the infraorbital canal (JARVIK, 1948a, p. 130, figs. 33B, 34; cf. STENSIÖ, 1947, figs. 20A, 29A, hc_1). If this connection really exists it may, as suggested by STENSIÖ (1947, fig. 29A, F), correspond to sensory line *ja* of SCHMALHAUSEN (*sl. x*, fig. 107B, C; j_1 HOLMGREN & PEHRSON, 1949, fig. 21).

VI. SUMMARY AND CONCLUSIONS

The Porolepiformes are a distinct group of fossil fishes which previously have generally been brought together with other groups (Osteolepiformes, Struniiformes, Coelacanthiformes) with an intracranial joint into a common systematic unit, the Crossopterygii.

The present study of the structure of the head of the Porolepiformes is based on almost all the relevant fossil material of this group known so far. Besides specimens from Great Britain, the Baltic area and Escuminac Bay the material includes large collections from the Lower Devonian of Spitsbergen and from the Middle and Upper Devonian of East Greenland. Of particular importance have been the excellent specimens of *Glyptolepis groenlandica* n. sp which in 1956 were found in the Middle Devonian deposits of Canning Land, East Greenland, and the grinding series of the head of one of these specimens that has been in progress since 1959.

On the basis of this large and on the whole well preserved fossil material an almost complete and partly very detailed description of the head and exoskeletal shoulder-girdle in the Porolepiformes has been given. Only the posterior parts of the braincase (otic capsules and postero-ventral ossification) and the dorsal parts of the post-hyoidean branchial arches which are contained in the yet unsectioned part of the skull of *G. groenlandica* are still imperfectly known.

Most of the new facts presented in the "Descriptive section" will be recorded below in connection with the comparisons with the Osteolepiformes and the Urodela, comparisons that now can be carried out on a much broader basis than hitherto has been possible. Moreover the much widened knowledge of the anatomy of the head not only of the Porolepiformes but also of the Osteolepiformes together with the important results gained by the embryologists during the last few decades have afforded new possibilities to attack the old problems as to the origin, composition and metamerism of the vertebrate skull, and attempts have been made to interpret the non-visceral parts of the braincase in terms of cranial vertebrae. Furthermore new interpretations of the urodele chondrocranium and of the median parts of the parasphenoid have been presented.

The main results may be summarised as follows:

Porolepiformes and Osteolepiformes

1. The accepted porolepiform genera, *Porolepis* (Lower Devonian), *Glyptolepis* (mainly Middle Devonian), and *Holoptychius* (Upper Devonian), and as far as they are known the remaining two Devonian genera *Heimenia* and *Laccognathus*, agree closely with each other in the structure of the skull, and disregarding the cosmine layer it is hardly possible to distinguish safely between the Porolepidae and the Holoptychiidae on the basis of cranial characters. The Porolepiformes are a most distinct and homogenous group of fishes.

2. As unequivocally demonstrated by all reliable and well documented investigations the Osteolepiformes, too, are a most distinct group and also in this group the differences in the head between the two accepted families, the Osteolepidae and the Rhizodontidae, refer mainly to the cosmine layer.

3. The most striking similarities between porolepiforms and osteolepiforms refer to characters (such as the intracranial joint), which for good reasons may be suspected to be primitive and which besides are shared with other groups. Whether also the choana is such a primitive feature or if it has arisen independently in the two groups is still an open question.

4. The common characters of porolepiforms and osteolepiforms indicating relationship are few. The most striking similarities of this kind are found in the lower jaw and in the antero-ventral part of the submandibular series, but there are also general similarities in the disposition of the dermal bones as whole, the pattern of the sensory line system, and the dentition; undoubtedly, porolepiforms and osteolepiforms are closer related to each other than to any other contemporaneous group of fishes and most likely they descended from a common ancestor. However, there are fundamental differences and because most of the specialisations characteristic of porolepiforms were developed as early as in the Lower Devonian it is evident that the two groups came into existence far back in pre-Devonian times.

5. One well-known difference between porolepiforms and osteolepiforms refers to the external shape of the paired fins. It has been shown that there is a corresponding great difference in the development of the endoskeleton of the pectoral fin and for that reason alone it is necessary to place porolepiforms and osteolepiforms in separate groups of a high systematic rank.

6. The exoskeletal shoulder-girdle has in each group a characteristic structure and it is easy to decide if isolated cleithra or clavicles pertain to a porolepiform or an osteolepiform.

7. The median extrascapular in porolepiforms overlaps, but is in

osteolepiforms overlapped by, the lateral extrascapular. The significance of this difference is unknown.

8. The view advanced by WESTOLL and supported by ROMER, PARRINGTON, and others that the frontal in osteolepiforms is a parietal and the parietal a postparietal, discussed and refuted in a previous paper (JARVIK, 1967b), is inconsistent also with the new facts presented in this paper (pp. 147–150, 266).

9. The fact that the area of the parietal shield, which in osteolepiforms is occupied by the parietal and the intertemporal, in porolepiforms shows a single large bone has been discussed and partly on the basis of new facts it has been concluded that this bone most likely is a compound parietointertemporal.

10. The posterior principal element of the fronto-ethmoidal shield in porolepiforms corresponds to the frontal and dermosphenotic in osteolepiforms and is probably a compound frontodermosphenotic.

11. In porolepiforms there is a single pineal plate, but no pineal foramen. The early osteolepiforms have a pineal foramen surrounded by a ring of small pineal plates. The fact that the pineal foramen in certain advanced osteolepiforms is lacking is due to secondary changes.

12. In porolepiforms there is a median rostral pierced by the ethmoidal commissure, whereas the lateral rostral components have fused with the premaxillary into a compound rostropremaxillary. In osteolepiforms, on the other hand, there is an independent lateral rostral, and in this group there are medial rostral components that have fused with the premaxillary. Moreover the complex bone thus formed generally includes nasal components and is a nasorostropremaxillary.

13. The lateral rostral in osteolepiforms is a highly specialised structure consisting of a pars facialis pierced by the infraorbital sensory canal, a pars palatina, and a large processus dermintermedius extending far into the cavity of the nasal capsule. This element has no equivalent in porolepiforms. The view held by PANCHEN and others that the lateral rostral is homologous with the porolepiform nariodal is rejected. No structure corresponding to the inwardly directed process of the anterior tectal in osteolepiforms is developed in porolepiforms.

14. In porolepiforms there are two openings in the exoskeleton for external nasal tubes, the fenestra exonarina anterior and the fenestra exonarina posterior, the latter bounded posteriorly by a notch in the lachrymal. These openings are separated by a small dermal bone, the nariodal, modified for this special purpose. No such bone exists in osteolepiforms in which the fenestra exonarina posterior and accordingly also the notch in the lachrymal are lacking.

15. The external cheek-plate in porolepiforms presents a large prespiracular plate and there are one upper and two or more lower squa-

mosals. Osteolepiforms always have a single squamosal and lack prespiracular plate. The characteristic anterior medially bent process of the maxillary in osteolepiforms has no equivalent in porolepiforms.

16. An important characteristic feature of porolepiforms is the presence of a preoperculosubmandibular plate situated behind the palatoquadrate, outside the symplectic. In osteolepiforms there is no symplectic and no preoperculosubmandibular.

17. The opercular and subopercular have in porolepiforms a characteristic shape and there are three or more branchiostegal rays and eight or nine submandibulars. In osteolepiforms there are no independent branchiostegal rays but a branchiostegosubmandibular plate and in front of that at most seven submandibulars.

18. In porolepiforms one of the principal gular plates overlaps that of the other side. In osteolepiforms no such overlapping occurs.

19. The parasymphysial dental plate and the part of the lower jaw that carries this plate have become modified in different ways in the two groups. In porolepiforms the parasymphysial dental plate is a strong arched structure carried by the correspondingly arched antero-medial lamina of the dentary, and it is provided with a row of three sigmoid tusks and lateral and medial rows of smaller teeth. A characteristic feature is moreover that the plate extends forwards to the anterior end of the jaw and that the anterior transverse part of the dorsal margin of the dentary lacks teeth. In osteolepiforms the dorsal margin of the dentary is toothed in front of the parasymphysial dental plate, which in primitive forms (osteolepids) is a thin lamina continuous with the anterior coronoid, and with a shagreen of small teeth (adsymphysial dental plate, JESSEN). In advanced osteolepiforms (rhizodontids) the postero-lateral part of the plate has become reduced and what remains is only a small plate ("predentary", VOROBYEVA) which is a vestige of the antero-medial part of the original plate.

20. The vomers in porolepiforms diverge forwards and there are no equivalents to the fossa apicalis, the prenasal pit, the intervomerine pit and the intervomerine canal of osteolepiforms. Nor has the vomer a posterior process, and there are no canals in the bone for branches of the r. palatinus VII corresponding to those found in osteolepiforms.

21. The parasphenoid in porolepiforms is a broad, thin plate anteriorly extending only to about the transition between the orbitotemporal and ethmoidal regions. It generally shows a slightly raised tooth-bearing portion and a distinct often toothed groove for the prespiracular gill-slit. The tooth-bearing portion is sometimes missing and is replaced by independent dental plates. The bone is pierced by a median foramen which contained the common opening of the right and left buccohypophysial ducts, and by paired canals for the a. carotis interna, a medial branch of

that artery, and the a. palatina. The parasphenoid in osteolepiforms is generally a long and narrow structure extending far forwards underneath the ethmoidal region. Its middle part is generally guttershaped and is provided with a high tooth-bearing ridge pierced in its posterior part by a long median buccohypophysial canal. Postero-laterally to that canal there is a distinct pocket which very likely is the area of origin for the subcranial muscle. The groove for the prespiracular gill-slit is indistinct, never toothed, and the bone may be pierced by a canal for the a. carotis interna, but there is no canal for a medial branch of that artery and no canal for the a. palatina.

22. With regard to the development and distribution of dental plates in the mouth cavity and pharynx there are also considerable differences between porolepiforms and osteolepiforms. In both groups there is a paraotic dental plate, in porolepiforms provided with a distinct ridge on its inner side. In front of that plate in porolepiforms there is a great number of partly strong upper oral plates in the roof of the mouth cavity, and there are also lower oral dental plates forming a median prolingual field, and a paired medial mandibular field in the intermandibular division. No such oral plates have been found in osteolepiforms. But in them there are a paired subotical dental plate and spiracular dental plates, the latter situated on the lateral side of the otoccipital.

23. Turning to the neural endocranium attention may first be paid to the very great differences which since 1942 have been known in the structure of the ethmoidal region and the snout as a whole.

One of the most conspicuous and well documented characteristics of the osteolepiform snout is no doubt the presence of the processus dermintermedius of the lateral rostral. The very similar development of this process and of the inwardly directed process of the anterior tectal can only mean that the anterior part of the nasal cavity in osteolepiforms in general is subdivided in the same way as in *Eusthenopteron* and that the processus intermedius, the crista intermedia, the lateral horizontal ridge of the prenasal wall etc. were developed. All these endo- and exoskeletal structures are completely lacking in porolepiforms in which the fenestra endonarina anterior, in sharp contrast to osteolepiforms, is a small simple opening in the lateral nasal wall.

Other fundamental differences refer to the absence of the posterior external nostril in osteolepiforms, the different course of the posterior external nasal duct in the two groups and to the different development of the walls of the lateral recess. The crista rostro-caudalis and Seydel's palatal process of porolepiforms have no quivalents in osteolepiforms and the same applies to the fenestra ventro-lateralis, the internasal cavity, the medial nasal wall, and the internasal ridge.

Because, furthermore, there are very great differences also in the course and position of the canals and other passages for nerves and vessels and in several other regards it is evident that we are concerned with two quite different types of snouts, each characterised by a great number of specialisations. It is certainly not easy to deduce the common ancestral type, and it is not surprising that the attempts to find intermediate forms made by supporters of the theory of a monophyletic origin of the Amphibia have been in vain.

24. In the structure of the orbitotemporal region, too, porolepiforms differ widely from osteolepiforms. The dorsal part of the interorbital wall in porolepiforms is thick and the tectum orbitale is well developed. The ventral part presents a large and deep fossa autopalatina bounded ventrally by the suborbital ledge which is much broader than in osteolepforms, shows one or two articular areas for the palatoquadrate on its dorsal side, and is supported ventrally by the broad parasphenoid. Moreover the bulbus olfactorius in porolepiforms was situated ventrolaterally to, but in osteolepiforms in front of, the hemisphere. Furthermore there are separate pineal and parapineal canals in porolepiforms and the pineal and parapineal organs were asymmetric in position. With regards to the development of the fossa hypophyseos and the canal connected with that fossa the differences are so great that a comparison at present is difficult, and a remarkable fact is that the buccohypophysial duct in porolepiforms was a short paired structure whereas it in osteolepiforms formed a long median tube.

25. The palatoquadrate in porolepiforms lacks a notch for the rr. mandibularis and maxillaris trigemini; it also lacks a paratemporal process and there is no paratemporal articulation. The anterior part of the palatoquadrate is a thin horizontal plate divided by a notch into an ethmoidal articular process, which although different in structure and morphological relations seems to correspond to the processus apicalis in osteolepiforms, and an antero-medial articular lamina, which occupies the fossa autopalatina. The ventral side of this lamina in one or, most often, two places articulates or has fused with the dorsal side of the suborbital ledge. In osteolepiforms the corresponding part of the palatoquadrate is bent upwards and a process of the dorsal margin of that part is received by a pit on the lateral side of the interorbital wall, situated well above the suborbital ledge.

26. With regard to the hyomandibula the most important difference seems to be that this element in porolepiforms distally diverges from the palatoquadrate, giving place for the symplectic which posteriorly articulates with the distal end of the hyomandibula and anteriorly with the posterior side of the pars quadrata. No symplectic exists in osteolepiforms (cf. Point No 16).

27. In the hyobranchial skeleton, too, differences of fundamental importance are met with. In osteolepiforms there are two basibranchials and all the branchial arches are complete ventrally, they are separate and articulate with the basibranchials. In porolepiforms, there is only one basibranchial, the posterior branchial arches are incomplete ventrally not reaching the basibranchial, and interarcual articulations have developed. Another important difference is that the external side of the ceratohyal shows impressions for muscles, whereas the corresponding side of the ceratohyal in osteolepiforms presents dental plates.

28. In the subbranchial series, finally, there are also very great differences. In osteolepiforms this series includes two elements, the sublingual rod and the urohyal. In porolepiforms the sublingual rod is lacking and the corresponding area of the floor of the mouth cavity shows a quite different structure, namely the prolingual field of dental plates (cf. Point No 22). Moreover the posterior part of the urohyal has a very different shape, in osteolepiforms forming a high median plate but in porolepiforms a horizontal plate, bifurcate posteriorly.

Porolepiformes and Urodela

The views that the Urodela are closely related to the Porolepiformes and descendants of primitive porolepiforms, whereas the Anura and other Eutetrapoda are closely akin to the Osteolepiformes now rest on a well-grounded basis. Founded originally on a detailed comparative study of the anatomy of the snout as a whole in lower gnathostomes (JARVIK, 1942) these views have later (1962, 1963a, 1964, 1965a, 1966, 1967b, 1968b) been confirmed by comparative studies also of other parts of the head and are strongly supported by the new evidence presented in this paper (the objections raised to these views, discussed and refuted in previous papers, have been disregarded, as have all demonstrably erroneous descriptions of osteolepiforms and porolepiforms; see JARVIK, 1962, 1964, 1965a, 1966, 1968b; see also p. 143).

The similarities between porolepiforms and urodeles indicating close relationship may be summarised as follows.

29. As established in 1942 the snout in urodeles is of the porolepiform type.

In porolepiforms and urodeles, but in no other group of vertebrates, there is a rostro-caudal crest in the nasal cavity and there is a fenestra ventro-lateralis. Judging from the similar development of the nasal cavities the nasal sac also in porolepiforms had a ventral diverticle situated as Jacobson's organ in larval urodeles, an antero-medial bulge, and a lateral diverticle divided by the rostro-caudal crest into dorsal and ventral divisions. Moreover there was probably a plica palatina supported by Seydel's palatal process.

The dorsal division of the lateral diverticle was also in porolepiforms continued backwards by the posterior external tube (ductus nasolacrimalis). In primitive forms (*Porolepis*) this tube was short, it ran obliquely backwards and downwards in a groove on the inner side of the lateral wall of the nasal cavity, bounded ventrally by the crista rostro-caudalis, to the fenestra exonarina posterior, where it opened outwards by the posterior external nostril. This short tube corresponds to the proximal or primitive portion of the nasolachrymal duct in urodeles which has a similar position, direction and extent. The oblique course is due to a ventral migration of the posterior external nostril which had occurred early in porolepiform phylogeny. This migration influenced also the underlying part of the infraorbital sensory line which became displaced in a ventral direction and as a consequence of the migration bends strongly downwards in the anterior part of the lachrymal in porolepiforms or in the corresponding place in larval urodeles (as regards the absence of independent lateral rostral in porolepiforms see p. 153). Later in phylogeny the part of the lateral nasal wall with the groove for the nasal tube—following the general trend to a retrogressive development of the skeleton—became reduced and the nasal tube was grasped from the outside by a small gutter-shaped dermal bone, the nariodal, known only in porolepiforms and urodeles.

An important fact is that the posterior external nasal tube in *Glyptolepis groenlandica* did not open by a posterior nostril in the fenestra exonarina posterior, an opening which in porolepiforms as in primitive urodeles is situated between the nariodal and the lachrymal, but made a sharp bend in that fenestra and continued upwards and backwards towards the eye in a groove on the external side of the anterior part of the lachrymal. A secondary prolongation of the posterior external nasal tube has thus developed in *Glyptolepis* and as explained in 1942 it is in this way the distal or secondary portion of the nasolachrymal duct in urodeles must have arisen, nota bene if it be true that urodeles have evolved from porolepiforms. The fact that the nasolachrymal duct in *Glyptolepis* made a sharp bend in the area of the fenestra exonarina posterior exactly as it does in larval urodeles and that, as was predicted in 1942 on the basis of the conditions in larval urodeles, its secondary portion ran obliquely backwards and upwards towards the eye in a groove on the outside of the lachrymal strongly support (together with other evidence) the view that urodeles are not only related to but descendants of primitive porolepiforms.

The presence of a wide medial profundus canal, one or more lateral profundus canals, numerous foramina in the roof of the nasal capsule, the direction of the grooves on the posterior side of the postnasal wall, etc. show that the n. ophthalmicus profundus in porolepiforms as in

urodeles, but in no other vertebrates, was strong and supplied also the lateral parts of the snout on the expanse of the r. maxillaris V, and that it broke up into numerous dorsal twigs within the nasal cavity. Moreover the discovery in the serial sections of *Glyptolepis* of ascending and descending canals in the area medially to the choana can only mean that a profundus-palatine nerve-anastomosis situated as that in urodeles was developed already in porolepiforms, and as is evidenced by the serial sections, too, the most anterior neuromasts of the infraorbital line also in porolepiforms were supplied by a buccalis branch passing forwards medially to the choana. In other words the peculiar type of innervation of the snout characteristic of urodeles was developed already in porolepiforms.

The occurrence of an internasal cavity is another important common character and of great interest is that a vestige of the internasal ridge is present in certain urodeles. The internasal cavity in urodeles houses the internasal ("intermaxillary") gland which is supplied by branches from the profundus-palatine anastomosis. The fact that a canal which no doubt carried a branch from that anastomosis opens into the internasal cavity in porolepiforms suggests that an internasal gland innervated in the way characteristic of urodeles was developed in porolepiforms.

But it is not only in the structure of the nasal capsule, the development of the nasal sac, the course of the nasolachrymal duct, the mode of innervation, etc. that porolepiform show exactly the same specialisations as are characteristic of urodeles.

The vomer, too, in porolepiforms agrees well as to position and shape with the vomer in certain urodeles and an ascending lamina lining the lateral wall of the internasal cavity and suggestive of that in *Holoptychius* is sometimes present in urodeles as well. In several urodeles the vomer is provided with a strong tooth-bearing process extending far backwards underneath the parasphenoid. In 1942 I claimed that this process is formed by fusion of dental plates and I found it reasonable to assume that such dental plates were present underneath the parasphenoid in the porolepiform ancestors. The serial sections of *Glyptolepis* confirmed that the postulated dental plates really exist.

The fact that this and other predictions made in 1942 have been verified when later a more complete fossil material became available is another strong support for the view as to the origin of the Urodela advanced in 1942.

30. In the orbitotemporal region the intracranial joint, the basipterygoid process and the fossa autopalatina of porolepiforms have disappeared in urodeles, and due to reductions of the ventral parts of the endocranium the parasphenoid has assumed a higher position. But in

many other respects there is a considerable agreement and of great interest is that the discovery of structural details in porolepiforms have stimulated to a search for corresponding details in urodeles, a search that has been successful and has led to the discovery of important new anatomical structures in urodeles.

A good example of this profitable method is provided by the epiphysial complex. Because both the pineal organ and the parapineal organ obviously were well developed in porolepiforms and because porolepiforms in so many important respects agree very closely with urodeles, I found the unanimous statements in the literature that the parapineal organ should be completely lacking in urodeles very peculiar. The elaborate wax-models of parts of the brain in the 18.5 and 33 mm stages of the primitive urodele *Hynobius retardatus* made by my colleague H. C. BJERRING demonstrate that the parapineal organ is retained in urodeles. Because the pineal and parapineal organs in porolepiforms (in contrast to osteolepiforms) are asymmetrical in position it is also of interest to note that the epiphysial complex in urodeles displays asymmetry.

Another example concerns canal *c. a. cib* in porolepiforms. This canal which is situated medially to the passage for the a. carotis interna was the only canal in the hypophysial area of porolepiforms that could not be interpreted on the basis of the information on urodele anatomy in the literature. However, knowing what to look for and where to search BJERRING in serially sectioned embryos of *H. retardatus* discovered a transient vessel which conceivably is a medial branch of the a. carotis interna.

The presence of this medial arterial branch in porolepiforms and urodeles—and the way it was discovered—support the view that these groups are related as does also the remarkable fact that not only canal *c. a. cib* but all other canals in the hypophysial area, the hypophysial fossa itself, and the adjoining portions of the cranial cavity in porolepiforms could be easily interpreted on the basis of the conditions in urodeles.

As is evident from the course and development of the canals in the hypophysial area and adjoining parts of the orbitotemporal region the nerves and vessels in this part of the head in porolepiforms ran very much as in urodeles, and like in them a strong optic vein emerged from the brain cavity through the opticus canal. As in urodeles the optic chiasma was marked by a ventral swelling of the brain stem and behind that there was probably a median eminence in the diencephalic floor and portal vessels. Of great interest is that it could be established—for the first time in an early fossil vertebrate—that the adenohypophysis was provided with a paired pars tuberalis. That this structure was long and slender, as it is in larval urodeles and emerged from a lateral lobe

of the adenohypophysis is only what is to be expected in ancestral urodeles.

The fact that the buccohypophysial duct in porolepiforms, in contrast to osteolepiforms, is paired is of interest because the adenohypophysis in urodeles arises from a paired primordium. However, the possibility is to be taken into consideration that the hypophysis was originally paired in vertebrates and if so we in this case are facing a primitive feature of little value for establishing relationship.

Of fundamental importance in this regard is, on the other hand, the fact that the bulbus olfactorius in porolepiforms was incorporated in the ventro-lateral side of the hemisphere as it is in urodeles. In this respect, too, porolepiforms and urodeles differ widely not only from osteolepiforms and anurans but also from elasmobranchs, dipnoans, actinopterygians, etc. in which the bulbus olfactorius lies in front of the hemisphere.

31. The parasphenoid in certain larval stage of urodeles is a broad thin plate which covers the ventral side the orbitotemporal region and in these and other respects it agrees well with the parasphenoid in porolepiforms.

32. The otical and occipital regions of the neural endocranium are still imperfectly known in porolepiforms. However, as demonstrated in a previous paper (1967b, pp. 194–196) urodeles and anurans differ fundamentally with regard to the occipital artery and the arterial supply of the orbit and the snout. It was established that an occipital artery running exactly as that in anurans was developed in osteolepiforms. No canal for the occipital artery has been found in porolepiforms and if this canal is absent it seems likely that the artery supplying the snout in porolepiforms passed ventrally to the otic capsule as in urodeles and not dorsally to that structure as in osteolepiforms and anurans.

33. Alleged similarities in the auditory region has been one of the main arguments for the view that recent Amphibia are monophyletic in origin. It has been demonstrated that urodeles at least in one important respect, namely the presence of the symplectic, agree with porolepiforms but differ from osteolepiforms, anurans and other eutetrapods. In view of this and other facts it seems likely that the auditory apparatus of urodeles has evolved independently from the porolepiform stage.

34. In the structure of the intermandibular division, too, urodeles as demonstrated in a previous paper (1963a), in a most striking way agree with porolepiforms. A great number of common specialisations not encountered in any other group were demonstrated (see pp. 257–262), and it was shown that the necessary prerequisites for the formation of a tongue of the urodele type were present in porolepiforms.

35. As to the external dermal bones of the head one remarkable

fact, also indicating relationship, is that the "parietal" in the phylogeny of porolepiforms underwent a lengthening forwards, in advanced forms (*Holoptychius*) extending about as far forwards as is characteristic of urodeles.

36. The parietal pit-lines of the cranial roof are in larval urodeles, as in porolepiforms, situated in front of the supratemporal pit-line, and provided the reinterpretations of the sensory lines of the cheek suggested above (pp. 269–271) be correct there is a close agreement with porolepiforms also in this part of the head and in the course of the sensory lines as whole.

37. The numerous similarities between porolepiforms and urodeles in the structure of the snout, in the orbitotemporal region, in the auditory apparatus, in the intermandibular division, etc. recorded in Points Nos 29–36, almost exclusively refer to structural features common to these two groups but not found in osteolepiforms and anurans, and with a few exceptions not in other groups of fishes either.

This fact that the Porolepiformes and the Urodela are distinguished by a great number of common specialisations not shared with other groups, that is characters of the kind we in the first hand have to rely on for establishing relationship (pp. 178–179), is in agreement and supports the conclusions as to the origin of the Urodela and the Tetrapoda as a whole I came to in 1942 on the basis of comparative studies of the snout.

These conclusions are further supported by the following conditions:

The fact that the Osteolepiformes differ widely from the Porolepiformes in the anatomy of the head and that the Osteolepiformes not only in the snout have a great number of specialisations in common with the Anura.

The fact that there are profound anatomical differences between urodeles and anurans also in those parts that cannot be discussed on a palaeontological basis (see JARVIK, 1968b, p. 514; see also e.g. STRAUS, 1946, p. 89; HUGHES, 1968, pp. 78, 196; PATTLE, 1969, p. 135).

The fact that the ontogenetic development of urodeles and anurans in several cases has been shown to be a recapitulation of the presumed phyletic evolution.

The fact that it has been possible to predict anatomical details both in porolepiforms and urodeles.

The fact that the tetrapod limb in urodeles ontogenetically arises in a different way than that in anurans and amniotes (see JARVIK, 1964, pp. 66–69, 1965a).

38. In view of all this strong evidence it is only to repeat the conclusions from 1942:

The Urodela are closely related to the Porolepiformes and descendants of primitive porolepiforms or porolepiform-like ancestors.

The Anura are closely related to the Osteolepiformes and have evolved from primitive osteolepiforms.

The Amphibia are diphyletic in origin.

The Amniota belong to the Osteolepiform-Tetrapod stock.

In consequence the Porolepiformes and the Urodela must be brought together into a common systematic unit, the Urodelomorpha (JARVIK, 1968b, p. 513). Systematic units such as Sarcopterygii, Crossopterygii, Rhipidistia and Lissamphibia are to be rejected as is also the new classification of the "Rhipidistia" recently proposed by ANDREWS & WESTOLL (1970b).

Another consequence is that due attention must be paid to the conditions in the ancestral fishes in discussions of the phylogeny and classification of the Urodela, the Anura or other groups of tetrapods. In view of the great differences between porolepiforms and osteolepiforms vague references to the "rhipidistids" are quite unsufficient and of little or no value from a scientific point of view.

39. In addition to the numerous specialisations distinguishing the Porolepiformes and the Urodela these two groups have several structural features in common which are general vertebrate characters or a heritage from the common ancestor of osteolepiforms and porolepiforms. Such primitive structures are e.g. the primordia of the three posterior infradentaries and the vestiges of the coronoid series in the lower jaw of larval urodeles, and to this category belong also the similarities as to cranial metamerism, the structure of the vertebral column, and the incorporation of dorsal elements of the three prootic visceral arches into the braincase to be dealt with in the next section.

Composition of skull and cranial metamerism

As shown in a previous paper (1954) gnathostomes (like cyclostomes) have three prootic visceral arches; the premandibular arch, the mandibular arch, and the hyoid arch, each with three dorsal elements (infrapharyngeal, suprapharyngeal and epal). It was also shown that certain of these elements have become incorporated into the braincase and that the palatoquadrate is a composite structure, in osteolepiforms including the epipremandibular and the suprapharyngo- and epimandibulars. Later (1959a, 1960) the view was advanced that the braincase includes also a cranial portion of the vertebral column which forms essential parts of the basis cranii, forwards to the fossa hypophyseos, and it was suggested that the intracranial joint of "crossopterygians" is a persisting vertebral joint and that certain embryonic elements in the parachordal area are arcual elements of true cranial vertebrae.

The widened knowledge of the cranial anatomy of porolepiforms and osteolepiforms, the descriptions of *Latimeria* by MILLOT & ANTHONY, the embryological studies of the head in sharks and other fishes started by HOLMGREN and continued by BERTMAR and BJERRING, and the embryological investigations of the head in primitive urodeles, notably by REGEL, LEBEDKINA and BJERRING, have made it possible to develop these ideas further and to discuss the cranial metamerism and the structure and composition of the basis cranii and of the skull as a whole from partly new points of view.

40. On the basis of comparisons with porolepiforms or, if better known, with osteolepiforms and embryological data new interpretations of the visceral parts of the urodele chondrocranium have been presented.

The symplectic of porolepiforms is retained in urodeles as the hyoid process of the palatoquadrate or is independent. The hyomandibula forms in urodeles the shaft of the columella but because of the forward displacement of the jaw articulation in phylogeny it has changed direction (see fig. 92). The ventral articular head of the hyomandibula has fused with the posterior end of the infrapharyngohyal which projects backwards into the fenestra ovalis and constitutes the foot-plate of the columella. The suprapharyngohyal (lateral commissure) has probably fused with the adjoining part of the palatoquadrate into the processus oticus which both in urodeles and anurans seems to be a double formation. The anterior main part of the infrapharyngohyal also in urodeles forms an otical shelf, hitherto generally mistaken for the basipterygoid (basitrabecular) process. The otical shelf, present also in osteolepiforms and anurans, has fused or articulates with the adjoining part of the palatoquadrate forming the paratemporal commissure or articulation (this articulation is initiated in osteolepiforms).

In the urodelan mandibular arch the epimandibular (postero-dorsal marginal portion of palatoquadrate) has been retained as the body of the palatoquadrate with the pars quadrata. The suprapharyngomandibular in urodeles, too, makes the processus ascendens of the palatoquadrate which articulates, or has fused, with the suprapterygoid process of the neural endocranium. Following a general trend the basipterygoid process has become reduced in urodeles and there is no basal process and no basal articulation. The infrapharyngomandibular is vestigial and forms part of the so-called trabecula cranii.

The commissural lamina of the palatoquadrate which in porolepiforms connects the epimandibular with the epipremandibular and carries the main part of the entopterygoid is together with the underlying dermal bone retained in urodeles and it forms the processus pterygoideus posterior. This process generally ends freely but is in certain larval stages still connected with the epipremandibular (processus pterygoideus anterior)

which in urodeles is a larval structure and together with the underlying dermal bones (dermopalatine, ectopterygoid) becomes reduced in the adult. As in the sectioned specimen of *Glyptolepis* the anterior end (ethmoidal articular process) of the epipremandibular in larval urodeles has fused with the infrapharyngopremandibular. The latter, as in porolepiforms, forms part of the solum nasi and carries the vomer. The suprapharyngopremandibular, in urodeles represented by the preocular (antorbital) process, forms part of the postnasal wall. The ventro-lateral process of the postnasal wall in porolepiforms is in urodeles prolonged backwards as the processus maxillaris posterior which may join a secondary antero-lateral process of the palatoquadrate.

41. It has been shown that the subcranial muscle in porolepiforms as to position, extent and relations to adjoining structures agrees with the basitrabecular commissure in larval urodeles. Because the latter no doubt represents the polar cartilage the only possible conclusion must be that *the subcranial muscle*, as earlier suggested by BJERRING, *is homologous with the polar cartilage.*

42. An important fact is also that the notochord, as recently demonstrated by BJERRING, most anteriorly has been modified into an endoskeletal structure, *the exchordal*, extending forwards in front of the buccohypophysial duct which pierces its posterior part. Noteworthy, too, is that the front part of the mesoderm from which the exchordal develops in early embryonic stages of urodeles has the potentiality to form true notochordal tissue (TAKOYA, 1953) and thus in this respect agrees with the corresponding part of the mesoderm in *Branchiostoma lanceolatum* ("*Amphioxus*"; see fig. 108B).

43. The head, like the trunk, displays a distinct metamerism, discernible as far forwards as the notochord, inclusive the exchordal, goes (fig. 108A). In order to avoid confusion with vertebral segmentation, the use of the term segmentation as a synonym of metamerism has been abandoned.

44. In each cranial metamere there is a *dorsal nerve* serially homologous with the dorsal roots of the spinal nerves, and a ventral nerve corresponding to the ventral nerve-roots in the trunk. The dorsal nerves in the five foremost metameres are; in the 1st the n. profundus, in the 2nd the n. trigeminus, in the 3rd the n. facialis, in the 4th the n. glossopharyngeus, and in the 5th the first portion of the n. vagus. Each dorsal nerve has a dorsal branch (the n. ophthalmicus profundus, the r. ophthalmicus trigemini, the n. acusticus, etc., see fig. 88), and a visceral trunk (r. maxillaris in the 1st metamere, r. mandibularis in the 2nd, etc.).

The discovery of the *n. tenuis* (BJERRING, 1970) made the series of *ventral nerves* complete. The ventral nerves are: the n. oculomotorius in

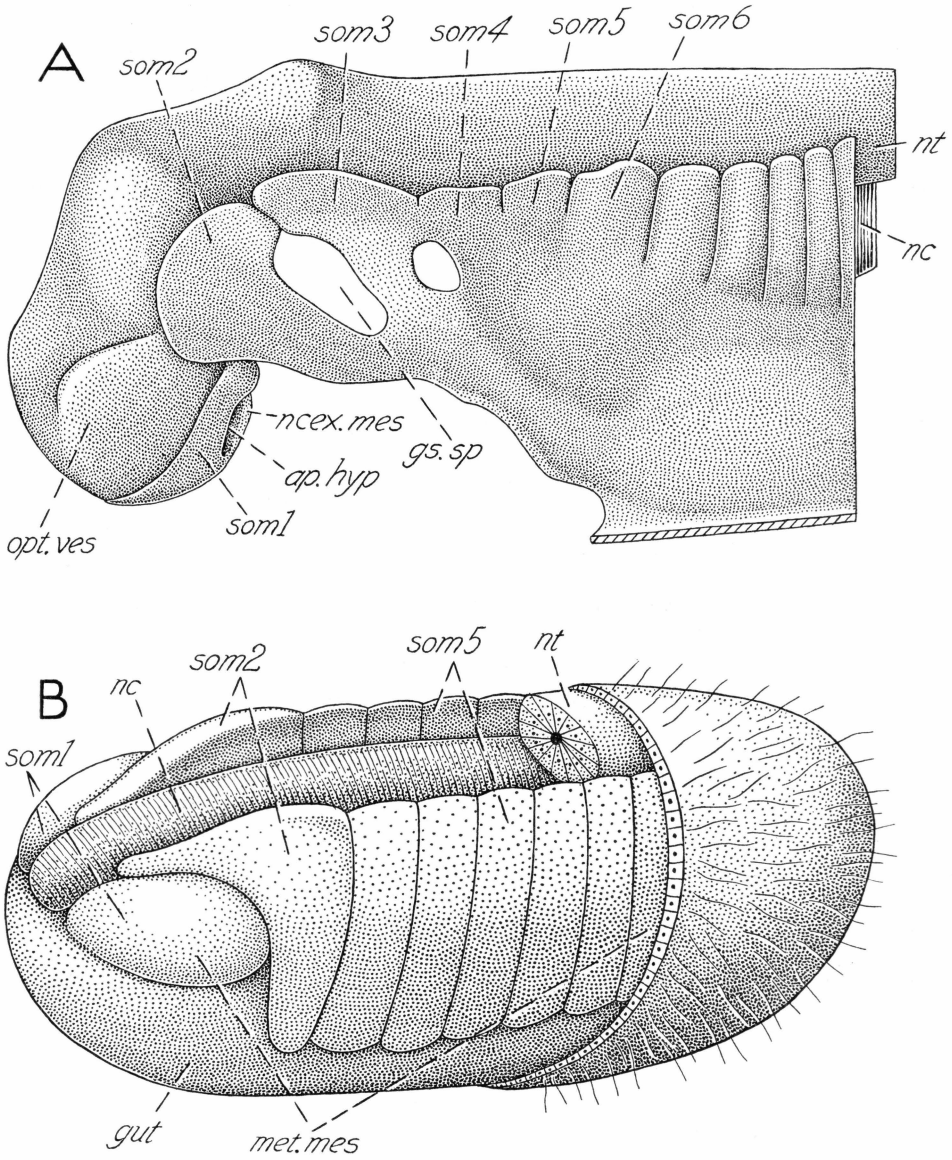


Fig. 108. Embryonic representations to illustrate similarities in anterior extension and metamerism of mesodern of, *A*, *Squalus acanthias* and, *B*, *Branchiostoma lanceolatum* ("*Amphioxus*"). Note the modifications in *A* of the somites and notochordal (exchordal) tissue of the 1st metamere (i.e. the so-called prechordal plate mesoderm) due to the pronounced cephalic flexure and the developing hypophysis. *A*, from Bjerring, 1967, fig. 19; *B*, from Bjerring, 1971, fig. 15.

ap. hyp, paired fenestration for hypophysis; *gs. sp*, fenestration caused by spiracular gill-slit; *gut*, gut tube; *met. mes*, metameric mesoderm; *nc*, notochord; *ncex. mes*, exchordal mesoderm; *nt*, neural tube; *opt. ves*, optic vesicle; *som1–som6*, somites of 1st–6th metameres or (in *B*) corresponding parts of metameric mesoderm.

the 1st metamere, the n. trochlearis in the 2nd, the n. abducens in the 3rd, the n. tenuis in the 4th and the n. occipitalis in the 5th.

45. The presence of one *visceral trunk* in each of the five foremost metameres (the conditions farther back have not been analysed) and other conditions (see p. 255 and Point No 51) show that *there is a correspondance between branchiomerism and metamerism.* The visceral arches belonging to the five foremost metameres are: the premandibular arch in the 1st, the mandibular arch in the 2nd, the hyoid arch in the 3rd, the first branchial arch in the 4th, and the 2nd branchial arch in the 5th.

46. In the head, as in the trunk, a paired somite is formed in each metamere (see fig. 108A), and *there is a continuous series of somites forwards to the foremost or premandibular somite which is developed in relation to the exchordal.* As a consequence mainly of the brain flexure in the early embryo and the development of the auditory vesicles (cf. fig. 108B) the cephalic somites have been modified but *no somite has disappeared* and exactly as in the trunk each cranial somite differentiates into a dermatome, a myotome and a sclerotome. The dermatomes which according to BJERRING in the 3rd and 4th metameres form parts of the lateral wall of the auditory capsule will not be further considered.

47. The *myotomes* also in the head form somatic muscles but an important fact first recognised by BERTMAR is that they may also produce skeletal tissues.

In the 1st metamere the myotomic material seems to be used up to form the four eye-muscles innervated by the n. oculomotorius. In the 2nd metamere the anterior part of the myotome develops into the eye-muscle (obliquus superior) innervated by the n. trochlearis, whereas the posterior part produces either the subcranial muscle or, in forms without intracranial joint, a skeletal structure, viz. the polar cartilage. In the 3rd metamere, too, the anterior part of the myotome produces an eye-muscle (rectus externus innervated by the n. abducens), whereas the posterior part forms both a muscle, basicranial muscle 3, and a skeletal structure known as the anterior basiotic lamina. Also in the 4th metamere arises a muscle, basicranial muscle 4, and a skeletal structure, viz. the posterior basiotic lamina. Behind the 4th metamere the myotomes generally form complete myomeres but an important fact is that the 5th myomere has a distinct basicranial portion, basicranial muscle 5, serially homologous with basicranial muscles 3 and 4 and probably also with the subcranial muscle which very likely is the basicranial muscle in the 2nd metamere.

48. The *basicranial muscles* are the ventral persisting portions of the cephalic myomeres and a remarkable fact is that there is one basicranial muscle in each metamere forwards to the 2nd. Basicranial muscles 3 and 4, discovered by REGEL, have hitherto been found with certainty only

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in larval urodeles but were probably present in the adult in osteolepiforms and porolepiforms. In urodeles they are transient structures. They soon become buried in the cartilage of the basiotic laminae and disappear and very likely the mesenchyme cells freed by the dedifferentiation of the muscles were used to form new cartilage. It is also very likely that this is what happened in the 2nd metamere when, in connection with the ankylosis of the intracranial joint at the transition from fish to tetrapod, the subcranial muscle, that is basicranial muscle 2, was replaced by the polar cartilage.

49. Basicranial muscle 5 is innervated by the ventral nerve of the 5th metamere, the n. occipitalis, and very likely basicranial muscle 4 is supplied by the n. tenuis and basicranial muscle 3 by the r. basioticus (BJERRING) of the n. abducens, although, because of the transient nature of both muscles and nerves, no contact hitherto has been observed. If the subcranial muscle is the basicranial muscle in the 2nd metamere it should be innervated by a branch of the ventral nerve of the metamere, that is the trochlearis. However, in *Latimeria* the nerve to the subcranial muscle emerges from the braincase together with the n. vagus and at the first sight it appears to belong to the 5th metamere. This anomaly has been discussed (pp. 239–241), and it has been suggested that the aberrant course of the nerve is due to a secondary displacement backwards of the same kind as has demonstrably happened to the ventral nerve (abducens) in the 3rd metamere. These matters have recently been discussed also by BJERRING (1971, 1972a), who demonstrated that the nerve to the subcranial muscle in osteolepiforms and early coelacanthiforms emerged from the braincase farther forward than in *Latimeria*.

50. Before turning to the derivatives of the cephalic sclerotomes it is necessary to include a few remarks on the *vertebral column*.

According to views developed in a previous paper (1965b) it is to be assumed that the early vertebrates were swimming animals with metameric muscles derived from the myotomes of metameric arranged somites. Like the radials in the paired fins the supporting endoskeletal elements in the trunk, that is the vertebrae, very likely are secondary formations. When in the phylogeny of the vertebrates the condensation of the sclerotomic mesenchyme began and skeletal elements arose, the vertebral joints—in consequence of the undulating swimming movements of the body—necessarily must be placed opposite the middle of the metameric muscles. This resulted in a primary subdivision or segmentation—not a "resegmentation"—of the sclerotomic mesenchyme and it explains why the vertebrae are intermetameric in position and are derived from two half-sclerotomes, one caudal from one metamere and one cranial from the metamere following next behind. Because the verte-

brae not only serve the purpose to give attachment to the metameric muscles, but also protect both the notochord and the overlying neural tube, it is easy to understand why there arose one paired dorsal and one paired ventral element in each half-sclerotome. Accordingly each vertebra will include four paired *primary* arcual elements, two anterior, the basidorsal and the basiventral, derived from the caudal half-sclerotome of one metamere and two posterior, the interdorsal and the interventral, formed from the cranial half-sclerotome of the metamere following next behind. The existence of these four paired primary components is documented by embryological investigations of various vertebrates (see e.g. SCHAUINSLAND, 1905, kraniale und kaudale dorsale und ventrale Bogenstücke) and I find no reason to reject GADOW's terms basidorsal, etc. for these elements.

In the vertebral column of *Eusthenopteron* (JARVIK, 1952) the two dorsal elements, the basidorsal and the interdorsal, are independent, whereas the two ventral elements, the basiventral and the interventral, have fused forming the ventral vertebral arch (see fig. 99B). In urodeles the conditions seem to be much the same (SCHAUINSLAND, 1905, pp. 499–501, fig. 284) but an interesting fact is that whereas in *Eusthenopteron* it is the basidorsals that form the neural arches such arches in the tail of urodeles may also be formed by the interdorsals. (Because the vertebral column in larval urodeles is of the "temnospondylous" type the objection against a close relationship between porolepiforms and urodeles raised by ANDREWS & WESTOLL, 1970b, p. 478, is invalid).

51. Turning to the *sclerotomic derivatives* in the head it is evident that the occipital region in *Eusthenopteron* is composed of vertebrae similar to those in the trunk; and a vertebra of the same kind no doubt forms the posterior end of the ethmosphenoid. This latter vertebra, *CV 1+2*, lies in front of the intracranial joint which is spanned by the subcranial muscle, that is basicranial muscle 2. Because *the intracranial joint* has the same relations to this muscle as have the vertebral joints to the metameric muscles in the trunk it very likely *is a persisting vertebral joint.* Behind this joint within the 2nd metamere there are in *Eusthenopteron* distinct traces also of the original vertebral joints within the 3rd, 4th and 5th metameres. These joints are represented by distinct fissurae in the otoccipital: the fissura oticalis ventralis anterior within the 3rd, the fissura oticalis ventralis posterior within the 4th, and the dorsal portion of the fissura occipitalis lateralis within the 5th metamere. A remarkable fact is that the basicranial muscles spanning these joints, judging from the impressions found on the ventral side of the otoccipital in *Eusthenopteron*, were retained in the adult.

In urodeles, too, there are distinct traces of the vertebral joints within the 3rd, 4th and 5th metameres, medially to the basicranial muscles

of these metameres. These joints are represented by the constrictions which separate the swellings described by REGEL in the parachordal part of the basis cranii of larval urodeles. Medially to the polar cartilage, which is homologous with basicranial muscle 2, there is also a constriction (between swellings 1 and 2) which obviously marks the position of the original joint within the 2nd metamere (as regards the joint within the 1st metamere see below).

The *cranial vertebrae* are named after the metameres to which they are supposed to belong (*CV 1*, *CV 1 + 2*, etc, figs. 89, 96, 97, 99). Each such vertebra, in larval urodeles represented by the swellings in the parachordal area, consists of a ventral portion serially homologous with the ventral vertebral arches in the trunk and a dorsal portion which forms part of the lateral wall of the cranial cavity. In *Eusthenopteron* and other "crossopterygians" the ventral vertebral arches which surround the cephalic portion of notochord in the same way as in the trunk may be independent, forming ventral arcual plates. The dorsal arcual plates between the notochordal canal and the cranial cavity seem to correspond to the epichordal commissure in larval anurans and probably there was originally one such plate in each vertebral segment. The dorsal ends of the dorsal vertebral portions of both sides, because of the strong development of the anterior part of the neural tube forming the brain, are far apart; they are joined by ectomesenchymatic material forming the endoskeletal cranial roof. In embryonic stages the dorsal portions form more or less distinct dorsal processes or pilae. The pila prefacialis in cranial vertebra *CV 2 + 3*, the pila oticalis anterior in *CV 3 + 4*, the pila oticalis posterior in *CV 4 + 5* and the pila occipitalis in *CV 5 + 6* all seem to be basidorsals serially homologous with the neural arches in the trunk. However, because of the fusion of the vertebrae and the formation of complete lateral cranial walls it seems likely that also the interdorsals, like in the tail of urodeles, may form neural arches. That this is so is evident in the vertebra forming the posterior end of the ethmosphenoid in *Eusthenopteron* and other "rhipidistids".

This vertebra, *CV 1 + 2*, is situated in front of the intracranial joint, that is the vertebral joint within the 2nd metamere, and accordingly we have to assume that it is composed of material derived from the anterior half-sclerotome of the 2nd metamere and the posterior half-sclerotome of the 1st metamere. However, as shown by HOLMGREN, the pila antotica, which obviously is the dorsal process of this vertebra, belongs to the 2nd metamere and consequently it must be formed from the cranial half-sclerotome of the metamere, which means that it is the interdorsal (see fig. 99 B).

As is well shown in *Eusthenopteron* the pila antotica (interdorsal 2) is provided with a strong antero-laterally directed process, the supra-

pterygoid process, articulating with the suprapharyngeal element (processus ascendens palatoquadrati) of the mandibular arch, that is the visceral arch of the 2nd metamere. This is of considerable interest because also the interdorsals of the 3rd and 4th metameres have lateral processes (processus oticalis anterior, processus oticalis posterior; see fig. 99C) which articulate with the suprapharyngeal elements of the visceral arches (hyoid arch, first branchial arch) belonging to these metameres. These conditions, too, illustrate the correspondance between branchiomerism and metamerism (as regards the premandibular arch see next paragraph).

In front of cranial vertebra *CV 1+2* there was probably an incomplete vertebra, *CV 1*, derived from the anterior half-sclerotome of the 1st metamere (fig. 99B). The dorsal process of this vertebra is the pila metoptica, which must be the interdorsal of the 1st metamere. However, in contrast to the interdorsals of metameres 2, 3, 4, interdorsal 1 has no lateral process articulating with the suprapharyngeal element of its metamere. As is well known the supra- and infrapharyngeal elements of the 1st or premandibular arch are situated far forwards and form parts of the walls of the nasal capsule. However, this almost certainly is due to a secondary displacement. The nasal sacs arise in ontogeny close to the hypophysis and when they in the phylogeny of the vertebrates, probably in connection with the prolongation of the rostral part of the head, moved forwards it is only to be excepted that the dorsal elements of the premandibular arch followed them.

It now remains to consider the ventral part of *CV 1* and the position of the original vertebral joint within the 1st metamere but for that purpose we have to turn to the parasphenoid.

52. As shown in a previous paper (1954) *the parasphenoid* in *Eusthenopteron* is composed of a median portion, the primitive parasphenoid, to which have been added infrapharyngeal dental plates of the mandibular arch. These plates form the processus ascendens anterior which is situated on the ventro-lateral side of the basipterygoid process, in the medial wall of the vestigial prespiracular gill-slit. In more advanced forms (palaeonisciform stage) the median portion, which in "crossopterygians" ends posteriorly at the intracranial joint, has become prolonged backwards to the fissura oticalis ventralis anterior and ascending infrapharyngeal dental plates corresponding to the spiracular dental plates in *Eusthenopteron* form a strong processus ascendens posterior in the medial wall of the spiracular gill-slit. In urodeles the basipterygoid process is reduced and there is no anterior ascending process. Nor is there a posterior ascending process in urodeles which is only what is to be expected in view of the fact that spiracular dental plates are lacking in porolepiforms.

In the median portion of the parasphenoid of the palaeonisciform stage three parts may be distinguished, anterior, middle, and posterior. The anterior part, situated below cranial vertebra *CV 1*, is represented by the prehypophysial parasphenoid primordium in larval urodeles and the corresponding parts of the parasphenoid in porolepiforms and osteolepiforms. The middle part, which covers cranial vertebra *CV 1+2* ventrally, is represented by the posthypophysial primordium in urodeles and the corresponding median parts of the parasphenoid in porolepiforms and osteolepiforms. The posterior part, situated on the ventral side of cranial vertebra *CV 2+3*, is independent in *Eusthenopteron* forming the paired subotical dental plate. The posterior margin of this plate (and of the corresponding median portion of the parasphenoid in palaeoniscids) coincides with the fissura oticalis ventralis anterior which is the vestigial vertebral joint within the 3rd metamere whereas the boundary between this plate and the part of the parasphenoid derived from the posthypophysial primordium lies at the intracranial joint which is the vertebral joint within the 2nd metamere. In view of these facts it seems reasonable to assume that the boundary between the pre- and posthypophysial primordia marks the position of the vertebral joint within the 1st metamere. This means that this joint originally was situated in the area of the buccohypophysial duct, a conclusion that also Bjerring (1971) has arrived at, but on the basis of other arguments.

53. Cranial vertebra *CV 1* is developed in relation to the exchordal endoskeleton which according to Bjerring represents a modified anterior part of the notochord. On this basis, and considering the fact that the prehypophysial primordium arises in connection with the so-called intertrabecular mesenchyma (see pp. 246, 253), it may be assumed that the braincase in the area of cranial vertebra *CV1* in a form like *Eusthenopteron* is composed of the following parts: 1) an endoskeletal midventral portion formed by the exchordal; 2) the ventral vertebral arch of *CV 1* derived from the intertrabecular mesenchyma; 3) the underlying portion of the parasphenoid descending from an element corresponding to the prehypophysial parasphenoid primordium; 4) the pila metoptica (interdorsal 1) forming the lateral endocranial wall just posterior to the opticus canal; 5) the portion of the endoskeletal cranial roof connecting the dorsal ends of the metoptic pilae of both sides and the overlying portion of the dermal cranial roof, both of which portions are ectomesenchymatic in origin; 6) a portion of the infrapharyngomandibular ("trabecula"); and 7) infrapharyngeal dental plates forming lateral parts of the parasphenoid.

54. As pointed out by Goodrich (1930, p. 219) "the head somites are of the same nature as and form a continuous series with those of the trunk". The 1st or premandibular somite lies at the anterior extremity

of the embryo (fig. 108A; cf. "*Amphioxus*", fig. 108B) and is developed in relation to the front part of the embryonic neural tube (brain) and the underlying modified foremost portion of the notochord, the exchordal. The relations of this and other somites to the notochord and the neural tube are exactly the same in head and trunk and because the hypophysial duct pierces the exchordal the hypophysis is not the important landmark in the metameric skull as it hitherto has been considered to be. Of great interest is also that the myotomes in the head form somatic muscles and as has been shown above there is a continuous series of metameric basicranial muscles—that is persisting portions of cephalic myomeres—extending forwards at any rate to the 2nd metamere. Finally, it has been demonstrated that the cephalic sclerotomes like those in the trunk form intermetameric vertebrae, composed of dorsal and ventral arcual elements, and that these vertebrae are separated by intrametameric vertebral joints spanned by the metameric basicranial muscles.

From the foregoing it seems likely that *there is no fundamental difference between head and trunk*; both regions are merely modifications of a simple common system. Thus if we try to visualise the vertebrate prototype there is good reason to believe that it was a metameric aquatic form to some extent suggestive of the one depicted in fig. 108B. This illustration is not an idle speculation but a drawing of an early embryo of "*Amphioxus*". The latter is of the same basic type as an early vertebrate embryo (fig. 108A) and in this way we have arrived at the common ancestry of the Craniata (Vertebrata) and the Acrania (see JARVIK, 1968b, fig. 4).

55. The new views as to the composition of the head presented in this and previous papers in the first hand rest on studies of the Devonian Porolepiformes and Osteolepiformes. It was the distinct serial arrangement of the dental plates in the roof of the mouth and pharynx and of the overlying supporting endoskeletal elements in *Eusthenopteron* that gave the key to the new interpretations of the dorsal parts of the premandibular, mandibular and hyoid visceral arches and of the braincase presented in 1954. However, as is now clear this regularity in arrangement of the visceral elements in osteolepiforms and porolepiforms is a consequence of the cranial metamerism inherited from the common ancestor of the Euchordata. The fact that early fossil porolepiforms and osteolepiforms, although specialised in many regards and in different ways, have retained so much of the original serial arrangement and in the adult show distinct traces in the head of the metamerism and the vertebral segmentation is in agreement with and supports the view advanced in previous papers (1968a, 1968b) that these two groups include the most primitive vertebrates known so far.

But as was also pointed out (1968b, p. 523) "Vertebrate Palaeontology alone cannot solve the problems". For the elaboration of the views as to the composition of the skull set forth above the results gained by the embryologists, in particular during the last few years, have certainly been of greatest importance. The fact that among extant vertebrates it is the embryonic stages of urodeles that display the most distinct traces of the original metamerism and vertebral segmentation in the head would scarcely be a surprise. This is just what should be expected in view of the fact that urodeles are closely related to and most probably direct descendants of primitive porolepiforms.

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Færdig fra trykkeriet den 29. december 1972.

PLATES

Plate 1

Glyptolepis groenlandica n. sp.

Holotype. Specimen No. P. 1488, Min. Mus., Copenh. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*). × 1/2. Head shown in text-fig. 3.

af, anal fin; *cdf*, *cvf*, dorsal and ventral lobes of caudal fin; *fdf*, first dorsal fin; *sdf*, second dorsal fin.

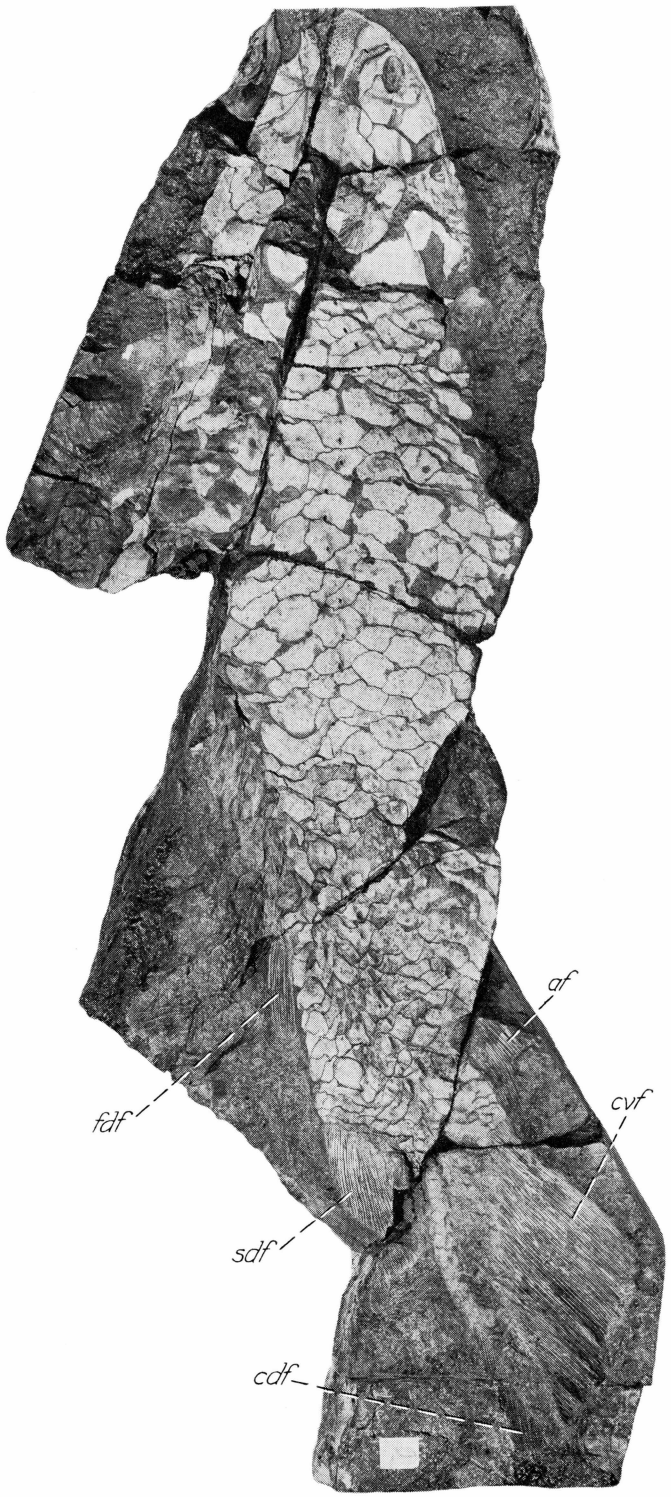

af
fdf
cvf
sdf
cdf

Plate 2

Porolepis brevis JARVIK

Flattened incomplete skull in dorsal view. Specimen No. P. 6963, Pal. Sect., Stockh. Coll. ENS. exp. 1939. Sigurdfjellet, Woodfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). Same specimen as in pl. 3. × 2/3.

FrD, frontodermosphenotic; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *PaIt*, parietointertemporal; *Po*, postorbital; *Prsp*, prespiracular plate; *Sq. u*, upper squamosal; *St*, supratemporal.

ahd, dorsal articular head of hyomandibula; *art. Sym*, articular area of hyomandibula for symplectic; *c. hy*, hyomandibular canal; *fe. o*, orbital fenestra; *gr. me*, *gr. mi*, grooves for rr. mandibularis externus and internus VII; *od. Ext. m*, area of parietal shield overlapped by median extrascapular.

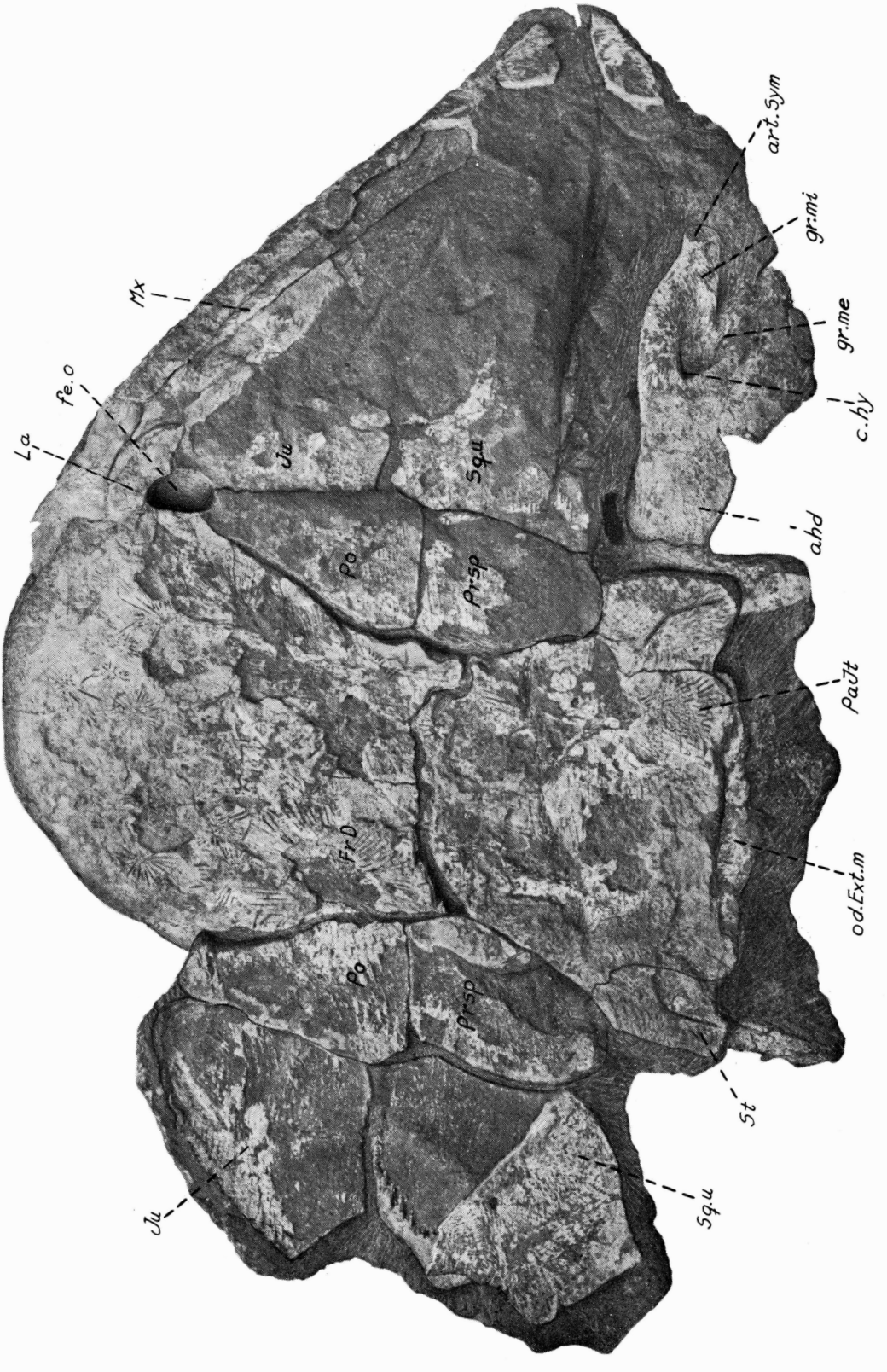

art.Sym
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Plate 3

Porolepis brevis JARVIK

Same specimen as in plate 2. Palatal aspect. × 2/3.

Enpt, entopterygoid; *Hy*, hyomandibula; *Mx*, maxillary; *Otoc*, otoccipital-*P*, parasphenoid; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate (epi; mandibular); *Pq. qu*, pars quadrata; *Vod*, ascending lamina of vomer.

ahv, ventral articular head of hyomandibula; *art. Ch*, articular area of hyomandibula, probably for ceratohyal; *cav. in*, internasal cavity; *fe. bc*, basicranial fenestra; *fe. ov*, fenestra ovalis; *fe. vl*, fenestra ventro-lateralis; *fo. aup*, fossa autopalatina; *fo. nc*, pit in posterior end of ethmosphenoid for notochord; *gr. a. dl*, groove for lateral dorsal aorta; *gr. orp*, posterior groove of orbito-rostral passage; *la. Vo*, vertical tooth-bearing lamina of vomer; *pr. b*, processus basalis of palatoquadrate; *pr. bp*, basipterygoid process; *pr. conn*, processus connectens; *p. Sym*, articular area for symplectic; *re. sh*, spiraculo-hyomandibular recess; *ri. in*, internasal ridge.

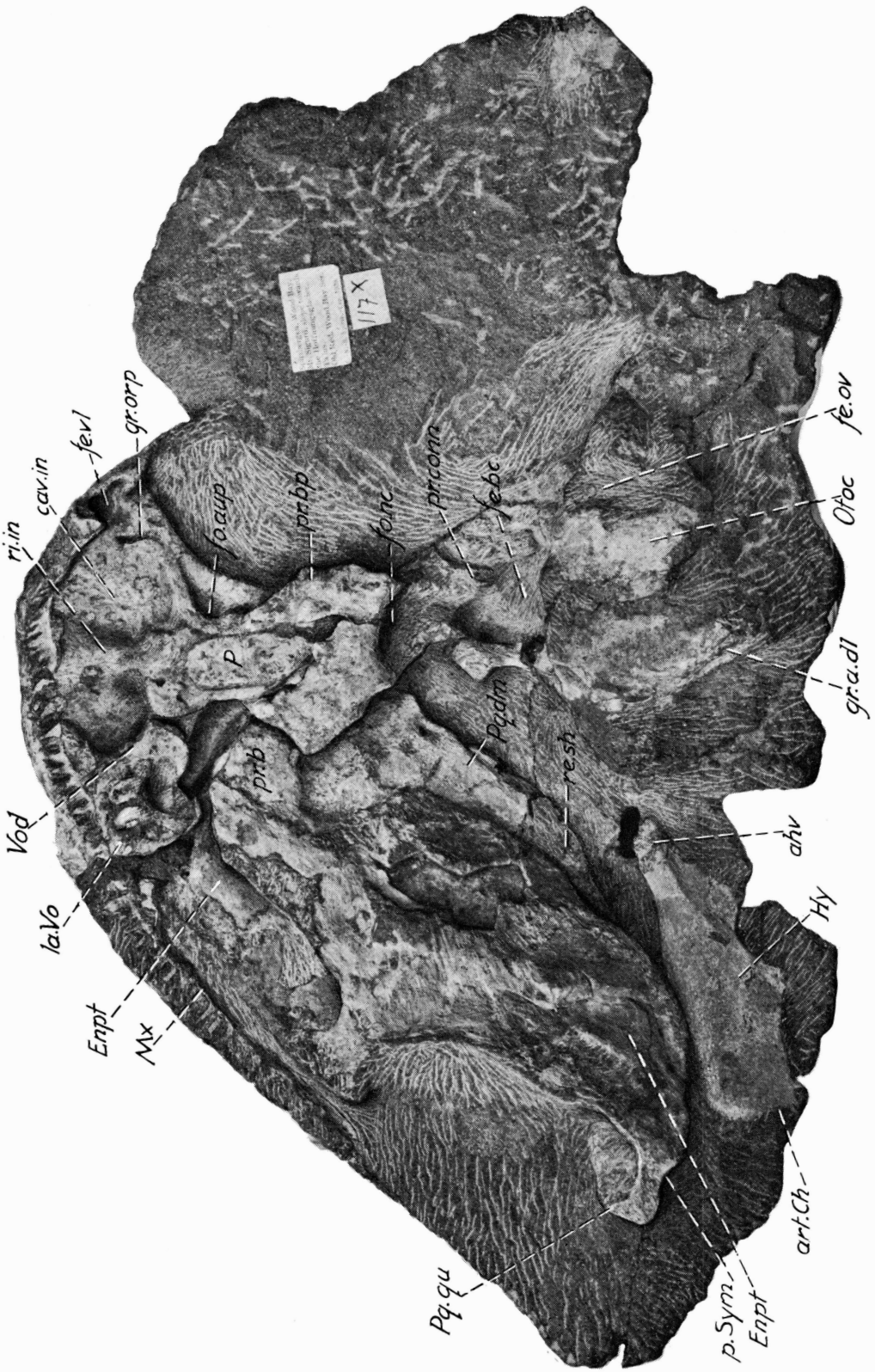

ri.in
cav.in
fevl
gr.orp
fo.aup
dprdd
fom
prdm
fe.bc
fe.ov
Ofoc
P
prb
Pq.dm
resh
gr.a.dl
Vod
la.Vo
Enpt
Mx
ahv
Hy
Pq.qu
p.Sym
Enpt
art.Ch

Plate 4

1. *Porolepis brevis* JARVIK. Flattened skull with anterior part of body in dorsal aspect. Specimen No. J. 554, Sedgwick Mus., Cambridge. Coll. Cambridge Spitsb. exp. 1965. Kronprinshøgda, Bockfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). × 5/6.

2. *Porolepis* sp. Left lower jaw. Lateral aspect. From same block (1964:41) as specimen figured in pl. 7:3, 4. Mus. de Paléont., Paris. Coll. French exp. (J.-P. Lehman) 1964. Grønhorg, Dicksondalen, Spitsbergen. Lower Devonian (Wood Bay Series). × 5/3.

Et, extratemporal; *Ext. l*, lateral extrascapular; *FrD*, frontodermosphenotic; *Ju*, jugal; *La*, lachrymal; *Mb. art*, pars articularis of meckelian bone; *Mx*, maxillary; *Op*, opercular; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *Pt*, posttemporal; *Sclm*, supracleithrum; *Sop*, subopercular; *Sq. u*, upper squamosal; *St*, supratemporal.

fe. exa, fenestra exonarina anterior; *fe. o*, orbital fenestra; *i. exp*, notch for posterior nasal tube; *pl. Id. 2*, *pl. Id. 4*, pit-lines of infradentaries 2 and 4.

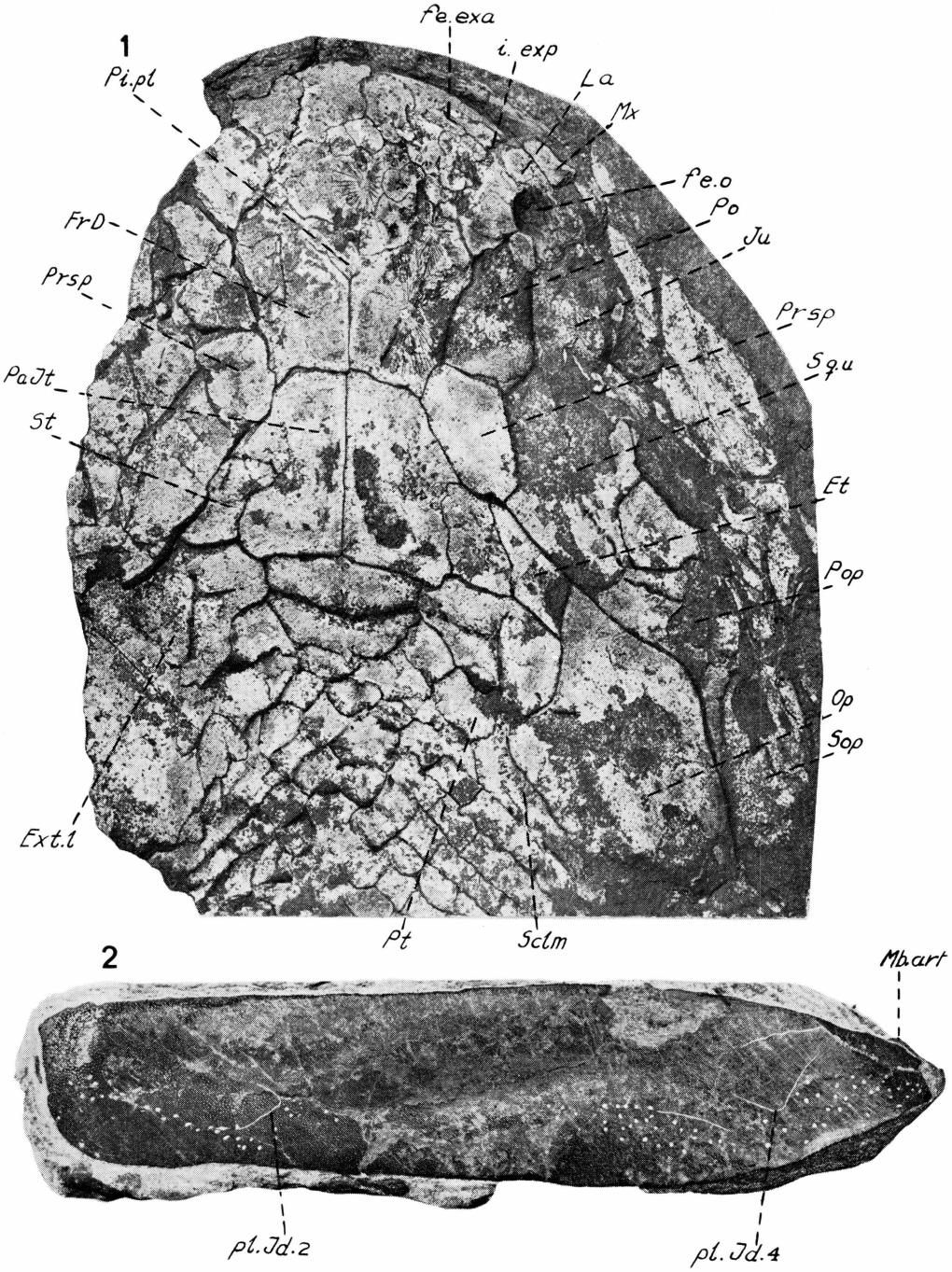

1
Fe.exa
i. exp
La
Mx
Pi.pl
Fe.o
Po
Ju
FrO
Prsp
Prsp
Sg.u
PaJt
St
Et
Pop
Op
Sop
Ext.t
Pt
Sclm
2
Mb.art
pl.Jd.2
pl.Jd.4

Plate 5

Porolepis brevis JARVIK

Incomplete specimen showing mainly parts of external cheek-plate, operculars, extrascapular series and exoskeletal shoulder-girdle together with some scales. Nos. A. 34004 and A. 34005, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Scott Keltiefjellet, Woodfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). × 2/3.

1. Photograph of specimen in lateral view.

2. Photograph of latex cast of counterpart.

Et, extratemporal; *Ext. l*, lateral extrascapular; *Ext. m*, median extrascapular; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Op*, opercular; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *Pt*, posttemporal; *Qj*, quadratojugal; *Sclm*, supracleithrum; *Sop*, subopercular; *Sq. l*, lower squamosals; *Sq. u*, upper squamosal.

fe. o, orbital fenestra; *fe. spir*, spiracular fenestra; *gr. msc*, groove marking course of main sensory canal; *i. La*, notch in lachrymal forming part of fenestra exonarina posterior; *od. Op*, area of supracleithrum overlapped by opercular.

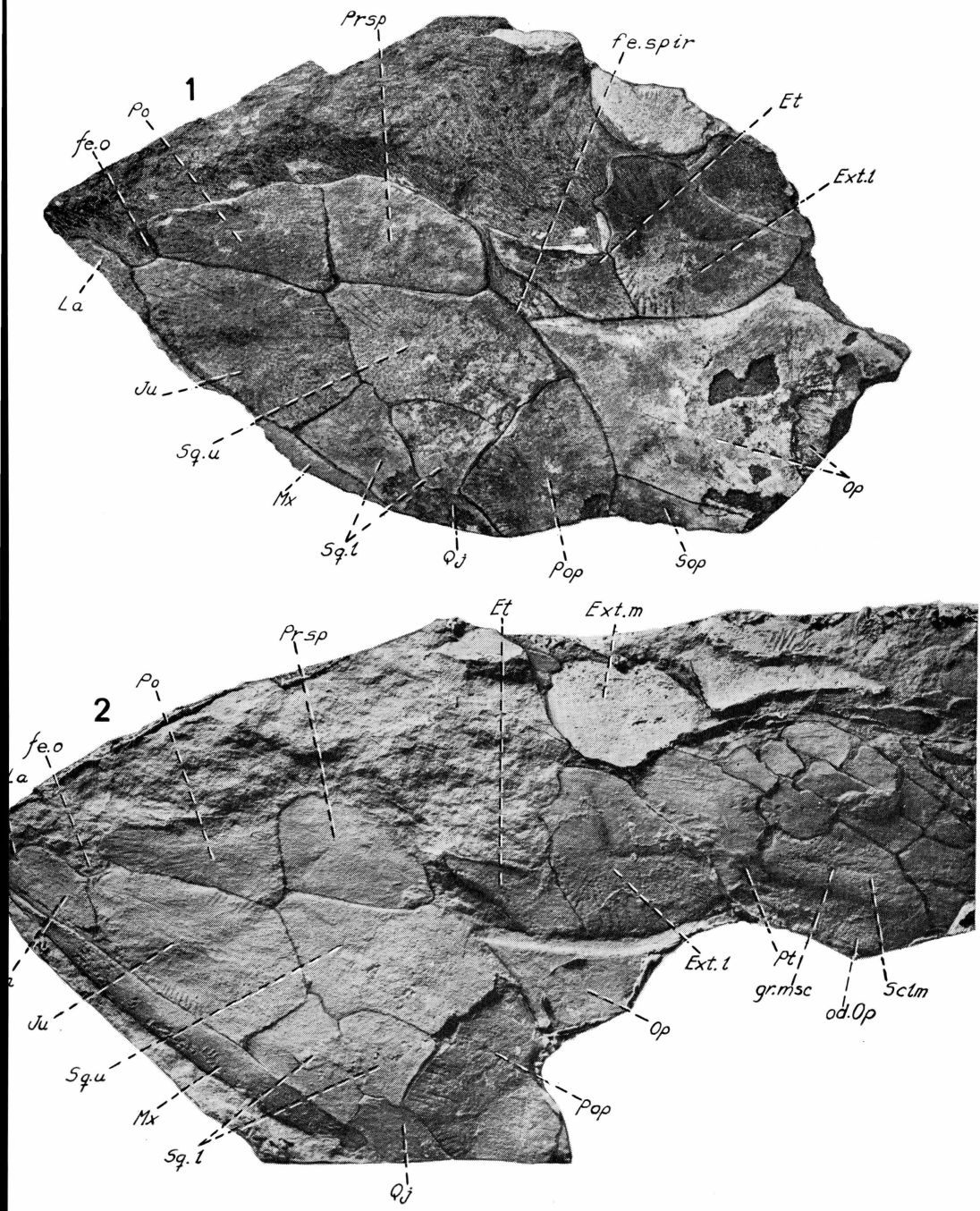

1
Prsp
fe.spir
Et
Ext.t
Po
fe.o
La
Ju
Sq.u
Mx
Sq.t
Qj
Pop
Sop
Op
2
Et
Ext.m
Pr.sp
Po
fe.o
Ju
Sq.u
Mx
Sq.t
Qj
Ext.t
Pt
gr.msc
od.Op
Sctm
Op
Pop

Plate 6

Porolepis brevis JARVIK

Two incomplete skulls collected by French Spitsbergen exp. in 1969 on top of Kronprinshøgda, Woodfjorden. Lower Devonian (Wood Bay Series). × 1/1.

1. Specimen No. SVB. 1, Mus. de Paléont., Paris. Lateral aspect.

2, 3. Specimen No. SVB. 2, Mus. de Paléont., Paris. Dorsal and ventral aspects.

Et, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *G*, principal gular plate; *Gm1*, *Gm2*, anterior and posterior median gular plate; *Ju*, jugal; *La*, lachrymal; *Lj*, lower jaw; *Mx*, maxillary; *Op*, opercular; *PaIt*, parietointertemporal; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Qj*, quadratojugal; *Rbr*, branchiostegal ray; *Sbm*, submandbular; *Sbm1*, *Sbm9*, submandibulars 1 and 9; *Sop*, subopercular; *Sq. l*, lower squamosals; *Sq. u*, upper squamosal; *St*, supratemporal; *Sy*, symphysial dermal bone.

fe. exa, *fe. exp*, fenestra exonarina anterior and posterior; *fe. o*, orbital fenestra; *od. G*, area of right principal gular overlapped by principal gular of left side; *od. Sbm*, area of principal gular overlapped by submandibulars; *pl. Ext. l*, pit-line of lateral extrascapular; *pl. Fr*, frontal pit-line; *pl. Gm*, pit-line of median gular; *pl. Id.2*, *pl. Id.4*, pit-lines of infradentaries 2 and 4; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. Qj*, *pl. Sq*, quadratojugal and squamosal pit-lines; *pl. Sq. l*, pit-line of lower squamosal; *pl. St*, supratemporal pit-line; *pl. tr. Pa*, transverse parietal pit-line.

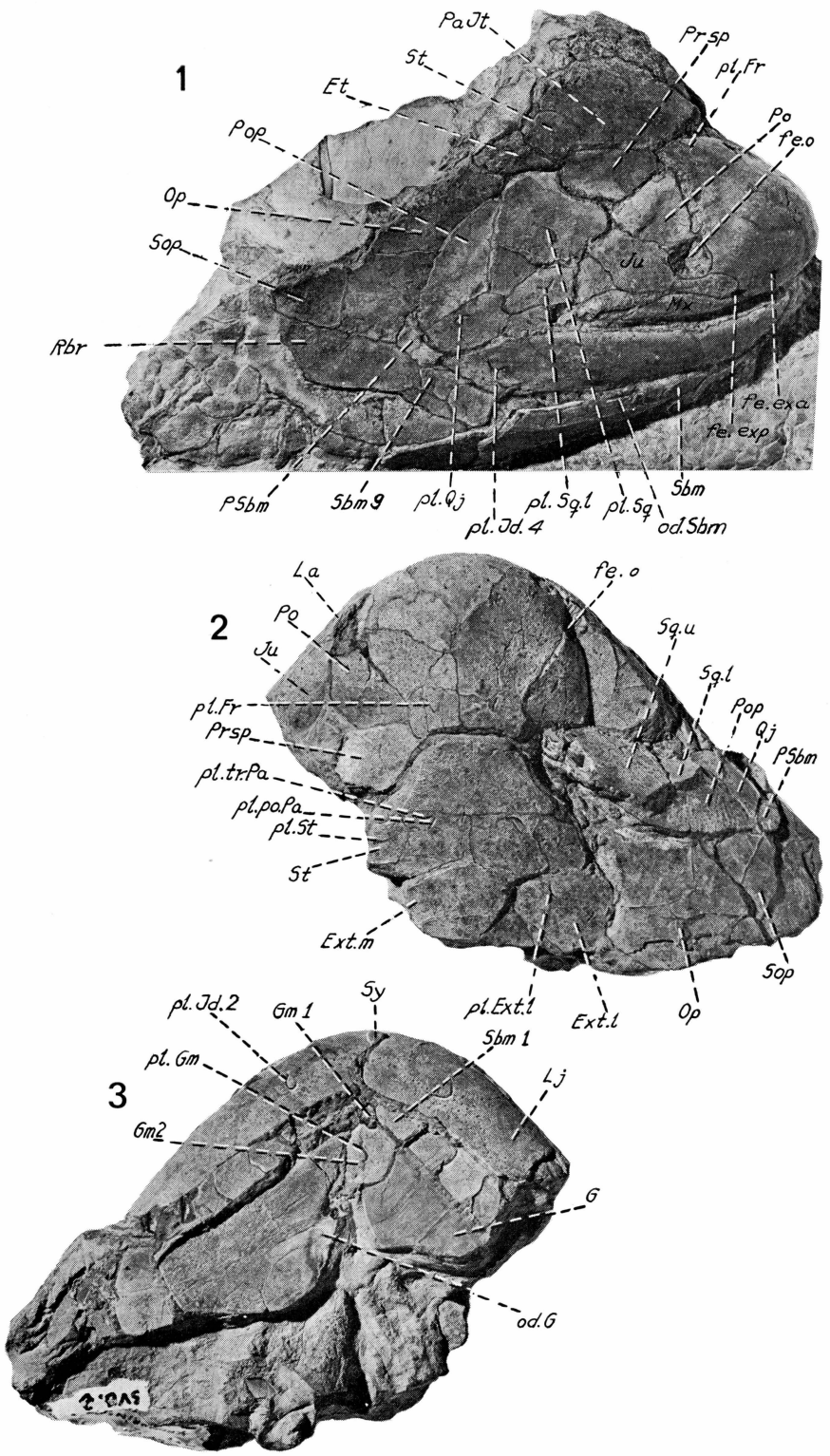

1
Pa.Jt
St
Pr.sp
pl.Fr
Et
Po
Fe.o
Pop
Op
Sop
Ju
Mx
Rbr
Fe.ex.a
Fe.exp
PSbm
Sbm 9
pl.Qj
pl.Jd.4
pl.Sq.l
pl.Sq
Sbm
od.Sbm
2
La
Fe.o
Po
Sq.u
Ju
Sq.l
pl.Fr
Pop
Qj
Prsp
PSbm
pl.tr.Pa
pl.pa.Pa
pl.St
St
Ext.m
Sop
Op
Ext.l
pl.Ext.l
3
pl.Jd.2
Gm 1
Sy
Sbm 1
pl.Gm
Lj
Gm2
G
od.G

Plate 7

1. *Porolepis* cf. *spitsbergensis*. Imperfect divisio cranialis anterior in ventral aspect. Specimen No. A. 33989, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Lower Devonian (Wood Bay Series), Spitsbergen. Same specimen as in pl. 8:2–4. × 9/4. In alcohol.

2. *Porolepis brevis* JARVIK. Fronto-ethmoidal shield in dorsal aspect. Superficial layer partly removed to show sensory canals and richly branching sensory canal tubes. Specimen No. P. 52688, Brit. Mus., London. Coll. ENS. exp. 1939. Garborgnuten, Ekmanfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). × 9/4. In xylol.

3, 4. *Porolepis brevis* JARVIK. Imperfect skull in dorsal and antero-lateral aspects. Specimen from block 1964:41, Mus. de Paléont., Paris. Coll. French exp. 1964. Grønhorg, Dicksondalen, Spitsbergen. Lower Devonian (Wood Bay Series). In alcohol. 3, × 9/8; 4, × 3/2.

Ju, jugal; *La*, lachrymal; *Lj*, lower jaw; *Mx*, maxillary; *PaIt*, parietointertemporal; *Po*, postorbital; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate; *Prart*, prearticular; *Prsp*, prespiracular plate; *St*, supratemporal.

c.a.ci, canal for a. carotis interna; *c.a.cib*, canal for medial branch of a. carotis interna; *co*, posterior corner of postnasal wall; *c. pap*, *c. pin*, parapineal and pineal canals; *et. com*, ethmoidal commissural canal; *fe. exa*, *fe. exp*, fenestra exonarina anterior and posterior; *fe. o*, orbital fenestra; *fe.vl*, ventro-lateral fenestra; *fo. nc*, pit for anterior end of notochord; *f. P*, foramen in parasphenoid for buccohypophysial duct; *gr. orp*, posterior groove of orbito-rostral passage; *i. exp*, notch in frontoethmoidal shield forming anterior part of fenestra exonarina posterior; *ioc*, infraorbital sensory canal; *la. De*, antero-medial lamina of dentary carrying parasymphysial dental plate; *om*, margin of orbital fenestra; *pl. Id. 4*, pit-line of infradentary 4; *pl. po. Pa*, posterior oblique parietal pit-line; *pr. bp*, basipterygoid process; *pr.pv*, ventro-lateral process of postnasal wall; *ri. in*, internasal ridge; *soc*, supraorbital sensory canal.

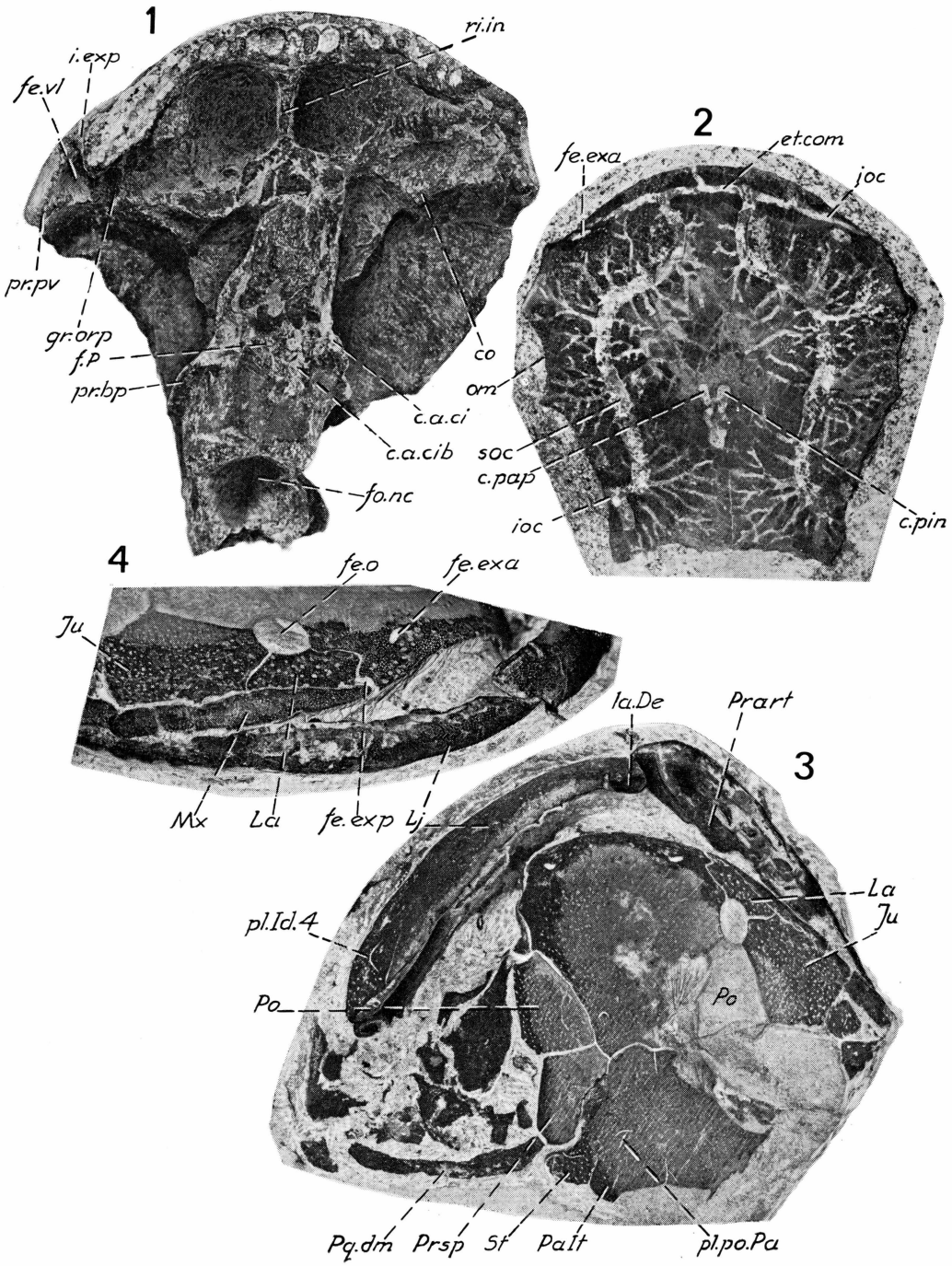

1
ri.in
i.exp
fe.vl
pr.pv
gr.orp
f.p
pr.bp
co
c.a.ci
c.a.cib
fo.nc
2
fe.exa
et.com
joc
om
soc
c.pap
ioc
c.pin
4
fe.o
fe.exa
Ju
Mx
La
fe.exp
Lj
3
la.De
Prart
La
Ju
pl.Id.4
Po
Po
Pq.dm
Prsp
St
Pa.It
pl.po.Pa

Plate 8

1. *Porolepis brevis* JARVIK. Imperfect fronto-ethmoidal shield. Inner side. Specimen No. P. 6980, Pal. Sect., Stockh. Coll. ENS. exp. 1939. Sigurdfjellet, Woodfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). × 5/3.

2, 3. *Porolepis* cf. *spitsbergensis*. Fronto-ethmoidal shield of specimen in pl. 7:1 in anterior and dorsal aspects. × 4/3.

4. Part of same shield in antero-dorsal view to show blister-like patches of cosmine. × 10/3.

FrD, frontodermosphenotic; *Na*, nasals; *Ptr*, postrostrals; *Te*, tectals.

cosm, blister-like patches of cosmine; *fe. exa*, fenestra exonarina anterior; *i. exp*, notch forming anterior part of fenestra exonarina posterior; *ioc*, infraorbital sensory canal; *od. La*, area of fronto-ethmoidal shield overlapped by lachrymal; *pl. Fr*, frontal pit-line; *soc*, supraorbital sensory canal.

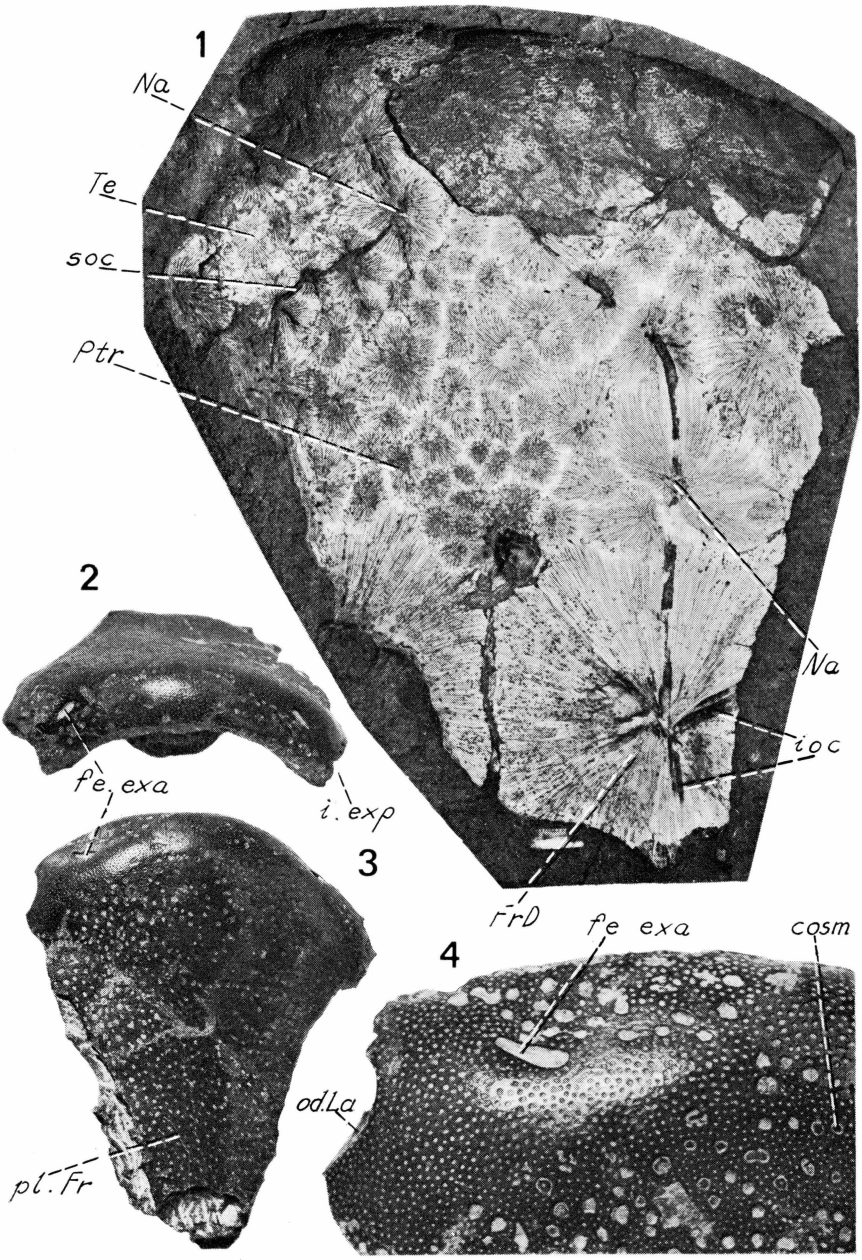

1
Na
Te
soc
ptr
Na
ioc
frO
2
fe exa
i. exp
3
pl. Fr
4
fe exa
cosm
od. La

Plate 9

Porolepis cf. *brevis*

1, 2. Imperfect divisio cranialis anterior in lateral and ventral aspects. Specimen No. A. 28626, Pal. Mus., Oslo. Coll. A. HEINTZ, 1960. Lykta, Dicksonfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). × 5/4.

art. am2, posterior area in floor of fossa autopalatina articulating with anteromedial articular lamina of palatoquadrate; *art. e*, area of postnasal wall articulating with ethmoidal articular process of palatoquadrate; *c. a. ci*, canal for a. carotis interna; *c. a. om*, canal for a. ophthalmica magna; *c. a. pal*, canal for a. palatina; *cav. in*, cavum internasale; *co*, posterior corner of postnasal wall *c. v. pit*, canal for pituitary vein; *e. pi*, pineal elevation; *fe. exa*, fenestra exonarina anterior; *fe. vl*, ventro-lateral fenestra; *fo. aup*, fossa autopalatina; *gr. psp*, prespiracular groove; *i. exp*, notch in margin of fronto-ethmoidal shield forming anterior part of fenestra exonarina posterior; *i. m. sc*, area of insertion of subcranial muscle; *od. La*, *od. Mx*, *od. Po*, areas of fronto-ethmoidal shield overlapped by lachrymal, maxillary and postorbital; *om*, margin of orbital fenestra; *pr. bp*, basipterygoid process; *ri. in*, internasal ridge; *tt. P*, teeth or pits for teeth of parasphenoid.

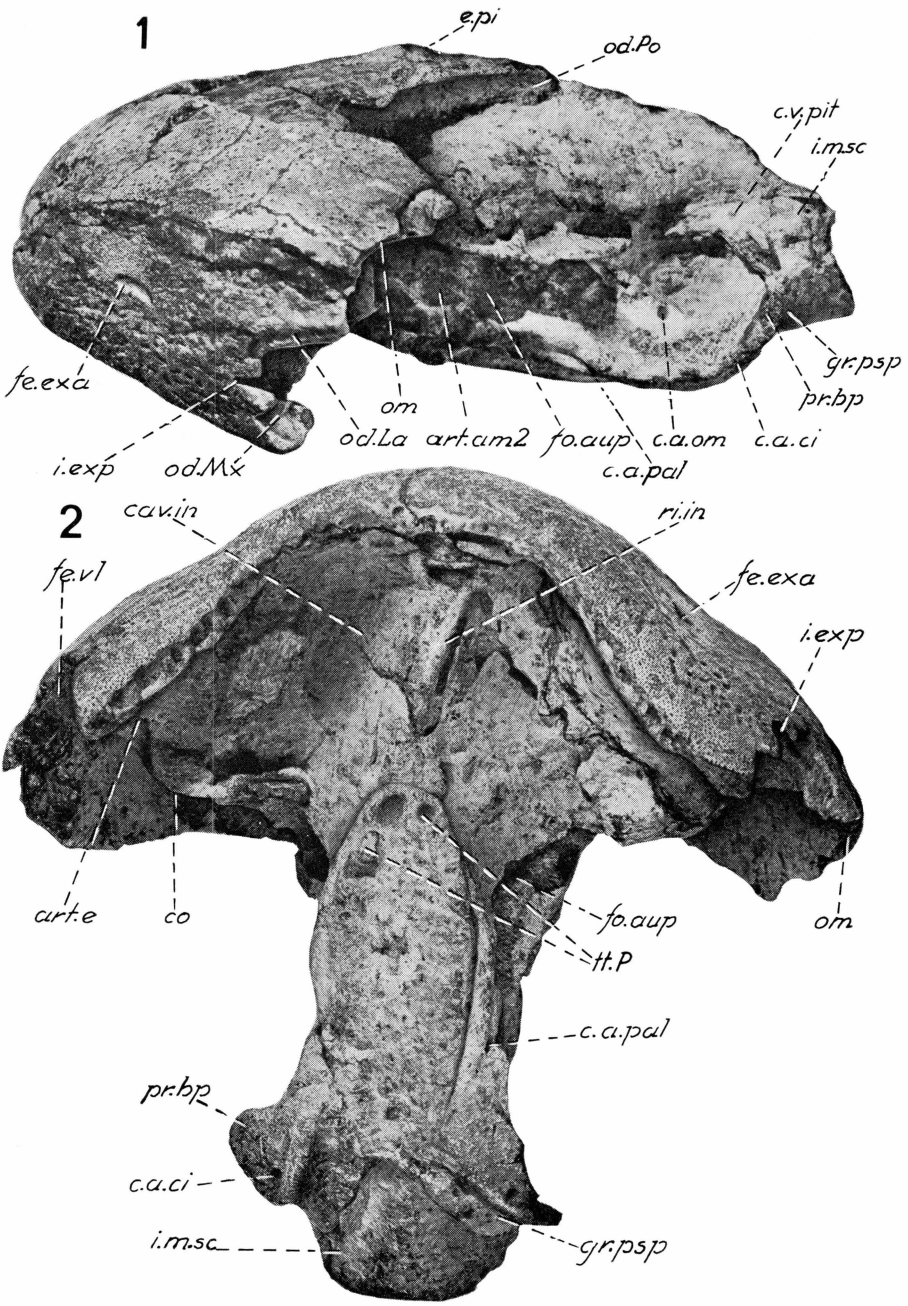

1
epi
od.Po
c.v.pit
i.m.sc
fe.ex.a
gr.psp
pr.hp
om
od.La
art.am2
fo.aup
c.a.om
c.a.ci
i.exp
od.Mx
c.a.pal
2
cav.in
ri.in
fe.v.l
fe.ex.a
i.exp
art.e
co
fo.aup
om
tt.P
c.a.pal
pr.hp
c.a.ci
i.m.sc
gr.psp

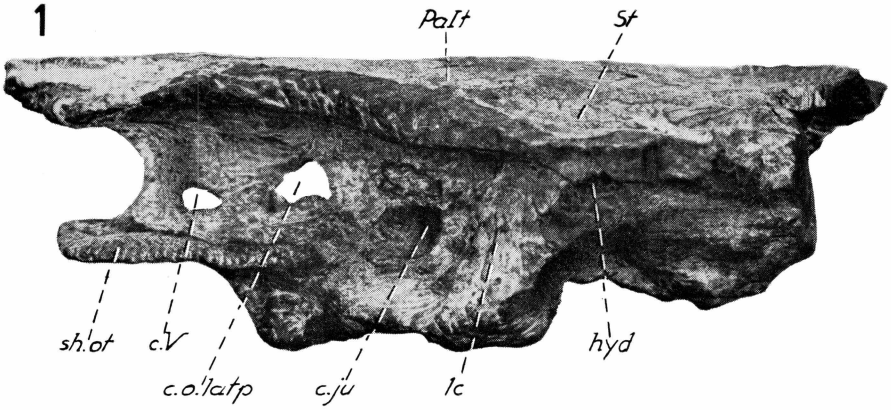
Plate 10

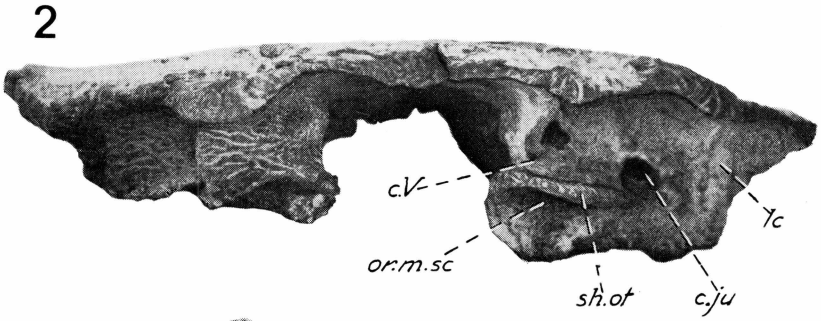
Porolepis sp.

1–3. Imperfect divisio cranialis posterior in lateral, anterior and ventral aspects. Specimen No. P. 6955, Pal. Sect., Stockh. Coll. ENS. exp. 1939. Kronprinshøgda, Woodfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). Same specimen as figured by BJERRING, 1967, pl. 13:A. × 5/4.

PaIt, parietointertemporal; *St*, supratemporal.

cav. cr, cranial cavity; *c. ju*, jugular canal; *c. o. latp*, canal for r. ophthalmicus lateralis VII (damaged); *c. V*, canal for n. trigeminus; *fe. ov*, fenestra ovalis; *hyd*, articular area for dorsal articular head of hyomandibula; *lc*, lateral commissure; *or. m. sc*, area of origin of subcranial muscle; *pr. po*, processus postoticalis; *ri. ju*, jugular ridge; *sh. ot*, otical shelf.


1
PaIt
St
sh.ot
c.V
c.o.latp
c.ju
lc
hyd


2
c.V
lc
or.m.sc
sh.ot
c.ju

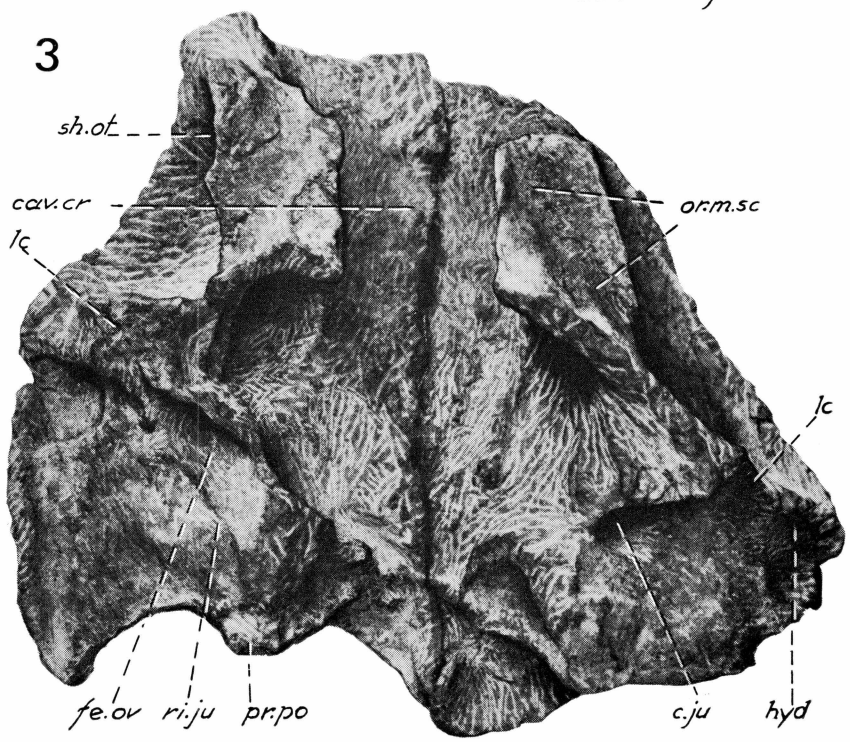

3
sh.ot
cav.cr
or.m.sc
lc
lc
fe.ov
ri.ju
pr.po
c.ju
hyd

Plate 11

All specimens from Lower Devonian (Wood Bay Series), Spitsbergen.

1. *Porolepis brevis* JARVIK. Almost complete fronto-ethmoidal shield. Dorsal aspect. Specimen No. A. 30483, Pal. Mus., Oslo. Coll. A. HEINTZ, 1964. Ekmanfjorden. × 9/8.

2, 5. *Porolepis spitsbergensis* JARVIK. Holotype. Incomplete divisio cranialis anterior in dorsal and lateral aspects. Specimen Nos. A. 34034, 34035, Pal. Mus., Oslo. Figured by JARVIK, 1942, pl. 1; pl. 2:2, 3. × 3/2.

3. *Porolepis brevis* JARVIK. Fronto-ethmoidal shield with anterior part of external cheek-plate. Dorsal view. Specimen No. A. 28633, Pal. Mus., Oslo. Coll. A. HEINTZ, 1960. Lykta, Dicksonfjorden. × 3/2 approx. In alcohol.

4. *Porolepis brevis* JARVIK. Fronto-ethmoidal shield. Dorsal aspect. Specimen No. P. 52686, Brit. Mus., Lond. Coll. ENS. exp. 1939. Lykta, Dicksonfjorden. × 3/2.

6. *Porolepis brevis* JARVIK. Incomplete fronto-ethmoidal shield in dorsal aspect. Specimen No. P. 52678, Brit. Mus., Lond. Coll. ENS. exp. 1939. × 3/1.

7. *Porolepis* sp. Incomplete parietal shield in dorsal view. Specimen No. A. 33991, Pal. Mus., Oslo. Coll. Norw. exp. Sigurdfjellet, Woodfjorden. × 9/8.

FrD, frontodermosphenotic; *Ju*, jugal; *La*, lachrymal; *Na*, nasal; *PaIt*, parieto-intertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Prsp*, prespiracular plate; *Ptr*, postrostral; *Sq. u*, upper squamosal; *St*, supratemporal.

c. o. lat, canal for r. ophthalmicus lateralis VII; *cr. rc*, crista rostro-caudalis; *e. pi*, pineal elevation; *fe. exa*, fenestra exonarina anterior; *fe. o*, orbital fenestra; *fe. vl*, fenestra ventro-lateralis; *i. exp*, *i. La*, notches forming anterior and posterior parts of fenestra exonarina posterior; *ioc*, infraorbital sensory canal; *od. La*, area overlapped by lachrymal; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. St*, supratemporal pit-line; *pl. tr. Pa*, transverse parietal pit-line.

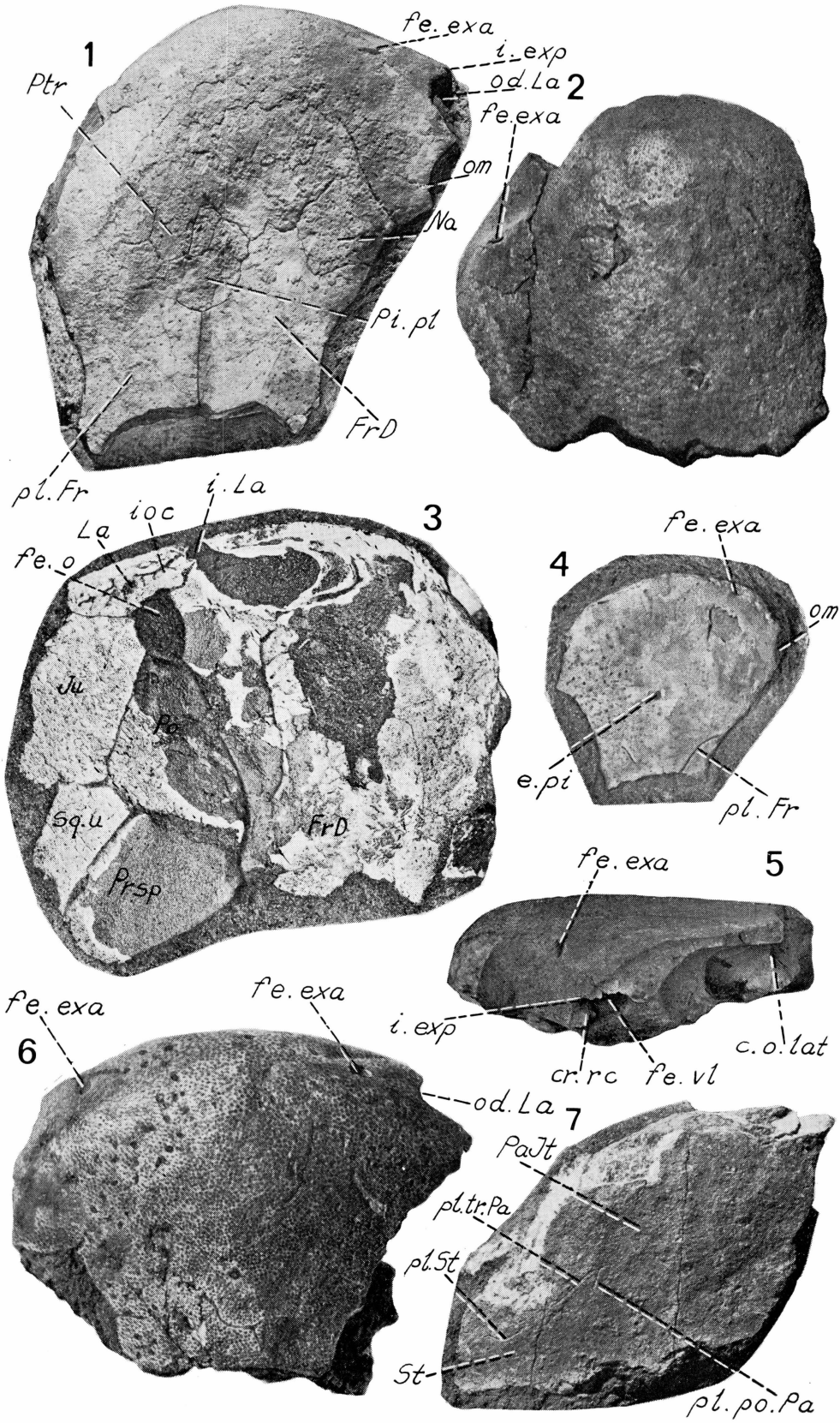

1
fe. exa
i. exp
od. La
Ptr
om
Na
pi. pl
FrD
pl. Fr
2
fe. exa
3
i. La
ioc
La
fe. o
Ju
Po
Sq. u
FrD
Prsp
4
fe. exa
om
e. pi
pl. Fr
5
fe. exa
i. exp
c. o. lat
cr. rc
fe. vl
6
fe. exa
fe. exa
od. La
7
PaJt
pl. tr. Pa
pl. St
St
pl. po. Pa

Plate 12

1–3. *Porolepis* sp. 1, 2, imperfect lower jaw in lateral and medial aspects. 3, anterior part of same jaw in dorsal aspect. Specimen No. A. 34002, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Lower Devonian (Wood Bay Series), Spitsbergen. × 9/10.

4. *Porolepis* sp. Anterior part of lower jaw in dorsal aspect. Photograph of latex cast. Specimen No. A. 34039, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Lykta, Nathorstdalen, Spitsbergen. Lower Devonian (Wood Bay Series). × 9/10.

5. *Porolepis* sp. Posterior part of imperfect lower jaw in lateral aspect. Specimen No. A. 34003, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Lykta, Dicksonfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). × 12/5.

6. *Heimenia* sp. Lower jaw in lateral aspect. Specimen No. P. 52674, Brit. Mus., Lond. Coll. ENS. exp. 1939. Jacobsenbukta, Woodfjorden, Spitsbergen. Lower or Middle Devonian (Verdalen Member of Stjördalen Division). × 3/5.

Prart, prearticular; *Psy*, bone fragment, probably of parasymphysial dental plate.

cot1, *cot2*, *cot3*, tusks of coronoids 1–3; *det*, teeth of dentary; *de. tl*, tooth-less anterior part of dorsal margin of dentary; *fo. ad*, adductor fossa; *gr. p-mc*, groove marking course of preoperculo-mandibular sensory canal; *i. Sy*, notches for symphysial dermal bones; *la. De*, antero-medial lamina of dentary carrying parasymphysial dental plate; *la. Co1*, *la. Co2*, *la. Co3*, vertical tooth-bearing laminae of coronoids 1–3; *plh. Id*, horizontal pit-lines of infradentaries; *pl. Id.2*, *pl. Id.4*, pit-lines of infradentaries 2 and 4.

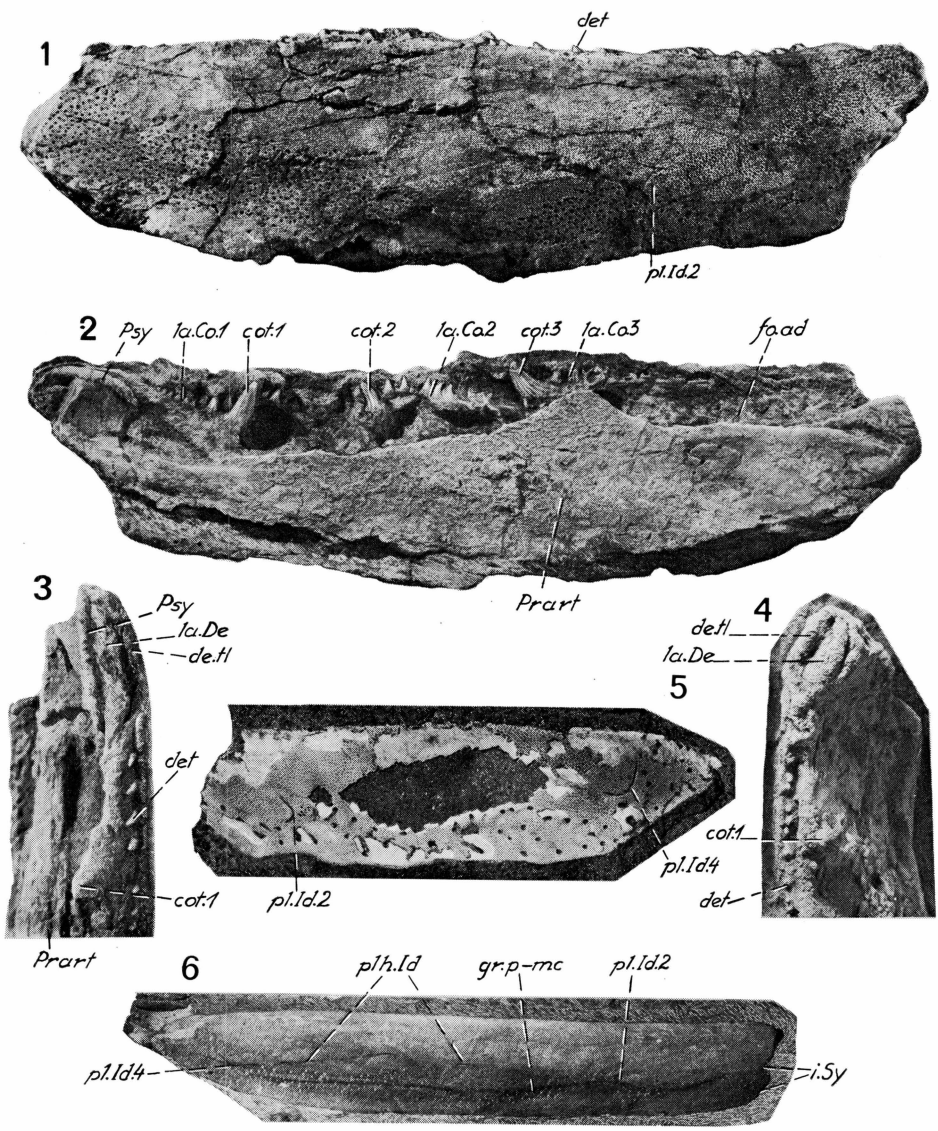

1
det
pl.Id.2
2
Psy
la.Co.1
cot:1
cot:2
la.Ca2
cot:3
la.Co3
fo.ad
Prart
3
Psy
la.De
de.tl
det
cot:1
Prart
pl.Id.2
4
det
la.De
5
cot:1
pl.Id.4
det
6
plh.Id
gr.p-mc
pl.Id.2
pl.Id.4
i.Sy

Plate 13

Porolepis spp.

All specimens from Lower Devonian (Wood Bay Series), Spitsbergen.

1. Left principal gular plate in external view. Specimen No. P. 6950, Pal. Sect., Stockh. Coll. ENS. exp. 1939. Kronprinshøgda, Bockfjorden. × 2/3.

2. Left principal gular plate in external view. Photograph of latex cast. Specimen No. P. 52690, Brit. Mus., Lond. Coll. ENS. exp. 1939. Kronprinshøgda, Bockfjorden. × 2/3.

3. Right cleithrum in external view. Photograph of latex cast. Specimen No. P. 6967, Pal. Sect., Stockh. Coll. ENS. exp. 1939. Fiskedalen, Dicksonfjorden. × 2/3.

4. Impression of external side of right cleithrum. No. P. 52702, Brit. Mus., Lond. Coll. ENS. exp. 1939. Stjørdalen, Woodfjorden. × 4/3.

3. Right cleithrum in inner aspect. Photograph of latex cast. Specimen No. A. 3987, Pal. Mus. Oslo. Coll. Norw. exp. Reinsdyrflya. × 2/3.

6. Right cleithrum. Impression of inner side. Specimen No. A. 34022, Pal. Mus., Oslo. Coll. ENS. exp. 1939. Borgen, Dicksonfjorden. × 2/3.

7. Right cleithrum in external view. Specimen from same block (1964:41) as specimens shown in text-fig. 2 and pl. 7:3, 4. Coll. French exp. 1964. Grønhorg, Dicksondalen. × 4/3.

ar. e. sh, area for attachment of endoskeletal shoulder-girdle; *ar. tri*, triangular area; *od. G*, area overlapped by principal gular of other side; *od. Gm*, area overlapped by median gular plates; *od. Op*, area overlapped by opercular; *od. Sbm*, area overlapped by submandibulars; *od1. Clav*, area overlapped by clavicle; *og. sc*, area overlapping scales.

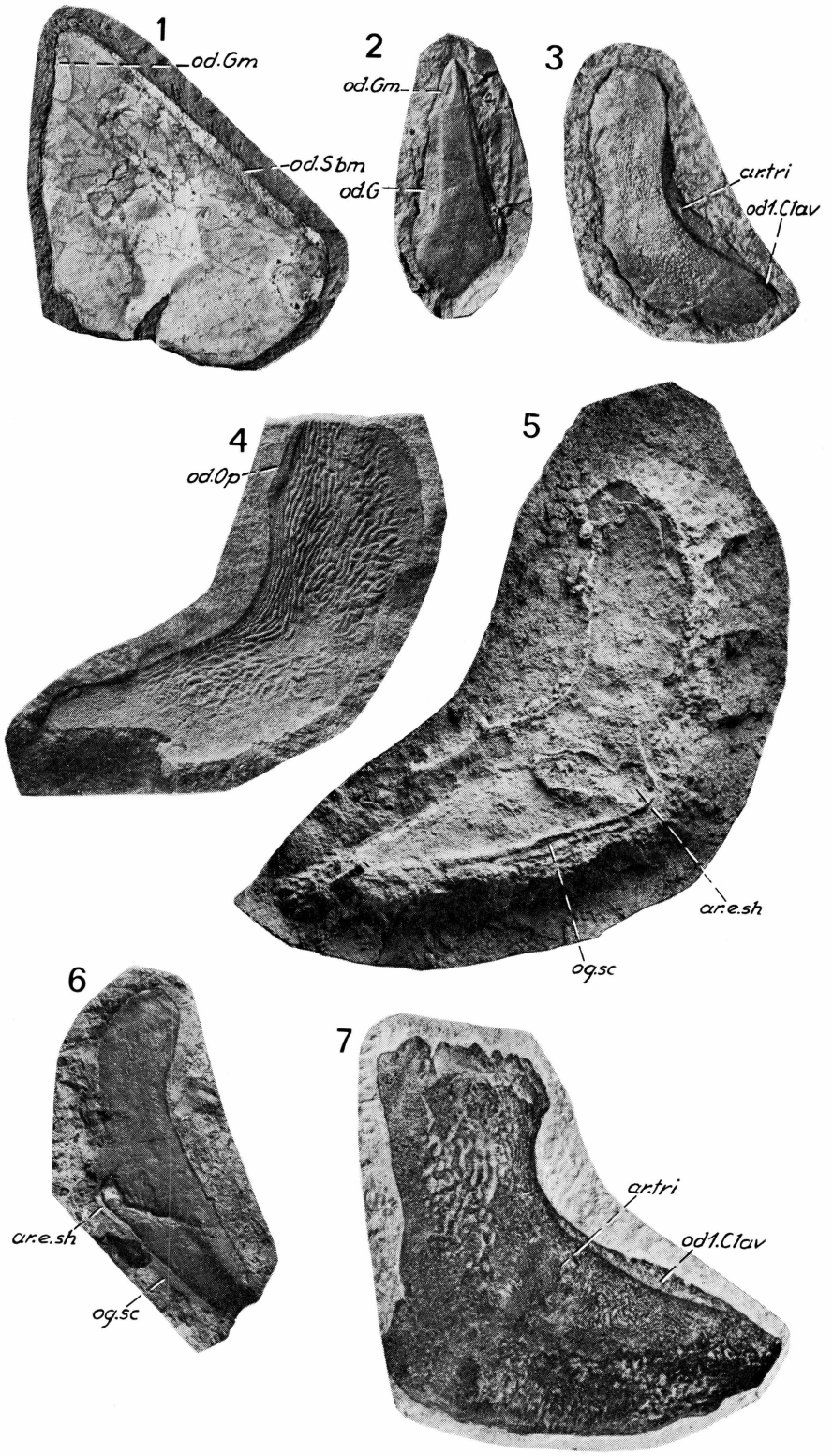

1
od.Gm
od.Sbm
2
od.Gm
od.G
3
ar.tri
od1.C1av
4
od.Op
5
ar.e.sh
og.sc
6
ar.e.sh
og.sc
7
ar.tri
od1.C1av

Plate 14

1, 2. *Glyptolepis?* cf. *paucidens*. Imperfect divisio cranialis anterior in lateral and ventral aspects. Specimen No. P. 47838, Brit. Mus., London. Coll. J. Saxon 1965. Thurso Bay, Caithness, Scotland. Middle Devonian. × 9/10.

3, 4. *Glyptolepis* sp. Imperfect divisio cranialis anterior in dorsal aspect (× 9/10) and posterior part in lateral aspect (× 9/5). Specimen No. 53382, Geol. Surv., Lond. Scotland. Middle Devonian. Same specimen as figured by Jarvik, 1954, fig. 19 C, D.

5. *Glyptolepis* sp. Imperfect divisio cranialis anterior in ventral aspect. Specimen No. 53388, Geol. Surv., London. Scotland. Middle Devonian. Same specimen as figured by Jarvik, 1954, fig. 19 A. × 6/5.

FrD, frontodermosphenotic; *Na*, nasal; *P*, parasphenoid; *Ptr*, postrostral.

ar. Vo, vomeral area; *c. a. ci*, canal for a. carotis interna; *c. a. cib*, canal for medial branch of a. carotis interna; *c. a. om*, canal for a. ophthalmica magna; *c. a. pal*, canal for a. palatina; *cav. in*, internasal cavity; *cav. nc*, cavity of nasal capsule; *c. bh*, canals for buccohypophysial ducts; *c. o. lat*, canal for r. ophthalmicus lateralis; *c. prl*, *c. prm*, lateral and medial profundus canals; *c. pr-p*, canal for combined profundus-palatine nerve; *c. prt*, canals for twigs of medial terminal profundus branch; *c. p. tub*, canal for pars tuberalis of adenohypophysis; *c. v. ca*, canal for v. cerebralis anterior; *c. II*, *c. III*, canals for n. opticus and n. oculomotorius; *c. IV*, canal and groove for n. trochlearis; *fe. vl*, fenestra ventro-lateralis; *fo. aup*, fossa autopalatina; *fo. hyh*, ventral horizontal portion of fossa hypophyseos; *fo. nc*, pit for anterior end of notochord; *gr. psp*, prespiracular groove; *gr. II*, groove for n. opticus; *ioc*, infraorbital sensory canal; *od. Po*, area overlapped by postorbital; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line; *pr. bp*, basipterygoid process; *pr. conn*, processus connectens; *pr. sp*, suprapterygoid process; *re. inf*, infundibular recess of cranial cavity; *re. lhy*, recess for lateral lobe of adenohypophysis; *ri. in*, internasal ridge; *ta. P*, raised tooth-bearing area of parasphenoid; *w. mn*, medial nasal wall.

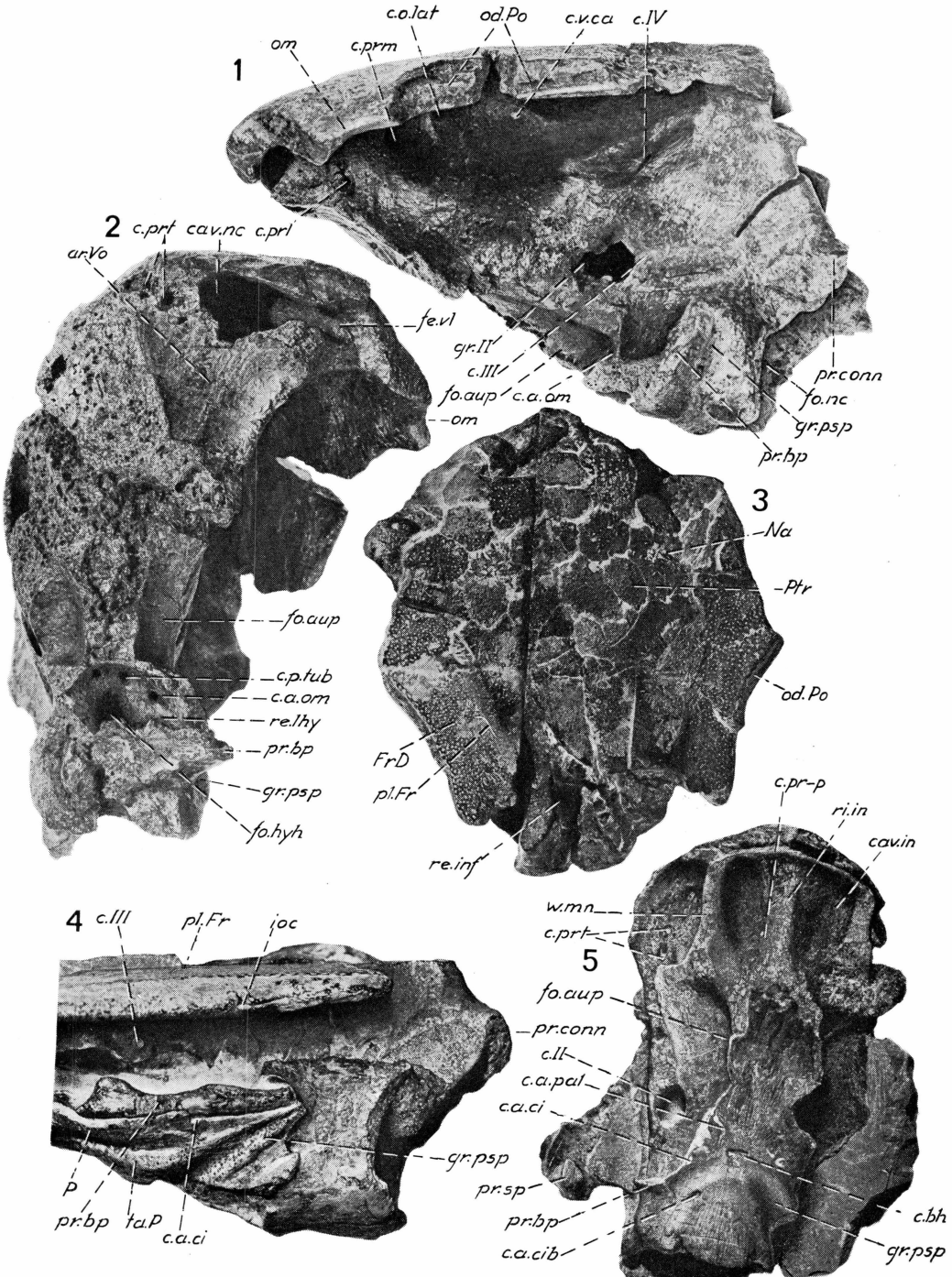

1
c.o.lat
od.Po
c.v.ca
c.IV
om
c.prm
2
c.prf
cav.nc
c.prl
ar.Vo
fe.vl
gr.II
c.III
fo.aup
c.a.om
om
pr.conn
fo.nc
gr.psp
pr.bp
3
Na
Ptr
od.Po
fo.aup
c.p.tub
c.a.om
re.lhy
pr.bp
gr.psp
fo.hyh
FrD
pl.Fr
re.inf
c.pr-p
ri.in
cav.in
4
c.III
pl.Fr
ioc
w.mn
c.prf
5
fo.aup
pr.conn
c.II
c.a.pal
c.a.ci
gr.psp
pr.sp
pr.bp
c.a.cib
c.bh
gr.psp
p
pr.bp
ta.p
c.a.ci

Plate 15

Glyptolepis groenlandica n. sp.

Flattened head with anterior part of body in dorsal aspect. Specimen No. P. 1523, Min. Mus., Copenh. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*). × 9/8.

Et, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *FrD*, frontodermosphenotic; *Ju*, jugal; *Lj*, lower jaw; *Op*, opercular; *PaIt*, parietointertemporal; *Pi. pl*, pineal plate; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Qj*, quadratojugal; *Sclm*, supracleithrum; *Sop*, subopercular; *Sq. u*, upper squamosal; *St*, supratemporal.

ioc, infraorbital sensory canal; *msc*, main sensory canal; *p-mc*, preoperculomandibular sensory canal.

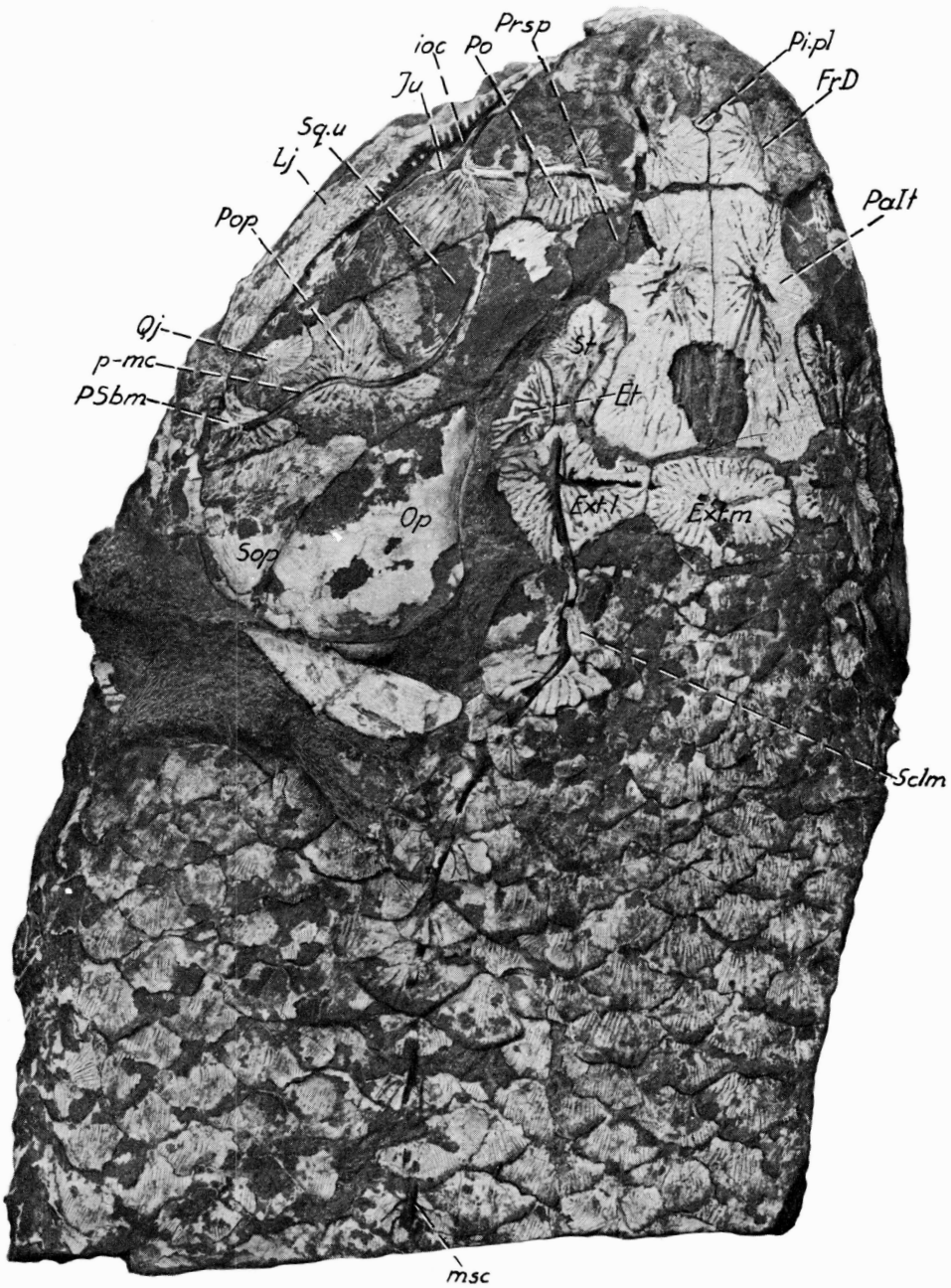

Prsp
ioc
Po
Pi.pl
Ju
FrD
Sq.u
Lj
PaIt
Pop
Qj
St
p-mc
PSbm
Et
Ext.l
Ext.m
Op
Sop
Sclm
msc

Plate 16

Glyptolepis groenlandica n. sp.

Skull compressed from lateral sides. Specimen No. P. 1518, Min. Mus., Copenh. Coll. 1956. Hesteskoen, Canning Land. Middle Devonian (Series with *Asterolepis saeve-soederberghi*). From same block as holotype. × 4/3.

1. Left side in external view.

2. External cheek-plate and adjoining parts of right side in inner view.

Clm, cleithrum; *De*, dentary; *Dpl*, dermopalatine; *E. sh*, endoskeletal shoulder-girdle; *Et*, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *Fr-et. sh*, fronto-ethmoidal shield; *G*, principal gular plate; *Ju*, jugal; *La*, lachrymal; *Lj*, lower jaw; *Mx*, maxillary; *Op*, opercular; *PaIt*, parietointertemporal; *Po*, postorbital; *Pop*, preopercular; *Pq*, palatoquadrate; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Pt*, posttemporal; *Oj*, quadratojugal; *Rbr*, branchiostegal ray; *Sbm*, submandibulars; *Sclm*, supracleithrum; *Sop*, subopercular; *Sq. l*, *Sq. u*, lower and upper squamosals; *St.* supratemporal.

fe. exa, fenestra exonarina anterior; *fe. o*, orbital fenestra; *i. La*, notch in lachrymal forming posterior part of fenestra exonarina posterior; *i. spir*, notch in upper squamosal forming part of spiracular fenestra; *p-mc*, preoperculo-mandibular sensory canal; *p. Sym*, articular pit on posterior side of pars quadrata for symplectic; *w. pn*, postnasal wall.

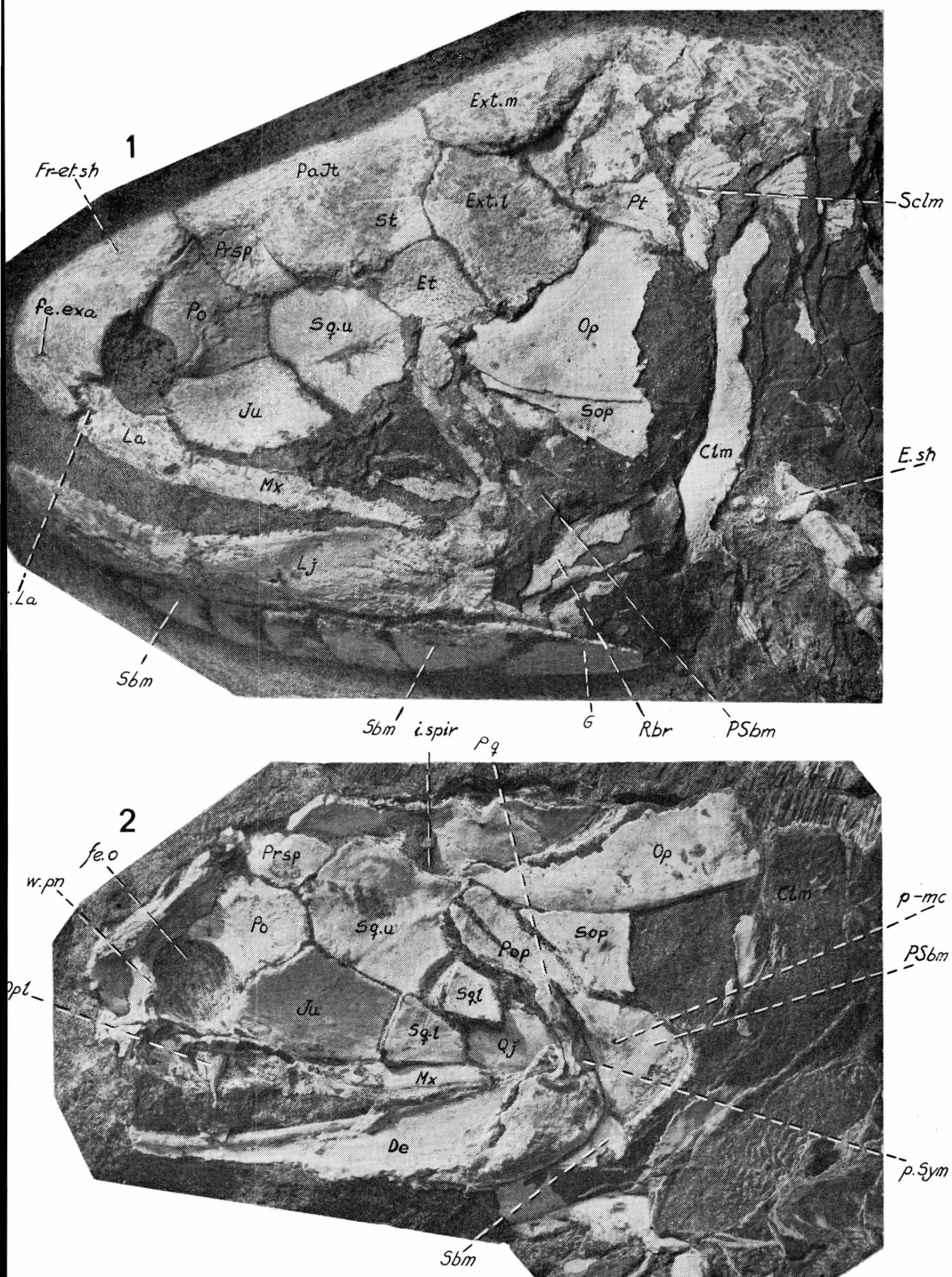

1
Fr-ef.sh
Ext.m
PaJt
Ext.l
Pt
Sclm
St
Prsp
Et
fe.exa
Po
Sq.u
Op
Ju
Sop
La
Clm
E.sh
Mx
Lj
Sbm
i.spir
Pq
G
Rbr
PSbm
2
fe.o
w.pn
Prsp
Op
Clm
p-mc
Po
Sq.u
Sop
Pop
PSbm
Sql
Ju
Sqt
Qj
Mx
De
p.Sym
Sbm

Plate 17

Glyptolepis groenlandica n. sp.

Dorso-ventrally flattened skull from same block as holotype prepared from ventral side to show hyobranchial apparatus. Same specimen as in pl. 18:1. Specimen No. P. 1510, Min. Mus., Copenh. Coll. 1956. Hesteskoen, Canning Land, East Greenland, Middle Devonian (Series with *Asterolepis saevesoederberghi*).

1. Skull in dorsal view. In alcohol. × 1/1.

2. Same in antero-lateral view to show groove of lachrymal for posterior external nasal tube. In alcohol. × 8/3.

3. Anterior part of skull in ventral aspect. In alcohol. × 8/3.

Bb, basibranchial; *Ch*, ceratohyal; *Enpt*, entopterygoid; *Ext. m*, median extrascapular; *HbI*, *HbII*, hypobranchials I and II; *Hh*, hypohyal; *Ju*, jugal; *La*, lachrymal; *Lj*, lower jaw; *Mx*, maxillary; *Op*, opercular; *P*, parasphenoid; *PaIt*, parietointertemporal; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *Rm*, median rostral; *Sclm*, supracleithrum; *Sq. u*, upper squamosal; *Sym*, symplectic; *Uh*, urohyal; *Vo*, vomer.

c. a. ci, canal for a. carotis interna; *cav. in*, internasal cavity; *dplt*, dermopalatine tusk; *fe. exa*, fenestra exonarina anterior; *fe. exp*, fenestra exonarina posterior; *fe. o*, orbital fenestra; *f. P*, foramen in parasphenoid for buccohypophysial ducts; *gr. La*, groove of lachrymal for posterior external nasal tube (nasolachrymal duct); *gr. psp*, prespiracular groove; *m. bhe. a*, area of attachment of musculus branchiohyoideus externus; *m. sarIa*, area of attachment of m. subarcualis rectus; *pl. Qj*, quadratojugal pit-line; *pr. b*, processus basalis; *pr. bp*, basipterygoid process; *p. Sym*, articular pit for symplectic in posterior side of pars quadrata; *ri. in*, internasal ridge.

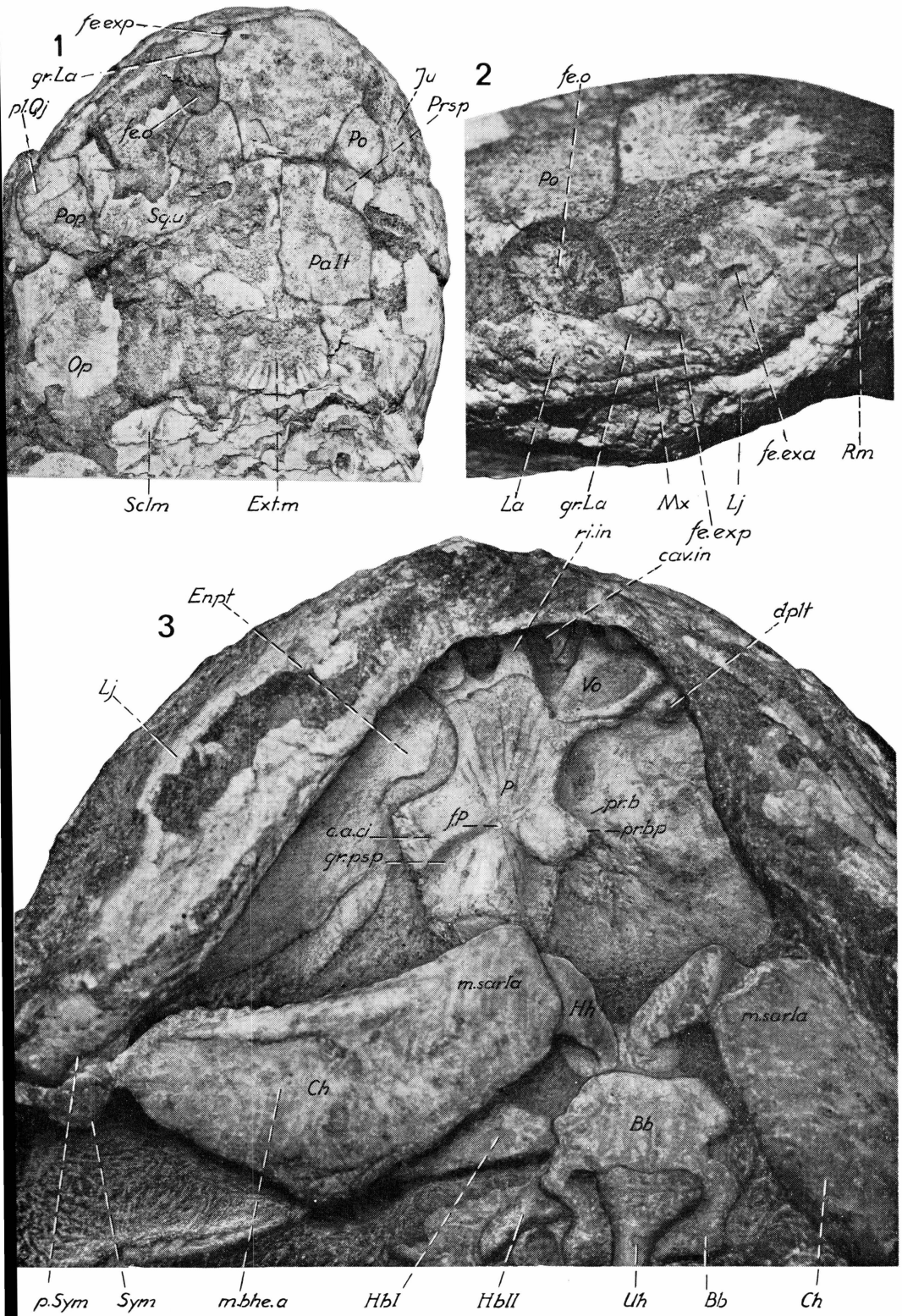

1
fe.exp
gr.La
pl.Qj
fe.o
Ju
Prsp
Po
Pop
Sq.u
Palt
Op
Sclm
Ext.m
2
fe.o
Po
fe.exa
Rm
La
gr.La
Mx
Lj
fe.exp
3
ri.in
cav.in
Enpt
dplt
Lj
Vo
Pl
pr.b
pr.bp
fp
c.a.cj
gr.ps.p
m.sarla
Hh
m.sarla
Ch
Bb
p.Sym
Sym
m.bhe.a
HbI
HbII
Uh
Bb
Ch

Plate 18

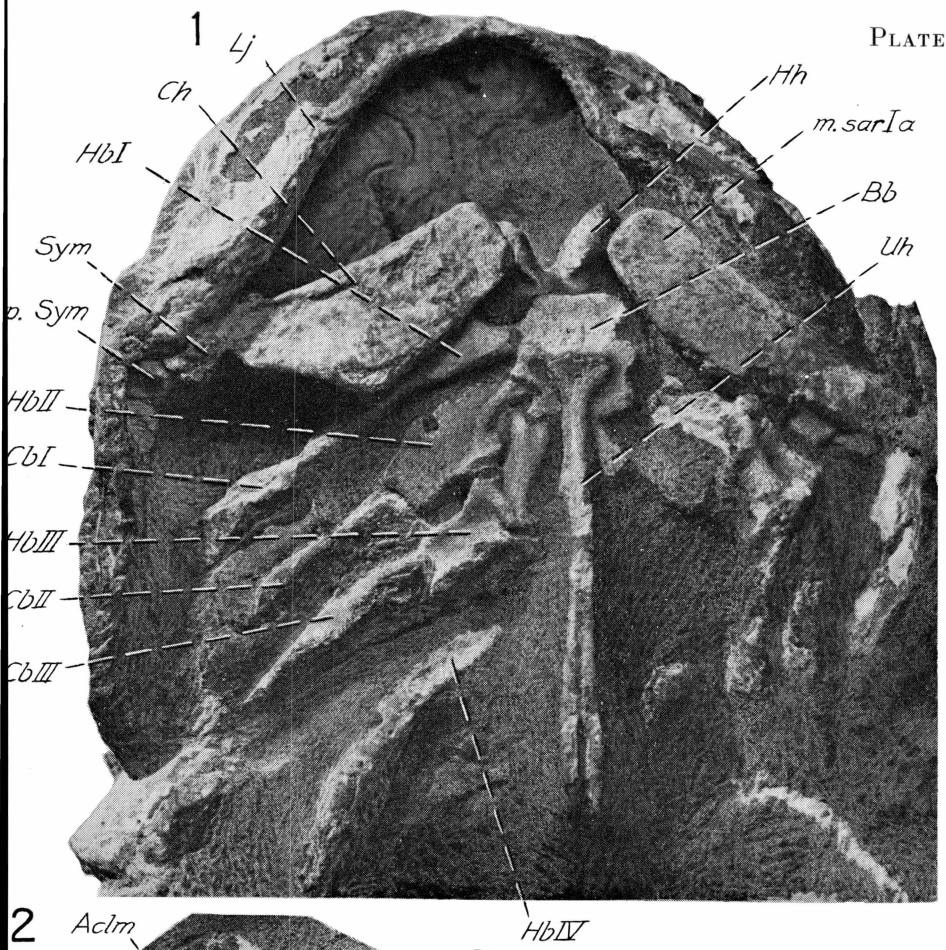
Glyptolepis groenlandica n. sp.

1. Same skull as in plate 17. Ventral aspect. × 3/2.

2. Same skull as in plate 16. External cheek-plate and operculars of right side removed to show palatoquadrate, visceral arches and exoskeletal shoulder-girdle. Lateral aspect. × 3/2.

Aclm, anocleithrum; *Bb*, basibranchial; *Cb*, ceratobranchials; *Cb I*, *Cb II*, *Cb III*, ceratobranchials I, II, and III; *Ch*, ceratohyal; *Clav*, clavicle; *Clm*, cleithrum; *Eb*, epibranchials; *Fr-et. sh*, fronto-ethmoidal shield; *Hb I*, *Hb II*, *Hb III*, *Hb IV*, hypobranchials I–IV; *Hh*, hypohyal; *Hy*, hyomandibula; *Lj*, lower jaw; *Otoc*, otoccipital; *Pa. sh*, parietal shield; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate; *Sclm*, supracleithrum; *Sym*, symplectic; *Uh*, urohyal.

ar. exp, exposed area of entopterygoid; *cav. nc*, cavity of nasal capsule; *cot1*, *cot2*, tusks of coronoids 1 and 2; *la. am*, antero-medial articular area of pars autopalatina of palatoquadrate; *la. com*, commissural lamina of palatoquadrate; *m.sarIa*, area of attachment of musculus subarcualis rectus; *pr. a*, processus ascendens palatoquadrati; *p. Sym*, articular pit for symplectic in posterior side of pars quadrata; *vot*, tusk of vomer.


1
Lj
Ch
HbI
Sym
p. Sym
HbII
CbI
HbIII
CbII
CbIII
Hh
m. sarIa
Bb
Uh
HbIV

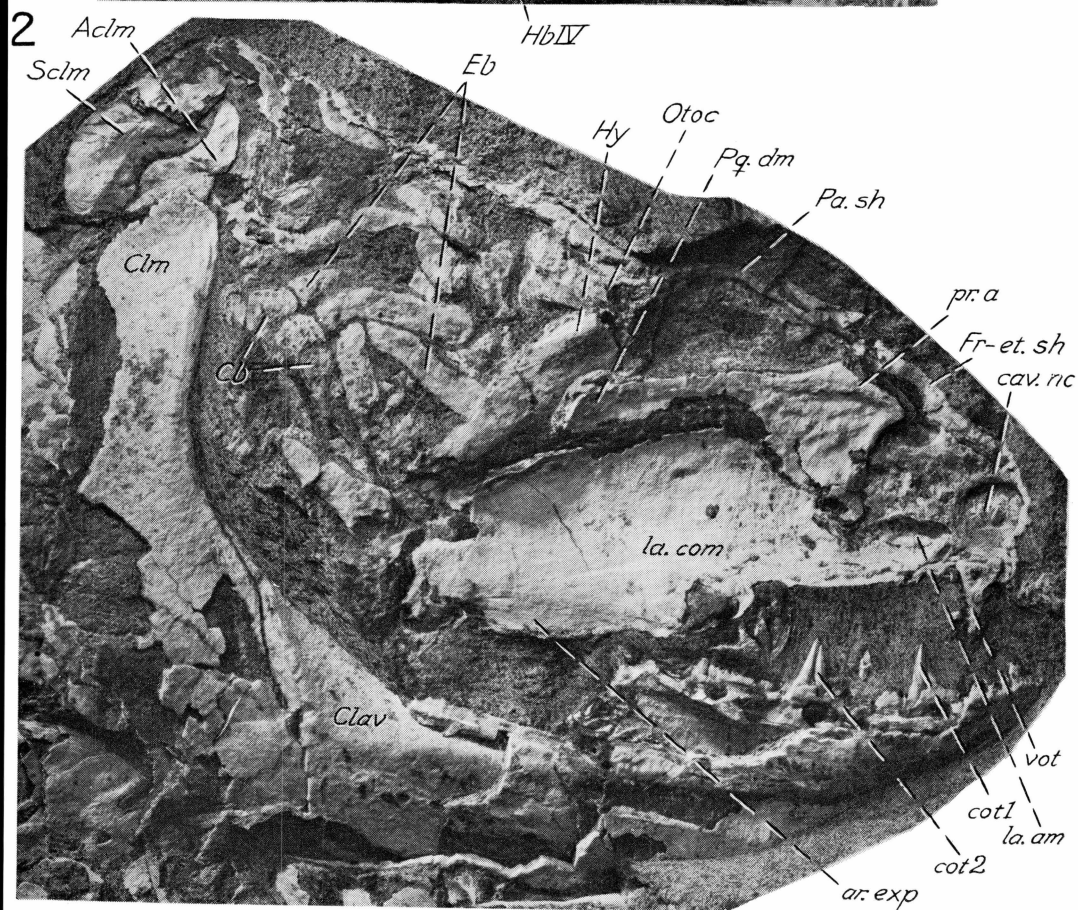

2
Aclm
Sclm
Clm
Cb
Eb
Hy
Otoc
Pq. dm
Pa. sh
pr. a
Fr-et. sh
cav. nic
la. com
Clav
vot
cot1
la. am
cot2
ar. exp

Plate 19

Glyptolepis groenlandica n. sp.

Dorso-ventrally compressed skull from same block as holotype, broken so that dermal cranial roof, external cheek-plate and operculars may be removed. Specimen No. P. 1490, Min. Mus., Copenh. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*). × 3/2.

1. Skull-roof and external cheek-plate in inner aspect.

2. Neural endocranium and parts of visceral endoskeleton in dorsal view.

Et, extratemporal; *Etsph*, ethmosphenoid; *Ext. l*, lateral extrascapular; *Hy*, hyomandibula; *Ju*, jugal; *Mb. art*, pars articularis of meckelian bone; *Op*, opercular; *Otoc*, otoccipital; *PaIt*, parietointertemporal; *Po*, postorbital; *Pop*, preopercular; *Pq. aup*, pars autopalatina of palatoquadrate; *Pq. dm*, postero-dorsal marginal portion of palatoquadrate; *Pq. qu*, pars quadrata; *Prart*, prearticular; *Prsp*, prespiracular plate; *PSbm*, preoperculosubmandibular; *Pt*, posttemporal; *Qj*, quadratojugal; *Sop*, subopercular; *Sq. u*, upper squamosal; *Sym*, symplectic.

cav. cr, cranial cavity; *cr. par*, crista parotica; *fe. o*, orbital fenestra; *fo. ad*, adductor fossa; *fo. br*, fossa bridgei; *gr. buca*, groove for medial buccalis branch; *gr. me*, *gr. mi*, grooves for rr. mandibularis externus and internus VII; *gr. v. fs*, groove for vena facialis superior; *la. am*, antero-medial articular lamina of palatoquadrate; *la. com*, commissural lamina; *lc*, lateral commissure; *pl. Fr*, frontal pitline; *pr. a*, processus ascendens palatoquadrati; *pr. av*, antero-ventral articular process of otoccipital; *pr. e*, ethmoidal articular process of palatoquadrate; *p. Sym*, articular pit for symplectic; *re. sh*, spiraculo-hyomandibular recess; *sh. m*, medial shelf; *sh. ot*, otical shelf; *stcc*, supratemporal commissural sensory canal; *t. tm*, taenia tecti medialis of otoccipital.

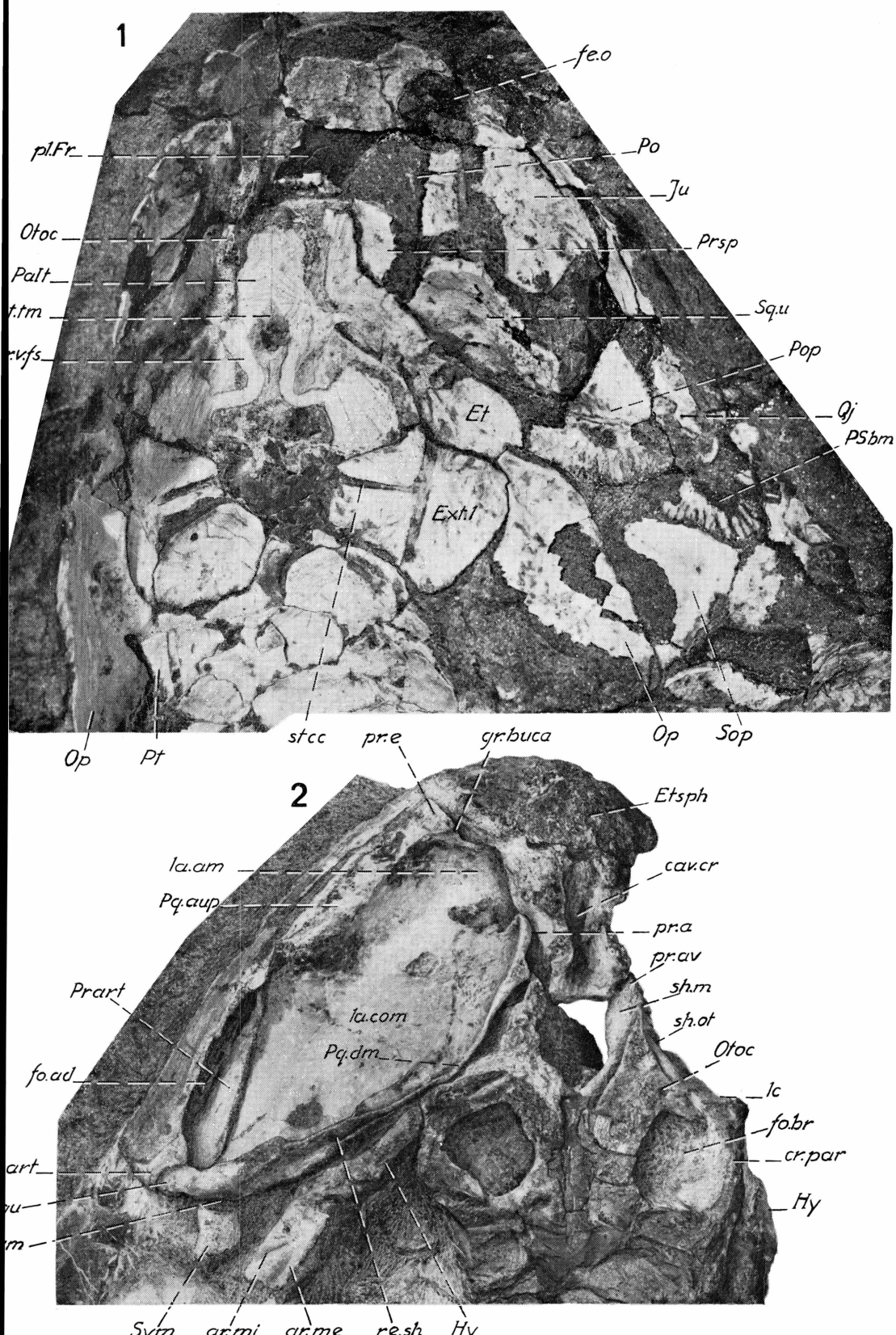

1
fe.o
pl.Fr
Po
Ju
Otoc
Prsp
Palt
t.tm
Sq.u
r.vfs
Pop
Et
Qj
PSbm
Exfl
Op
Pt
st.cc
pr.e
gr.buca
Op
Sop
2
Etsph
la.am
cav.cr
Pq.aup
pr.a
pr.av
Prart
sh.m
la.com
sh.ot
Pq.dm
Otoc
fo.ad
lc
fo.br
art
cr.par
Hy
Sym
gr.mi
gr.me
re.sh
Hy

Plate 20

Glyptolepis groenlandica n. sp.

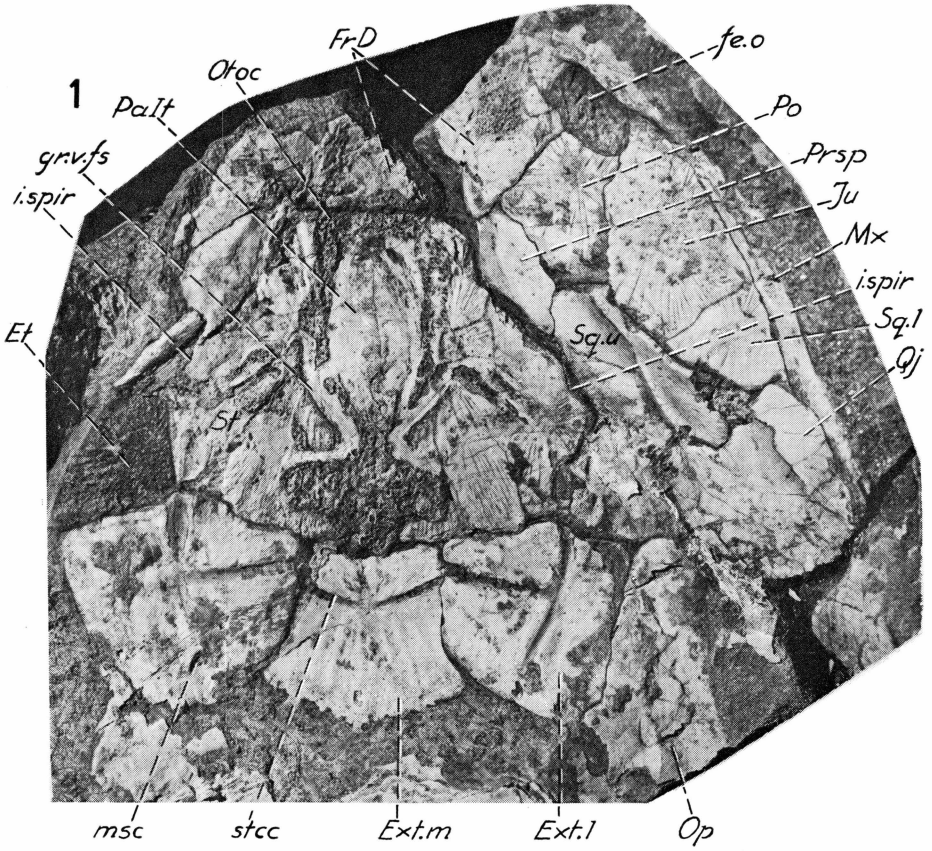
Imperfect dermal cranial roof with adjoining parts of external cheek-plate of two specimens from same block as holotype in inner aspects. Coll. 1956. Hesteskoen, Canning Land, East Greenland (Series with *Asterolepis saevesoederberghi*). × 3/2.

1. Specimen No. P. 1497, Min. Mus., Copenh.

2. Specimen No. P. 1496, Min. Mus., Copenh.

Et, extratemporal; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *FrD*; frontodermosphenotic; *La*, lachrymal; *Ju*, jugal; *Mx*, maxillary; *Op*, operculare *Otoc*, otoccipital; *PaIt*, parietointertemporal; *Po*, postorbital; *Prsp*, prespiracula, plate; *Qj*, quadratojugal; *Sq. l*, *Sq. u*, lower and upper squamosals; *St*, supratemporal.

fe. o, fenestra orbitalis; *gr. v. fs*, groove for vena facialis superior; *ioc*, infraorbital sensory canal; *i. spir*, spiracular notch in margin of supratemporal; *msc*, main sensory canal; *p. p*, *p. pp*, pits for pineal and parapineal organs on inner side of pineal plate; *soc*, supraorbital sensory canal; *stcc*, supratemporal commissural sensory canal.


1
Fr.D
fe.o
Otoc
Pa.lt
Po
gr.v.fs
Prsp
i.spir
Ju
Mx
i.spir
Et
Sq.u
Sq.l
Qj
St
msc
st.cc
Ext.m
Ext.l
Op

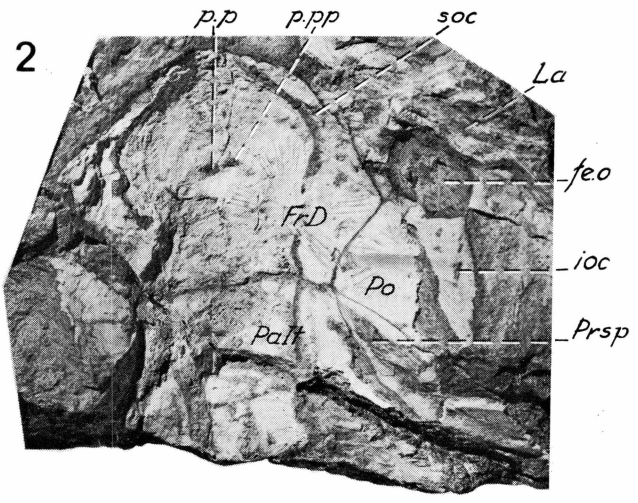

2
p.p
p.pp
soc
La
fe.o
Fr.D
ioc
Po
Prsp
Pa.lt

Plate 21

Glyptolepis groenlandica n. sp.

Specimens from same block as holotype. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*. × 6/5.

1. Incomplete dermal cranial roof with part of external cheek-plate and dorsal parts of neural endocranium. Ventral aspect. Specimen No. P. 1522, Min. Mus., Copenh.

2, 3. Sectioned specimen. 2, dermal cranial roof with dorsal parts of neural endocranium and parts of external cheek-plates. Ventral aspect. 3, counterpart in dorsal aspect. Photographs before the two pieces were glued together.

Et, extratemporal; *Etsph*, ethmosphenoid; *Ext. l*, *Ext. m*, lateral and median extrascapulars; *Op*, opercular; *Otoc*, otoccipital; *PaIt*, parietointertemporal; *Po*, postorbital; *Prsp*, prespiracular plate; *St*, supratemporal.

cav. in, cavum internasale; *cav. nc*, cavity of nasal capsule; *fe. o*, orbital fenestra; *fo. br*, fossa bridgei; *gr. v. fs*, groove for vena facialis superior; *stcc*, supratemporal commissural canal; *t. tm*, taenia tecti medialis of otoccipital.

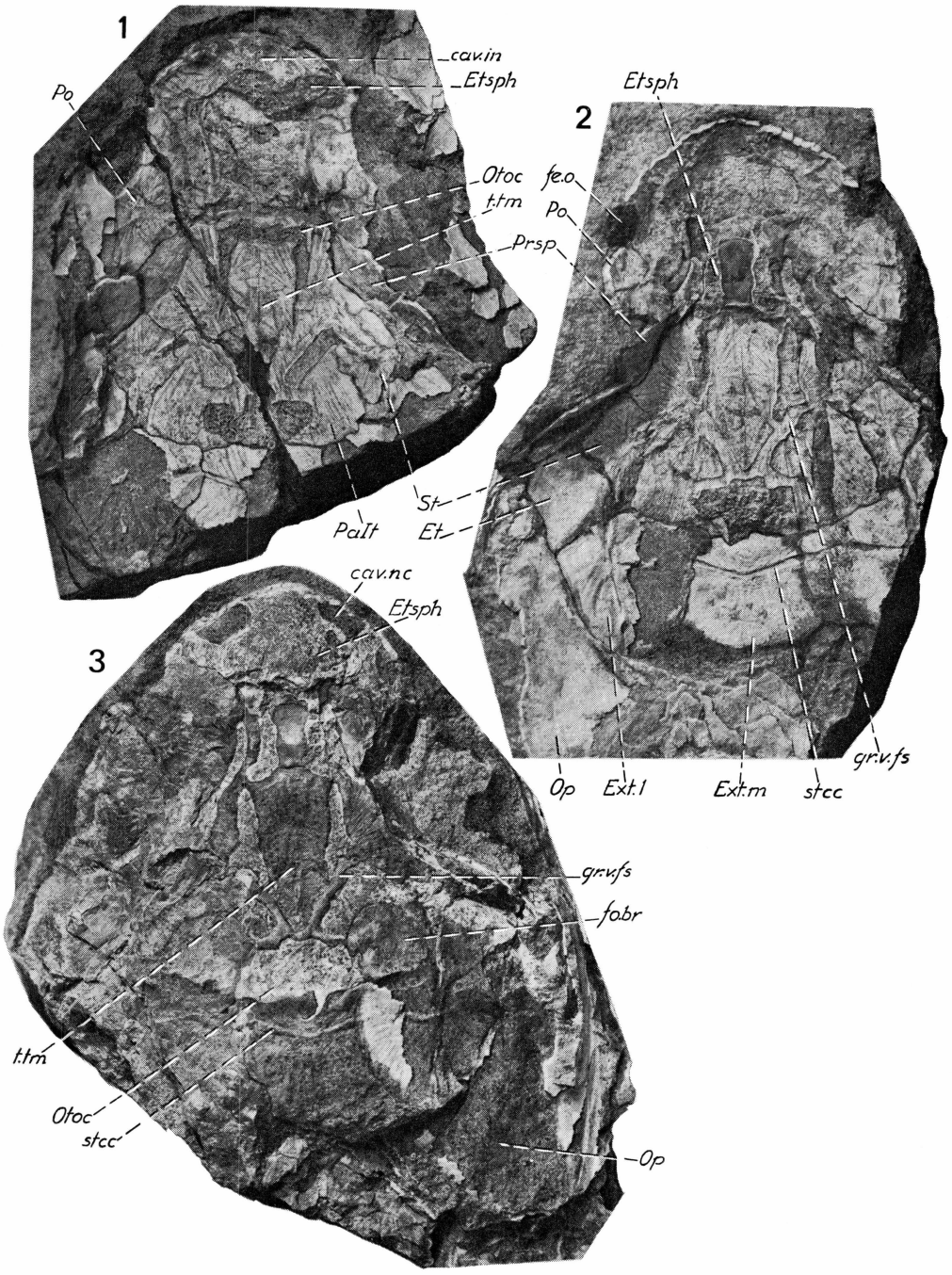

1
cav.in
Etsph
Po
Otoc
t.tm
Prsp
St
Pal.t
Et
2
Etsph
fe.o
Po
Op
Ext.l
Ext.m
st.cc
gr.v.fs
3
cav.nc
Etsph
gr.v.fs
fo.br
t.tm
Otoc
st.cc
Op

Plate 22

Glyptolepis groenlandica n. sp.

Specimens from same block as holotype. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*).

1. Dorso-ventrally compressed skull. Palatal aspect. Specimen No. P. 1515, Min. Mus., Copenh. × 3/2 approx.

2–5. Basibranchial of same specimen in ventral, dorsal, anterior and lateral aspects. × 9/4.

6. Anterior part of imperfect skull in ventral aspect showing oral dental plates. × 9/4.

Aplv, subchordal arcual plate; *Dpl*, dermopalatine; *Ju*, jugal; *Lj*, lower jaw; *Mx*, maxillary; *Vo*, vomer.

art. HbI, *art. HbII*, *art. HbIII*, articular areas for hypobranchials I–III; *art. Hh*, articular area for hypohyal; *dplt*, dermopalatine tusk; *fe. exch*, fenestra exochoanalis; *fo. bb*, ventral basibranchial fossa; *gr. psp*, prespiracular groove; *la. Dpl*, *la. Vo*, vertical tooth-bearing laminae of dermopalatine and vomer; *m. sarIa*, area of ceratohyal for attachment of musculus subarcualis rectus; *odp*, oral dental plates; *or. m. sc*, area of origin of subcranial muscle; *pr. av*, antero-ventral articular process of otoccipital; *pr. conn*, processus connectens; *pr. ling*, lingual process; *ri. in*, internasal ridge; *ri. vl*, ventro-lateral ridge of ceratohyal; *sh. ot*, otical shelf; *vot*, vomerine tusk.

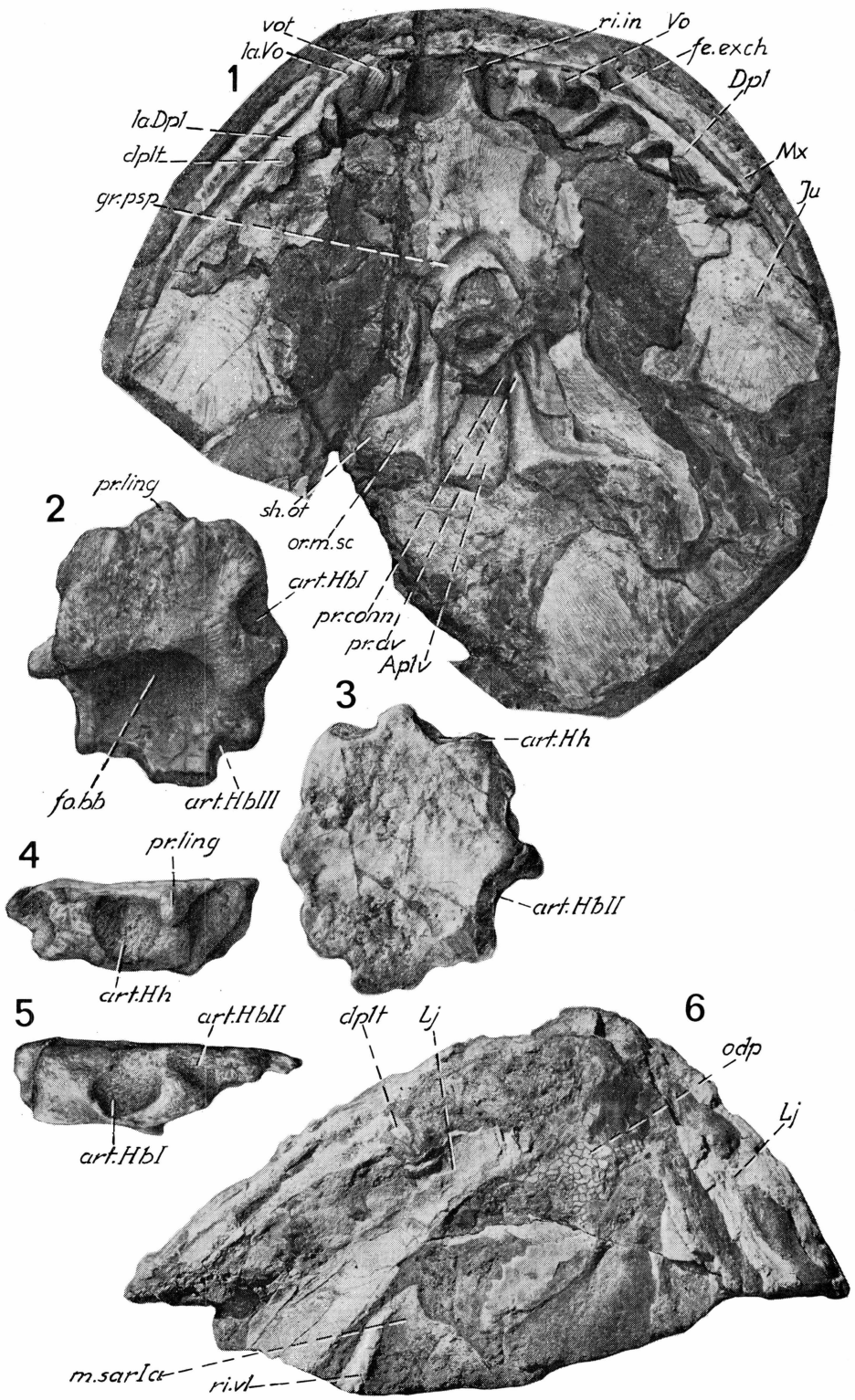

1
vot
la.Vo
ri.in
Vo
fe.exch
Dpl
la.Dpl
dplt
Mx
gr.psp
Ju
2
pr.ling
sh.ot
or.m.sc
art.Hbl
pr.conn
pr.dv
Apl
fo.bb
art.HblII
3
art.Hh
art.HblI
4
pr.ling
art.Hh
5
art.HblI
art.HblI
6
dplt
Lj
odp
Lj
m.sarlat
ri.vl

Plate 23

1, 2, 4. *Glyptolepis groenlandica* n. sp. Specimens from same block as holotype. Coll. 1956. Hesteskoen, Canning Land, East Greenland. Middle Devonian (Series with *Asterolepis saevesoederberghi*).

1. Impression of ventral side of anterior part of head with parts of lower jaws and submandibular series. Dorsal aspect. Specimen No. P. 1522, Min. Mus., Copenh. × 3/2.

2. Similar impression of another specimen. Specimen No. P. 1508, Min. Mus., Copenh. × 3/2.

4. Clavicle in medial aspect. Specimen No. P. 1505, Min. Mus., Copenh. × 9/8.

3. *Holoptychius* sp. Opercular in medial view. Specimen No. P. 1631, Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal, Gauss Halvø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 9/8.

G, principal gular plate; *Lj*, lower jaw; *Sbm1*, *Sbm7*, *Sbm8*, submandibulars 1, 7 and 8.

fo. l, lateral fossa on inner side of clavicle; *pl. G*, pit-line of principal gular; *p-mc*, preoperculo-mandibular sensory canal; *pr. Clav*, ascending process of clavicle; *p. pr. Op*, pit, probably for opercular process of hyomandibula; *ri. vm*, rodlike continuation of ascending clavicular process on inner side of ventro-medial plate.

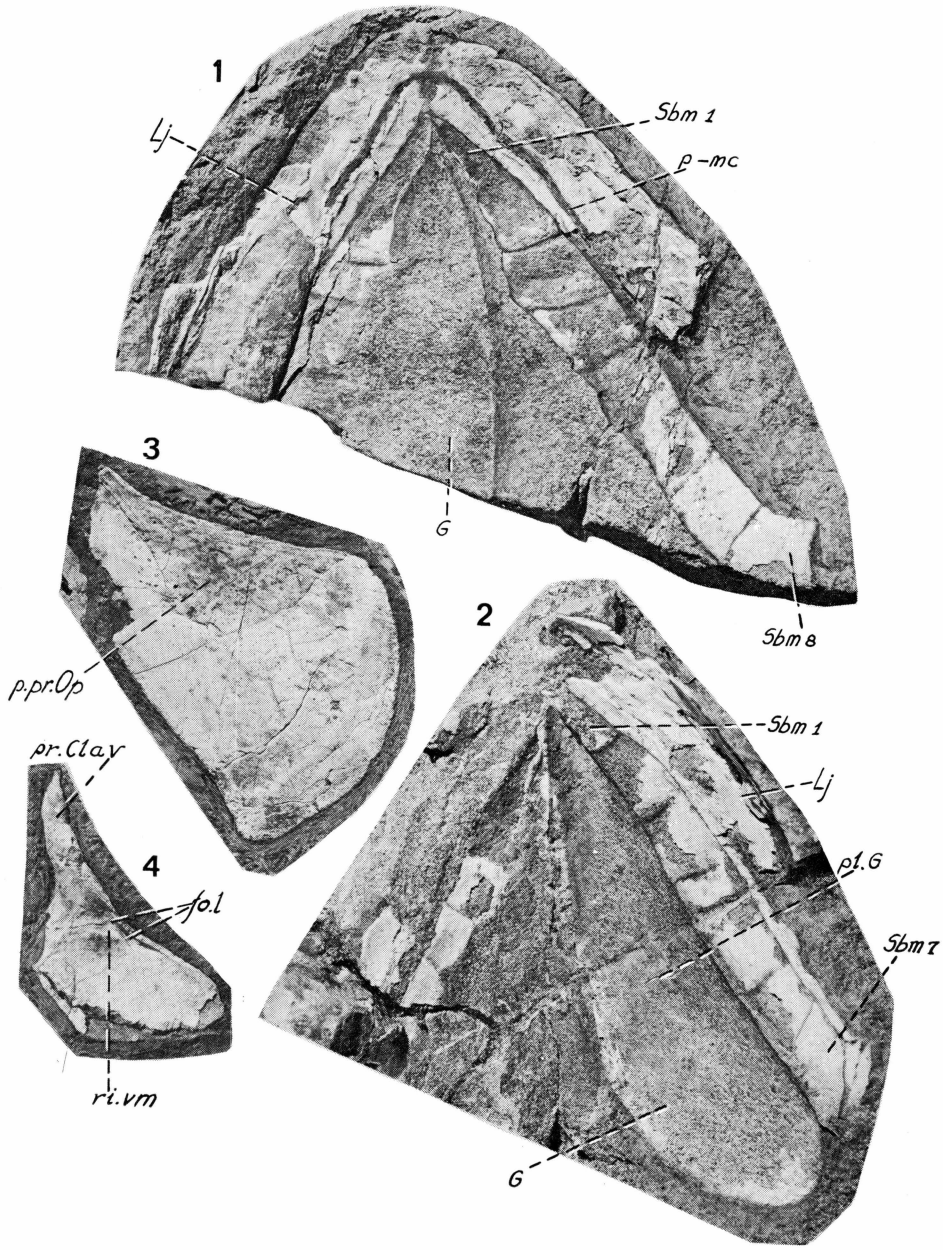

1
Lj
Sbm 1
p-mc
G
Sbm 8
3
p.pr.Op
2
Sbm 1
Lj
pr.Clav
4
fo.l
pl.G
Sbm 7
ri.vm
G

Plate 24

Holoptychius spp.

1. Parts of fronto-ethmoidal shield and external cheek-plate in inner aspect. Same specimen as in pl. 26:1–3, pl. 31:1 (see also text-fig. 36A and JARVIK 1942, fig. 33). Specimen No. 496, Min. Mus., Copenh. Coll. 1934. Kerstin Dal, Gauss Halvø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 2/1 approx.

2, 3. Imperfect divisio cranialis posterior in ventral and dorsal aspects. Same specimen as in pl. 30:3; figured by JARVIK, 1950a, fig. 36. Specimen No. P. 1593, Min. Mus., Copenh. Coll. 1947. S. side of Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 3/4.

4. Imperfect head in lateral aspect. Specimen No. 1840.14.15, RSM, Edinb. Clashbennie, Scotland. Upper Devonian.

Apv, paired posterior subchordal arcual plate; *Ext. m*, median extrascapular; *FrD*, frontodermosphenotic; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasals; *Op*, opercular; *PaIt*, parietointertemporal; *Po*, postorbital; *Pop*, preopercular; *Prsp*, prespiracular plate; *Qj*, quadratojugal; *RP*, rostropremaxillary; *So*, supraorbital; *Sq. l*, *Sq. u*, lower and upper squamosals; *St*, supratemporal; *Te*, tectal.

fe. bc, basicranial fenestra; *fe. ex*, fenestra exonarina communis; *fe. ov*, fenestra ovalis; *i. La*, notch in anterior margin of lachrymal forming posterior part of fenestra exonarina posterior; *i. lig*, depression probably for ligament; *or. m. sc*, area of origin of subcranial muscle; *pl. Fr*, frontal pit-line; *pl. po. Pa*, posterior oblique parietal pit-line; *pl. St*, supratemporal pit-line; *pl. tr. Pa*, transverse parietal pit-line; *sh. ot*, otical shelf; *soc*, supraorbital sensory canal.

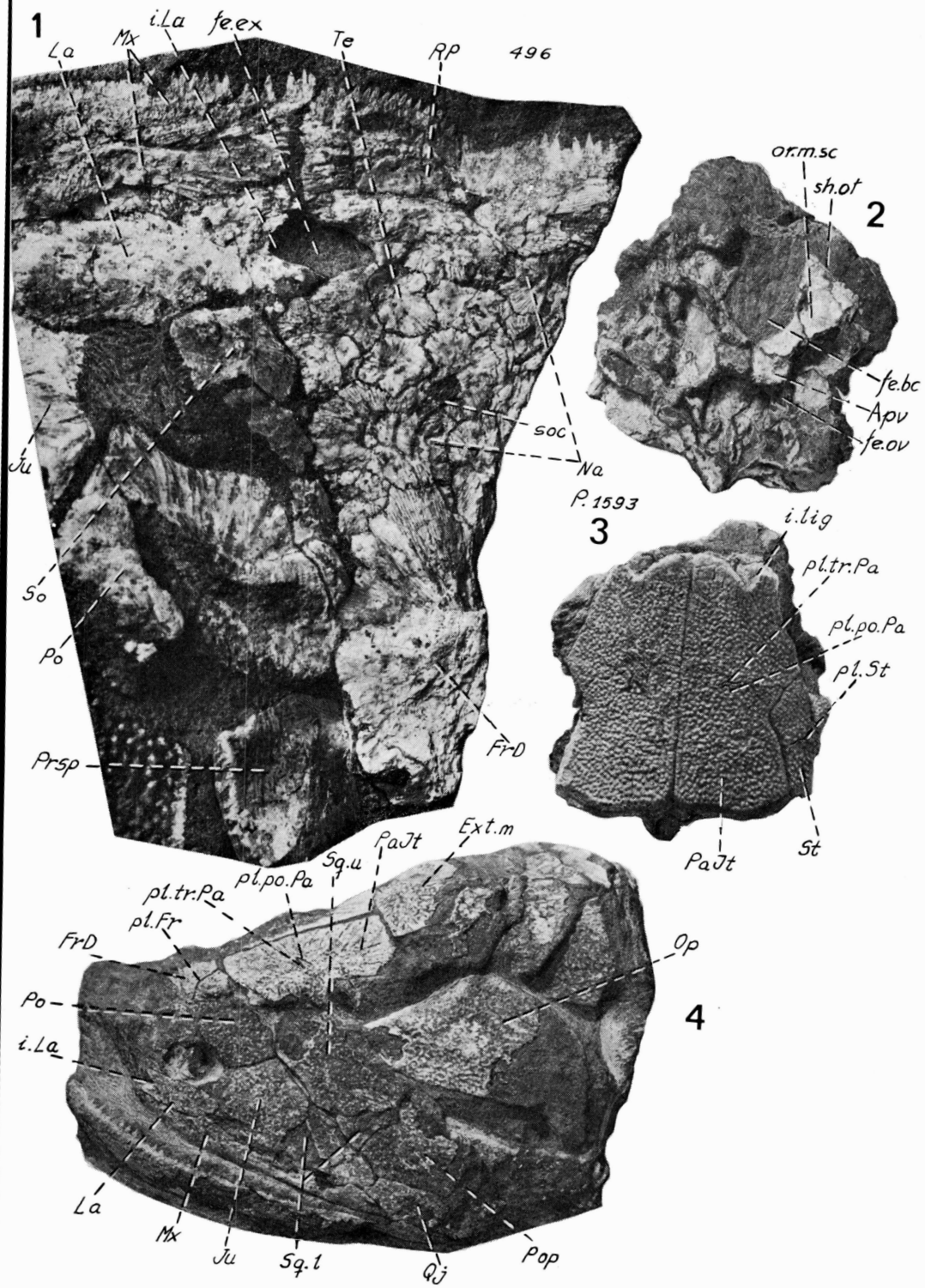

1
La
Mx
i.La
fe.ex
Te
RP
496
Ju
So
Po
Prsp
soc
Na
Fr.D
P. 1593
2
or.m.sc
sh.ot
fe.bc
Apv
fe.ov
3
i.lig
pl.tr.Pa
pl.po.Pa
pl.St
St
PaJt
4
Ext.m
PaJt
Sq.u
pl.po.Pa
pl.tr.Pa
pl.Fr
Fr.D
Op
Po
i.La
La
Mx
Ju
Sq.t
Qj
Pop

Plate 25

Holoptychius spp.

Imperfect anterior cranial divisions of two specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland.

1–4. Imperfect divisio cranialis anterior in dorsal, ventral, lateral and posterior aspects. Figured by JARVIK, 1942, fig. 44, 1954, fig. 3. Specimen No. 478, Min. Mus., Copenh. Coll. 1932. N. side of Celsius Bjerg, Ymers Ø. × 3/2.

5, 6. Imperfect divisio cranialis anterior in posterior and lateral aspects. Figured by JARVIK, 1954, fig. 19B. Specimen No. P. 1601, Min. Mus., Copenh. Coll. 1947. S. side of Celsius Bjerg, Ymers Ø. 5, × 3/2; 6, × 9/5.

FrD, frontodermosphenotic; *Frx*, independent part of frontal; *Na*, nasal; *P*, parasphenoid; *Pi. pl*, pineal plate; *Ptr*, postrostral; *RP*, rostropremaxillary; *Vo*, vomer; *Vod*, ascending lamina of vomer.

c. a. ci, canal for a. carotis externa; *c. a. cib*, canal for medial branch of a. carotis interna; *c. a. om*, canal for a. ophthalmica magna; *c. a. pal*, canal for a. palatina; *cav. cr*, cranial cavity; *cav. in*, internasal cavity; *cav. nc*, cavity of nasal capsule; *c. v. pit*, canal for pituitary vein; *c. III*, *c. IV*, canals for n. oculomotorius and n. trochlearis; *et. com*, ethmoidal commissure; *fe. vl*, fenestra ventro-lateralis; *fo. aup*, fossa autopalatina; *fo. nc*, pit for anterior end of notochord; *f. P*, foramen in parasphenoid for bucco-hypophysial ducts; *gr. orp*, posterior groove of orbito-rostral passage; *gr. psp*, prespiracular groove; *gr. v. o*, groove for v. optica; *gr. II*, groove for n. opticus; *i. m. sc*, area of insertion of subcranial muscle; *i. pr. ad*, impression for antero-dorsal articular process of otoccipital; *la. Vo*, tooth-bearing lamina of vomer; *le. so*, suborbital ledge; *pr. bp*, basipterygoid process; *pr. conn*, processus connectens; *pr. sp*, suprapterygoid process; *ri. in*, internasal ridge; *shh*, horizontal shelf; *vot*, vomerine tusk.

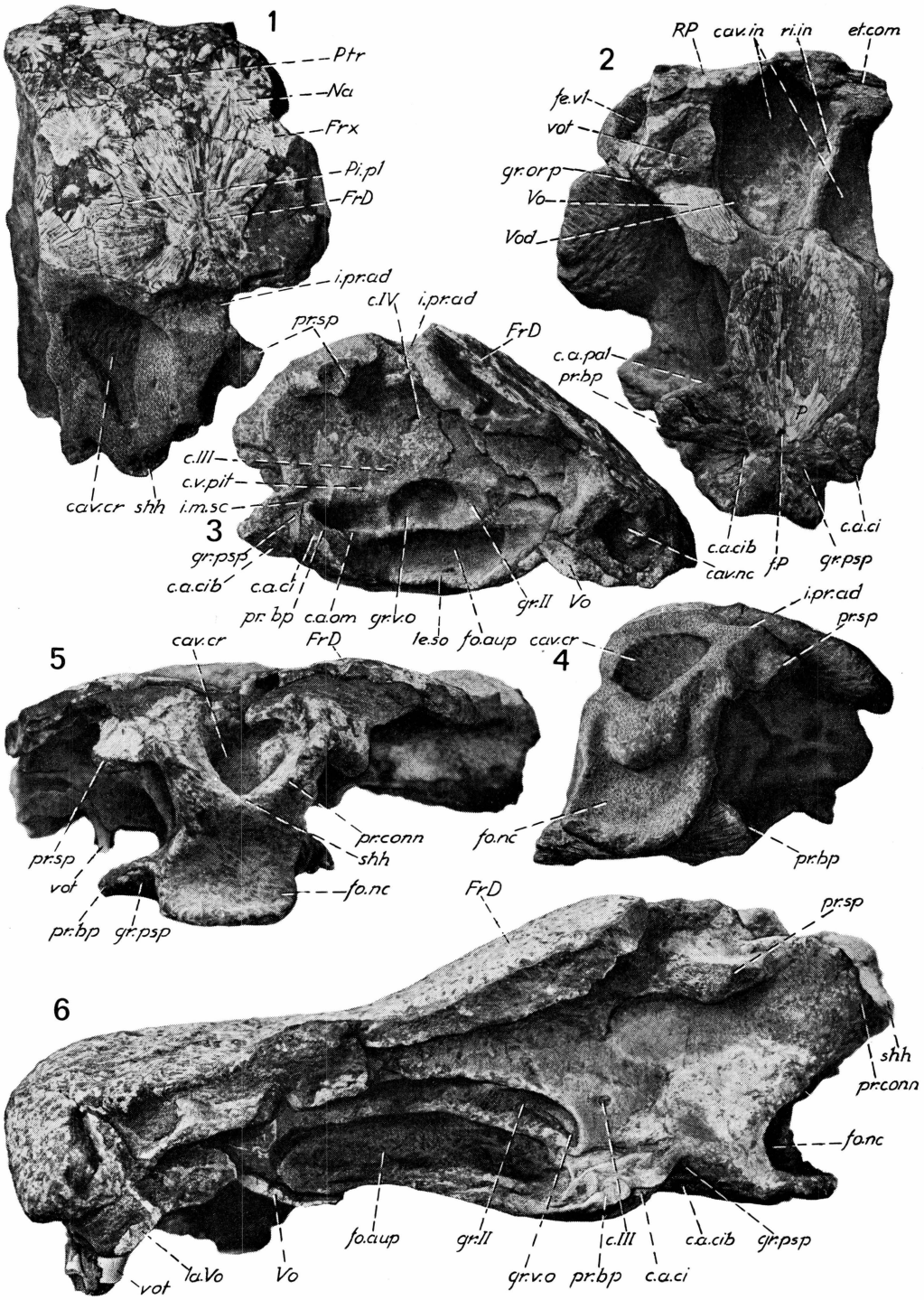

1
Ptr
Na
Frx
Pi.pl
FrD
i.pr.ad
cav.cr
shh
i.m.sc
c.v.pit
c.III
3
gr.psp
c.a.cib
c.a.ci
pr.bp
c.a.om
gr.v.o
pr.sp
c.IV
i.pr.ad
FrD
le.so
fo.aup
gr.II
Vo
2
RP
cav.in
ri.in
et.com
fe.vl
vot
gr.or.p
Vo
Vod
c.a.pal
pr.bp
p
f.p
c.a.cib
cav.nc
c.a.ci
gr.psp
4
i.pr.ad
pr.sp
cav.cr
fo.nc
pr.bp
5
cav.cr
FrD
pr.conn
shh
pr.sp
vot
fo.nc
pr.bp
gr.psp
6
FrD
pr.sp
shh
pr.conn
fo.nc
fo.aup
gr.II
c.III
c.a.cib
gr.psp
vot
la.Vo
Vo
gr.v.o
pr.bp
c.a.ci

Plate 26

1–5. *Holoptychius* spp. Two specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland, showing parasymphysial dental plates.

1. Part of incomplete skull in anterior aspect. Specimen No. 496, Min. Mus., Copenh. Coll. 1934. Kerstin Dal, Gauss Halvø. Same specimen as in pl. 24:1, pl. 31:1. × 2/3.

2. Detail of same specimen to show parasymphysial dental plates in their natural position. × 2/1.

3. Parasymphysial plates of same specimen in posterior aspect. × 2/1.

4, 5. Detached parasymphysial dental plate in dorso-lateral and lateral aspects. Photograph of latex cast whitened with ammonium chloride. Specimen No. P. 1605, Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal. × 8/3.

6. *Porolepis?* Detached parasymphysial dental plate in dorsal view. Photograph of latex cast whitened with ammonium chloride. Specimen No. P. 6965, Pal. Sect., Stockh. Coll. ENS. exp. 1939. Kronprinshøgda, Bockfjorden, Spitsbergen. Lower Devonian (Wood Bay Series). Figured by JESSEN, 1967, pl. 3:D. × 2/1.

Dpl, dermopalatine; *Ecpt*, ectopterygoid; *P*, parasphenoid; *Psy*, parasymphysial dental plate; *Psy. d*, *Psy. s*, parasymphysial dental plates of right and left sides; *Vo*, vomer.

cot1, tusk of coronoid 1; *f.P*, foramen in parasphenoid for buccohypophysial ducts; *psyt*, tusks of parasymphysial dental plate; *psytt*, rows of small teeth of parasymphysial dental plate; *sy*, symphysis of lower jaws; *uodp*, upper oral dental plates; *vot*, tusk of vomer.

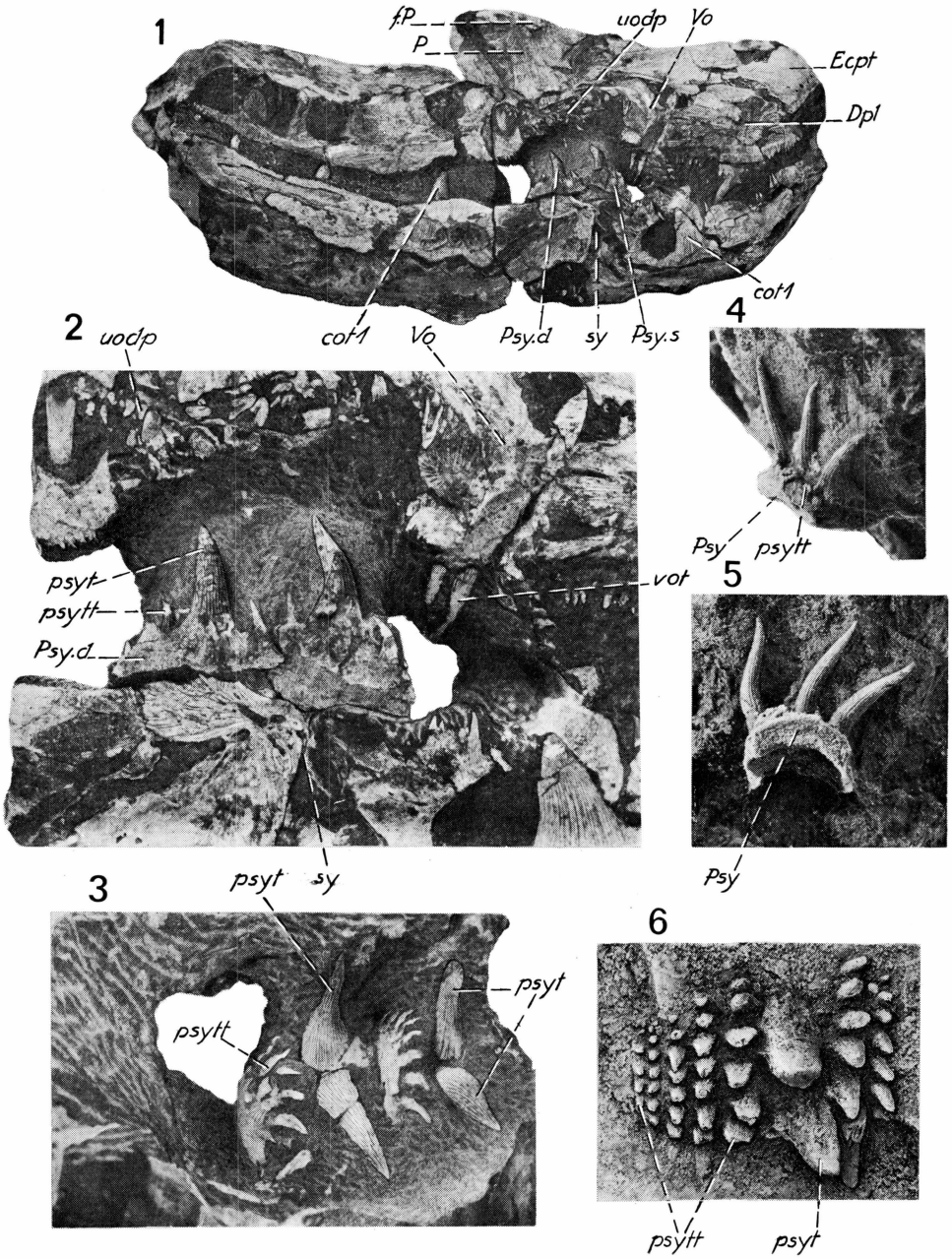

1
fP
P
uodp
Vo
Ecpt
Dpl
cot1
cot1
2
uodp
Vo
Psy.d
sy
Psy.s
psyt
psytt
Psy.d
vot
4
Psy
psytt
5
Psy
3
psyt
sy
psyt
psytt
6
psytt
psyt

Plate 27

Holoptychius sp.

1–4. Incomplete fronto-ethmoidal shields in inner aspects (see also text-figs. 36 B, 35 D, 35 C, 35 F). Specimens Nos. P. 1596, P. 1598, P. 1595 and P. 1652, Min. Mus., Copenh. Coll. 1934, 1951. 1215 m, Sederholms Bjerg, Paralleldal, East Greenland, Upper Upper Devonian (*Remigolepis* Series). × 3/2.

FrD, frontodermosphenotic; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *Pi. pl*, pineal plate; *Ptr*, postrostral; *Rm*, median rostral; *RP*, rostropremaxillary; *Te*, tectal.

et. com, ethmoidal commissure; *ioc*, infraorbital sensory canal; *iocv*, ventrally curving part of infraorbital sensory canal; *pl. Fr*, frontal pit-line; *prspc*, prespiracular sensory canal; *soc*, supraorbital sensory canal.

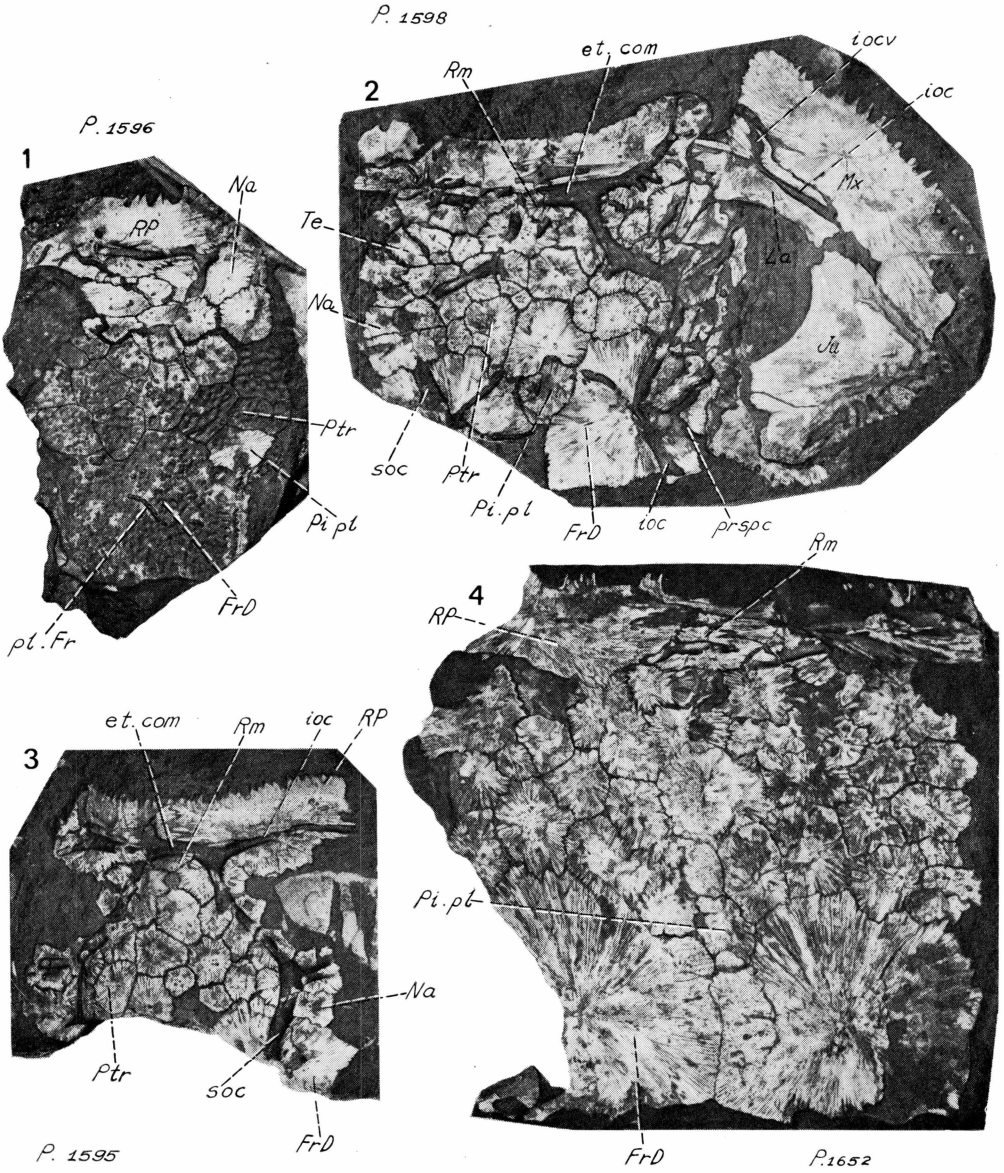

P. 1598
et. com
Rm
iocv
ioc
2
Mx
La
Ju
Te
Na
ptr
soc
Pi.pl
FrO
prspc
P. 1596
1
Na
RP
ptr
Pi.pl
FrO
pl.Fr
Rm
4
RP
Pi.pt
FrO
P. 1652
et. com
Rm
ioc
RP
3
Na
ptr
soc
FrO
P. 1595

Plate 28

Holoptychius spp.

Fronto-ethmoidal shields of four specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland, in inner aspects.

1. Specimen No. P. 1599, Min. Mus., Copenh. Coll. 1932. N. side of Celsius Bjerg, Ymers Ø. × 3/2.

2. Specimen No. 495, Min. Mus., Copenh. Coll. 1934. 1215 m, Sederholms Bjerg, Paralleldal. × 3/2.

3. Specimen No. P. 1597, Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal (see also text-fig. 36 D). × 1/1.

4. Specimen No. P. 1594, Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal. In alcohol. × 3/2.

FrD, frontodermosphenotic; *Na*, nasal; *PaIt*, parietointertemporal; *Pi.pl*, pineal plate; *Ptr*, postrostral; *Rm*, median rostral; *RP*, rostropremaxillary; *So*, supraorbital; *Te*, tectal.

et. com, ethmoidal commissure; *ioc*, infraorbital sensory canal; *prspc*, prespiracular sensory canal; *soc*, supraorbital sensory canal.

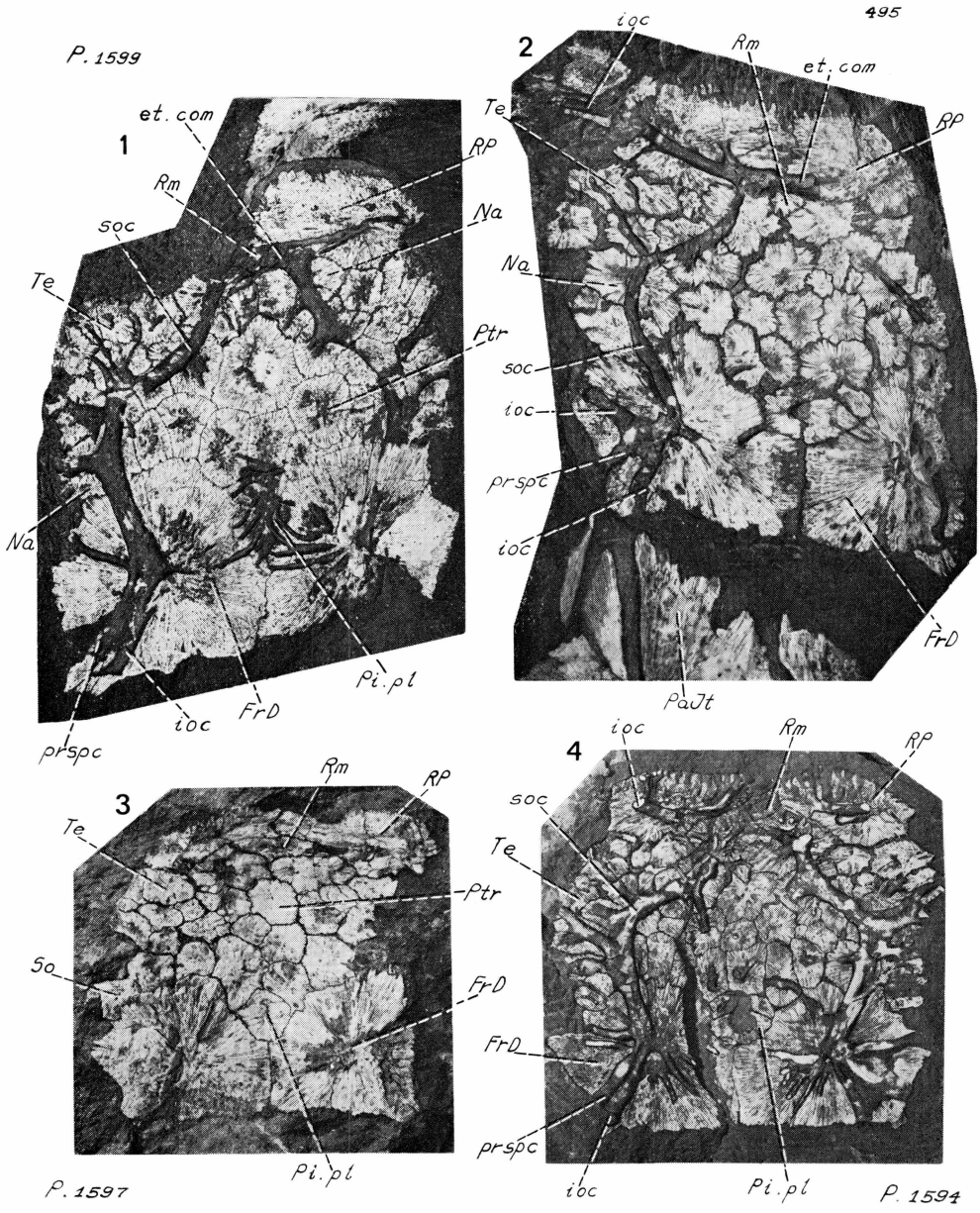

P. 1599
1
et. com
RP
Rm
soc
Na
Te
Ptr
Na
prspc
ioc
FrD
Pi. pl
495
2
ioc
Rm
et. com
Te
RP
Na
soc
ioc
prspc
ioc
FrD
PaJt
3
Rm
RP
Te
Ptr
So
FrD
Pi. pl
P. 1597
4
ioc
Rm
RP
soc
Te
FrD
FrD
prspc
ioc
Pi. pl
P. 1594

Plate 29

Holoptychius spp.

All specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland.

1, 2. Incomplete fronto-ethmoidal and parietal shields of two specimens preserved as impressions (see also text-figs. 37 A, B). Photographs of latex casts. Dorsal views. Specimens Nos. P. 1607 and P. 1606, Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal. 1, ×5/3; 2, × 1/1.

3. Fronto-ethmoidal shield and adjoining anterior part of external cheek-plate of flattened incomplete skull (see also text-fig. 37 C). Dorsal aspect. Specimen No. 494, Min. Mus., Copenh. Coll. 1934. 1215 m, Sederholms Bjerg, Paralleldal. × 4/3.

4. Incomplete fronto-ethmoidal shield in inner view. Specimen No. P. 1600, Min. Mus., Copenh. Coll. 1947. S. side of Celsius Bjerg, Ymers Ø. × 2/3.

5. Lachrymal in inner view (see also text-fig. 36 C). Specimen No. P. 1602, Min. Mus., Copenh. Coll. 1936. Sederholms Bjerg, Paralleldal. × 2/1.

FrD, frontodermosphenotic; *Ju*, jugal; *La*, lachrymal; *Mx*, maxillary; *Na*, nasal; *PaIt*, parietointertemporal; *Pi.pl*, pineal plate; *Po*, postorbital; *Rm*, median rostral; *RP*, rostropremaxillary; *St*, supratemporal; *Te*, tectal.

i. La, notch forming posterior part of fenestra exonarina posterior; *i. lig*, notches in adjoining parts of margins of fronto-ethmoidal and parietal shields conceivably for connecting ligament; *ioc*, infraorbital sensory canal; *iocv*, ventrally curving part of infraorbital sensory canal; *om*, margin of orbital fenestra; *pl. Fr*, frontal pit-line.

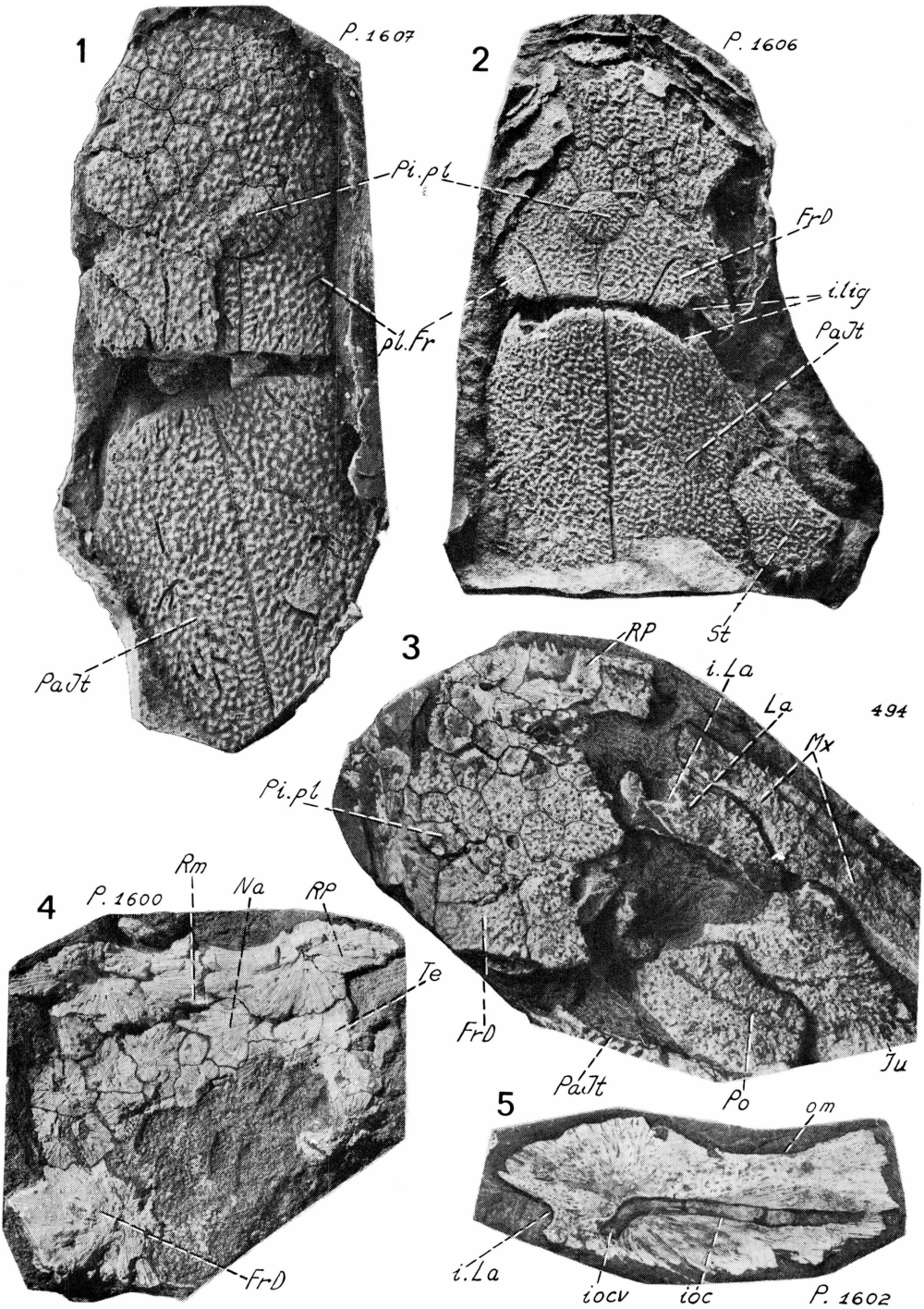

1
P. 1607
Pi.pl
pl.Fr
PaJt
2
P. 1606
FrO
i.lig
PaJt
St
3
RP
i.La
La
Mx
494
Pi.pl
FrO
PaJt
Po
Ju
4
P. 1600
Rm
Na
RP
Te
FrO
5
om
i.La
iocv
ioc
P. 1602

Plate 30

Holoptychius spp.

All specimen from Upper Upper Devonian (*Remigolepis* Series), East Greenland. × 2/3.

1. Impression of external side of right lower jaw and adjoining parts of head. Photograph of latex cast. Specimen No. P. 1590, Min. Mus., Copenh. Coll. 1948. Wimans Bjerg, Gauss Halvø.

2. Impression of external side of incomplete lower jaw. Specimen No. P. 1586, Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal.

3. Imperfect lower jaw in lateral aspect. Same specimen as in pl. 24:2, 3. Specimen No. P. 1593, Min. Mus., Copenh. Coll. 1947. S. side of Celsius Bjerg, Ymers Ø.

4. Right principal gular plate in external view. Photograph of latex cast. Specimen No. P. 1588, Min. Mus., Copenh. Coll. 1932. N. side of Celsius Bjerg, Ymers Ø.

5. Right principal gular plate in external view. Photograph of latex cast. Specimen No. P. 1577, Min. Mus., Copenh. Coll. 1954. S. side of Celsius Bjerg, Ymers Ø.

6. Impression of external side of left principal gular plate. Specimen No. P. 1529, Min. Mus., Copenh. Coll. 1936. Kerstin Dal, Gauss Halvø.

De, dentary; *G*, principal gular plate; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentaries 1–4; *Qj*, quadratojugal; *Sbm*, submandibular.

cot, coronoid tusk; *fo. Lj*, foramina in sutures between infradentaries; *i. mgc*, area overlapped by soft flap of mandibular gill-cover; *od. G*, area of principal gular overlapped by gular plate of other side; *od. Sbm*, area overlapped by submandibulars; *pl.G*, pit-line of principal gular plate; *pl.Id.2*, *pl.Id.4*, pit-lines of infradentaries 2 and 4; *pl.Qj*, *pl.Sbm7*, pit-lines of quadratojugal and submandibular 7.

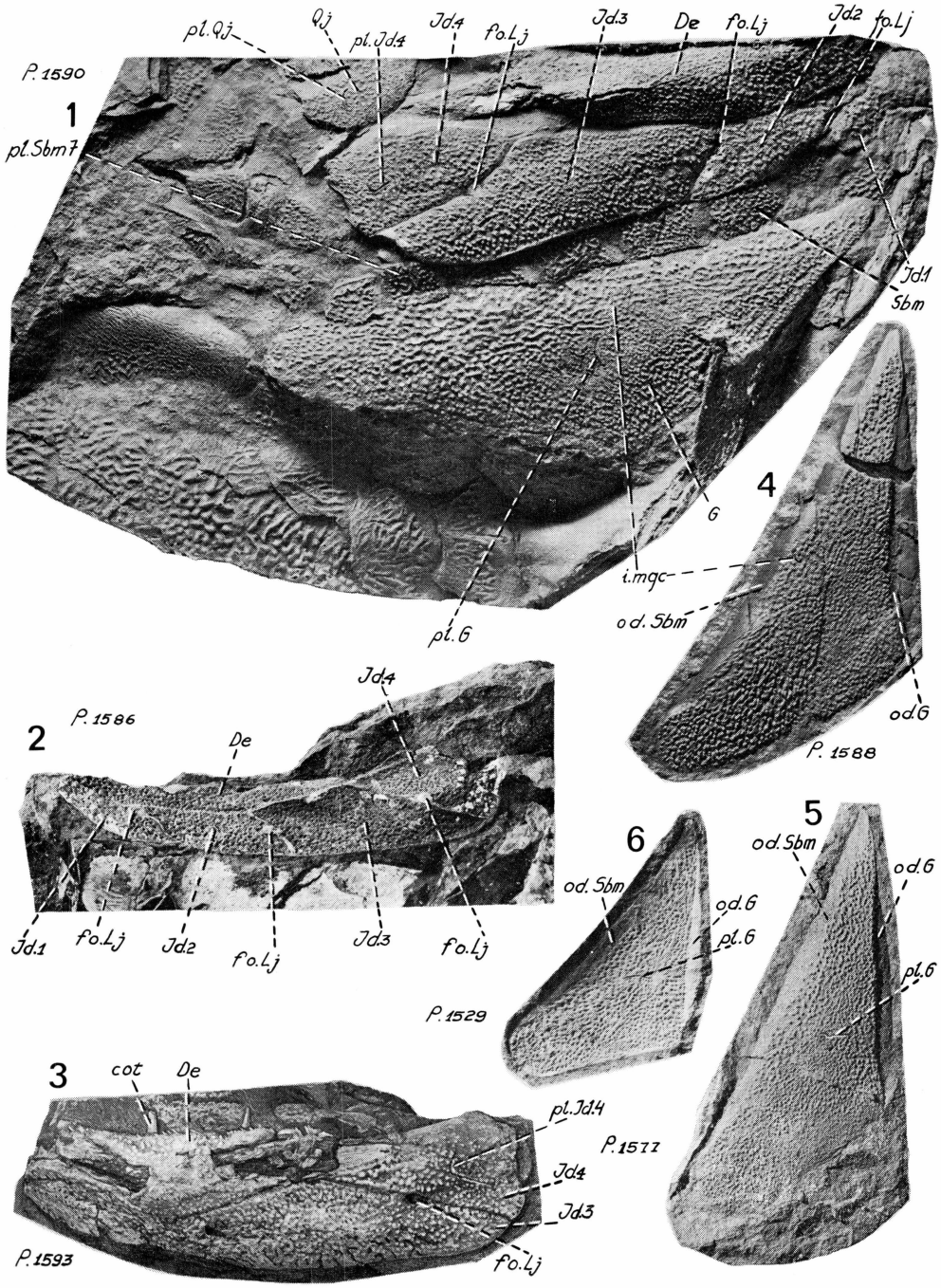

P. 1590
1
pl. Sbm 1
pl. Qj
Qj
pl. Jd 4
Jd 4
fo. Lj
Jd 3
De
fo. Lj
Jd 2
fo. Lj
Jd 1
Sbm
G
pl. G
i. mgc
od. Sbm
4
od. G
P. 1588
2
P. 1586
Jd 4
De
Jd 1
fo. Lj
Jd 2
fo. Lj
Jd 3
fo. Lj
6
od. Sbm
od. G
pl. G
P. 1529
5
od. Sbm
od. G
pl. G
3
cot
De
pl. Jd 4
Jd 4
Jd 3
fo. Lj
P. 1577
P. 1593

Plate 31

Holoptychius spp.

All specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland.

1. Slab with cranial remains of two individuals. Above imperfect cranial roof with parts of external cheek-plate and lower jaws in inner aspect. Same individual as in pl. 24:1 and pl. 26:1–3. Below imperfect skull-roof in inner aspect. Specimen No. 496, Min. Mus., Copenh. Coll. 1934, Kerstin Dal, Gauss Halvø. × 2/3.

2. Imperfect left lower jaw in external view. Specimen No. P. 1628, Min. Mus., Copenh. Coll. 1954. N. side of Celsius Bjerg, Ymers Ø. × 4/3.

3. Posterior part of right lower jaw in external aspect. Specimen No. P. 1629 Min. Mus., Copenh. Coll. 1951. 1215 m, Sederholms Bjerg, Paralleldal. × 2/1.

De, dentary; *FrD*, frontodermosphenotic; *Id.1*, *Id.2*, *Id.3*, *Id.4*, infradentaries 1–4; *Ju*, jugal; *Mx*, maxillary; *Na*, nasal; *PaIt*, parietointertemporal; *Po*, postorbital; *Prsp*, prespiracular plate; *RP*, rostropremaxillary; *Sq. u*, upper squamosal; *St*, supratemporal.

fe. ex, fenestra exonarina communis; *fo. Lj*, foramina in sutures between infradentaries; *ioc*, infraorbital sensory canal; *i. spir*, spiracular notch; *orc*, *p-mc*, oral and preoperculo-mandibular sensory canals; *prspc*, prespiracular sensory canal; *sy*, symphysis of lower jaws.

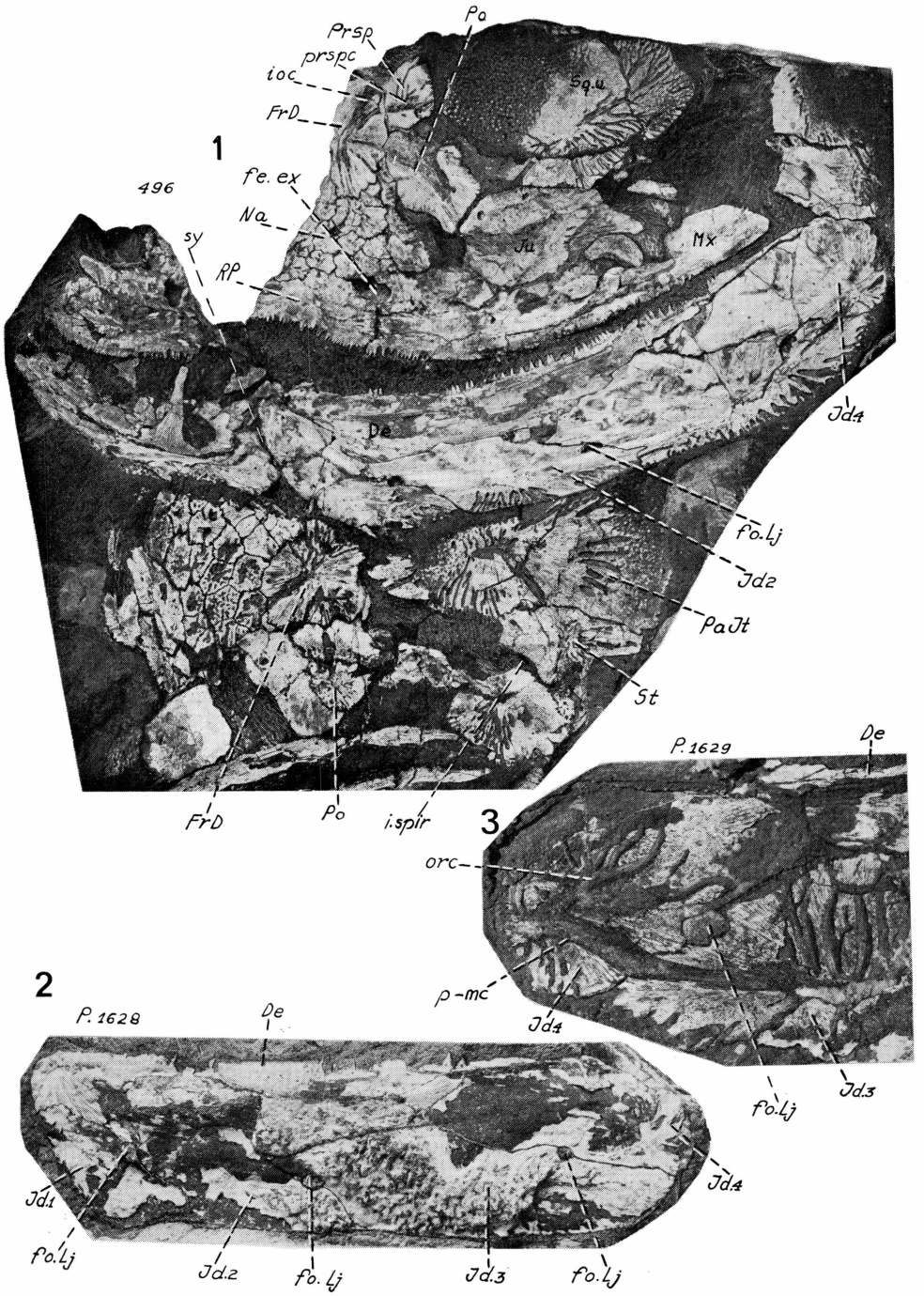

1
496
Prsp
prspc
ioc
FrO
Po
Sq.u
fe. ex
Na
sy
RP
Ju
Mx
Jd4
De
fo.Lj
Jd2
PaJt
St
FrO
Po
i.spir
3
P. 1629
De
orc
p-mc
Jd4
fo.Lj
Jd3
2
P. 1628
De
Jd4
Jd1
fo.Lj
Jd2
fo. Lj
Jd3
fo.Lj

Plate 32

1. *Holoptychius* sp. Left lower jaw in medial aspect (cf. fig. 47 A) and two scales in external aspect. Photograph of latex cast. Specimen No. P. 1587, Min. Mus., Copenh. Coll. 1954. S. side of Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 2/3.

2. Anterior part of lower jaw of same specimen in dorsal aspect. × 4/3.

3, 4. *Holoptychius* sp. Incomplete dentary in dorsal and medial aspects. Photographs of latex cast. Specimen No. P. 1588, Min. Mus., Copenh. Coll. 1954. S. side of Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 4/3.

5. *Glyptolepis baltica* Gross. Anterior end of right lower jaw in medial aspect. Specimen No. P. 829, Pal. Sect., Stockh. Ehrmann bei Ligat, Latvia. Upper Middle Devonian or Lower Upper Devonian (Oredesch Beds). × 8/3.

Co1, coronoid 1; *De*, dentary; *Id. 1*, infradentary 1; *Prart*, prearticular; *Prart. dp*, prearticular dental plate.

cot1, *cot3*, tusks of coronoids 1 and 3; *det*, teeth of dentary; *de. tl*, tooth-less anterior part of dorsal margin of dentary; *la. Co2*, vertical tooth-bearing lamina of coronoid 2; *la. De*, antero-medial lamina of dentary carrying parasymphysial dental plate; *p-mc*, preoperculo-mandibular sensory canal.

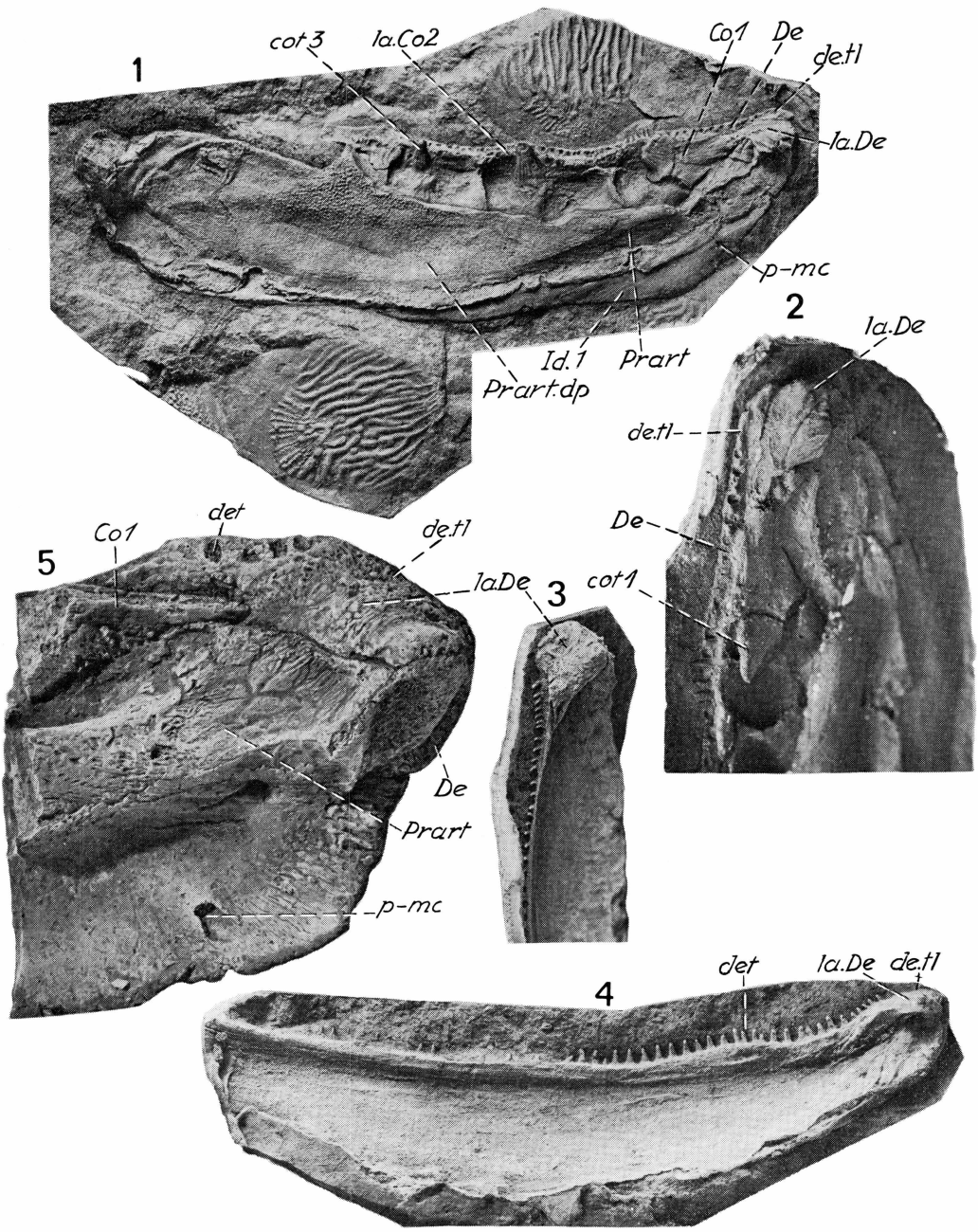

1
cot3
la.Co2
Co1
De
de.tl
la.De
p-mc
Id.1
Prart
Prart.dp
2
la.De
de.tl
De
cot1
3
5
Co1
det
de.tl
la.De
De
Prart
p-mc
4
det
la.De
de.tl

Plate 33

1, 2. *Holoptychius* sp. Maxillary in external and internal views. Photographs of latex casts. Specimen No. P. 1692, Min. Mus., Copenh. Coll. 1948. Wimans Bjerg, Gauss Halvø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 6/5.

3. *Porolepis* sp. Maxillary in external view. Specimen No. A. 34031, Pal. Mus., Oslo. Coll. Norw. exp. Lower Devonian (Wood Bay Series), Spitsbergen. × 4/5.
4. *Holoptychius* sp. Opercular in external view. Specimen P. 1579, Min. Mus., Copenh. Coll. 1934. Sederholms Bjerg, Paralleldal, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 4/5.

5. *Holoptychius* sp. Opercular. Impression of external side. Specimen No. P. 1534, Min. Mus., Copenh. Coll. 1951. Sederholms Bjerg, Paralleldal, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 4/5.

6. *Holoptychius* sp. Incomplete parietal shield with prespiracular plate in internal aspect. Specimen No. P. 1589, Min. Mus., Copenh. Coll. 1931. N. side of Celsius Bjerg, Ymers Ø, East Greenland. Upper Upper Devonian (*Remigolepis* Series). × 4/5.

FrD, frontodermosphenotic; *Mxp*, palatal lamina of maxillary; *PaIt*, parieto-intertemporal; *Prsp*, prespiracular plate; *St*, supratemporal.

ioc, infraorbital sensory canal; *no. Et*, notch of supratemporal for extratemporal; *no. La*, notch of maxillary for lachrymal; *od. Ext. l*, area overlapped by lateral extrascapular; *od. Ju*, area overlapped by jugal; *prspc*, prespiracular sensory canal.

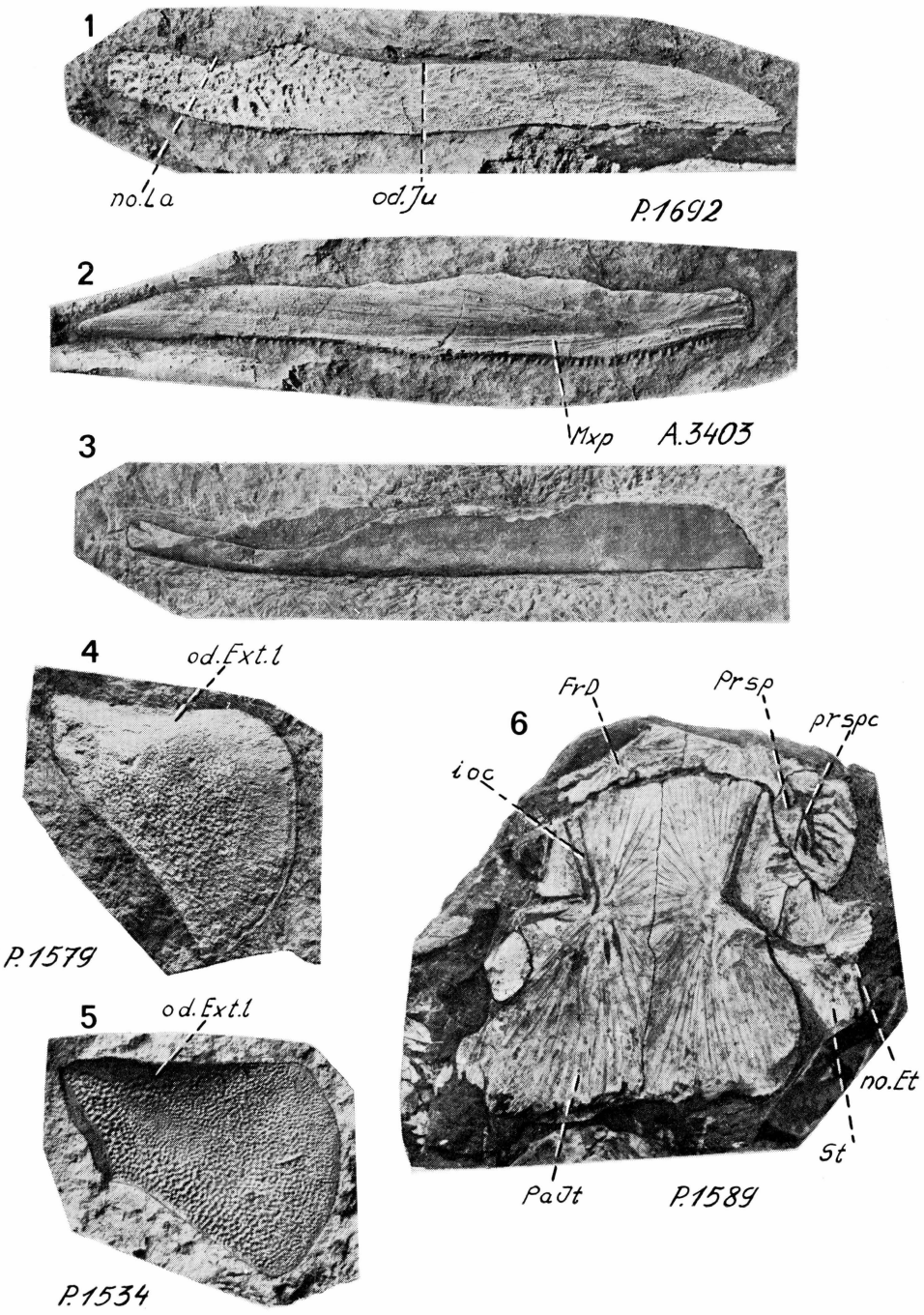

1
no.La
od.Ju
P.1692
2
Mxp
A.3403
3
4
od.Ext.l
P.1579
5
od.Ext.l
P.1534
6
FrD
Prsp
prspc
ioc
no.Et
St
PaJt
P.1589

Plate 34

1–4. *Holoptychius* spp. Cleithrum in external and (4) internal aspects. All specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland. Photographs of latex casts. × 4/5.

1. Specimen No. P. 1555, Min. Mus., Copenh. Coll. 1932. N. side of Celsius Bjerg, Ymers Ø.

2. Specimen No. P. 1558. Min. Mus., Copenh. Coll. 1933. Nathorsts Bjerg, Gauss Halvø. See also text-fig. 51 A.

3. No. P. 1536, Min. Mus., Copenh. Coll. 1934. Sederholms Bjerg, Paralleldal. See also text-fig. 51 F.

4. Specimen No. P. 1547, Min. Mus., Copenh. Coll. 1949. 1174 m, Sederholms Bjerg, Paralleldal.

5. *Glyptolepis* sp. Interclavicle in external view (cf. Gross, 1936, fig. 8G). Specimen No. P. 180, Pal. Sect., Stockh. Ehrmann bei Ligat, Latvia. Upper Middle Devonian or Lower Upper Devonian (Oredesch Beds). × 4/5.

ar. e. sh, area for attachment of endoskeletal shoulder-girdle; *ar. tri*, triangular area; *od. Op*, area overlapped by opercular; *od1. Clav*, area of cleithrum overlapped by clavicle; *od2. Clav*, area of interclavicle overlapped by clavicle.

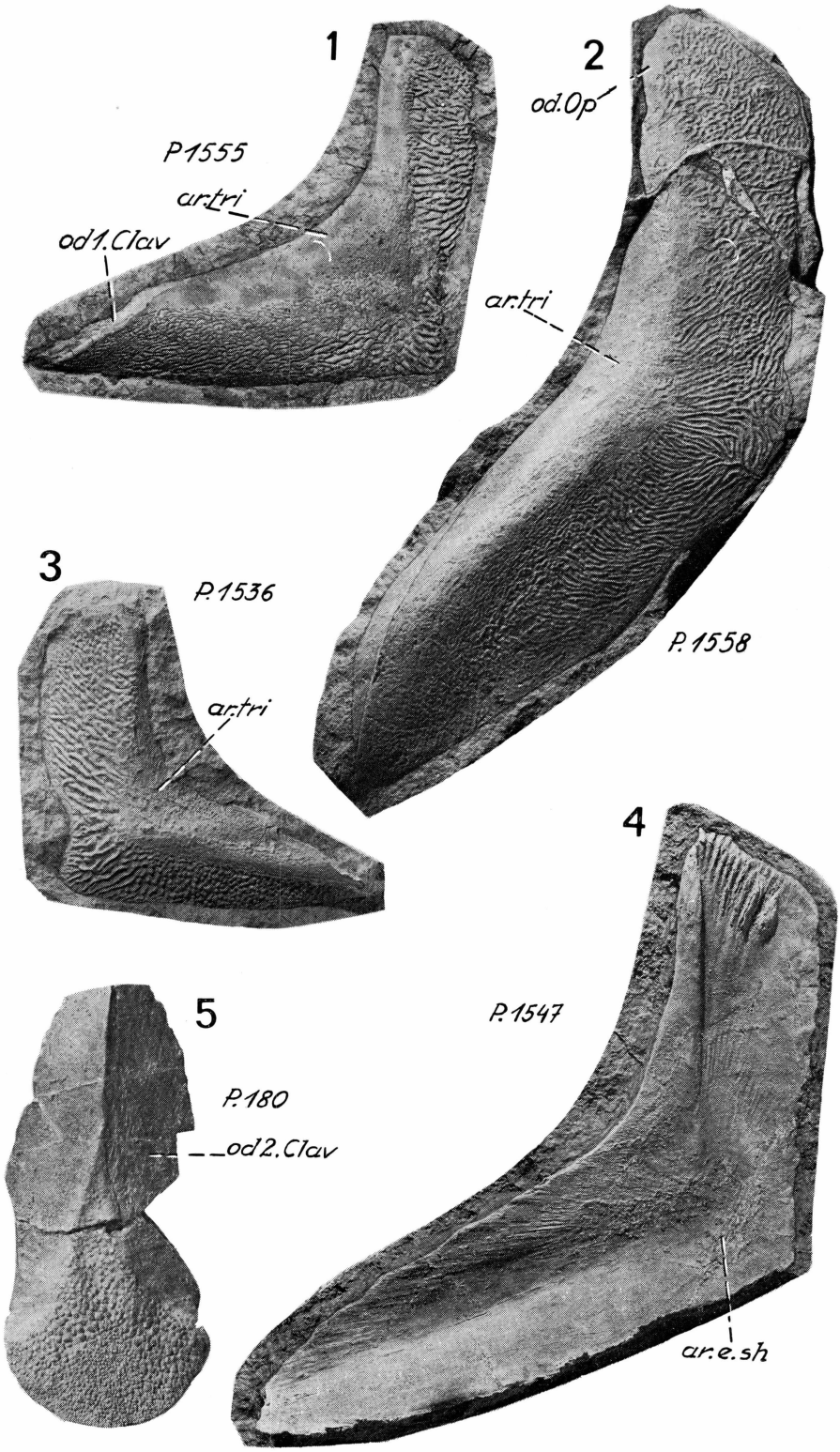

1
P.1555
ar.tri
od1.Clav
2
od.Op
ar.tri
P.1558
3
P.1536
ar.tri
4
P.1547
ar.e.sh
5
P.180
od2.Clav

Plate 35

Holoptychius spp.

All specimens from Upper Upper Devonian (*Remigolepis* Series), East Greenland.

1, 2. Right clavicle in medial and antero-dorsal aspects. Specimen No. P. 1566, Min. Mus., Copenh. Coll. 1955. Smith Woodwards Bjerg, Gauss Halvø. × 9/10.

3. Right clavicle in lateral aspect. Photograph of latex cast. Specimen No. P. 1531, Min. Mus., Copenh. Coll. 1934. Sederholms Bjerg, Paralleldal. × 3/5.

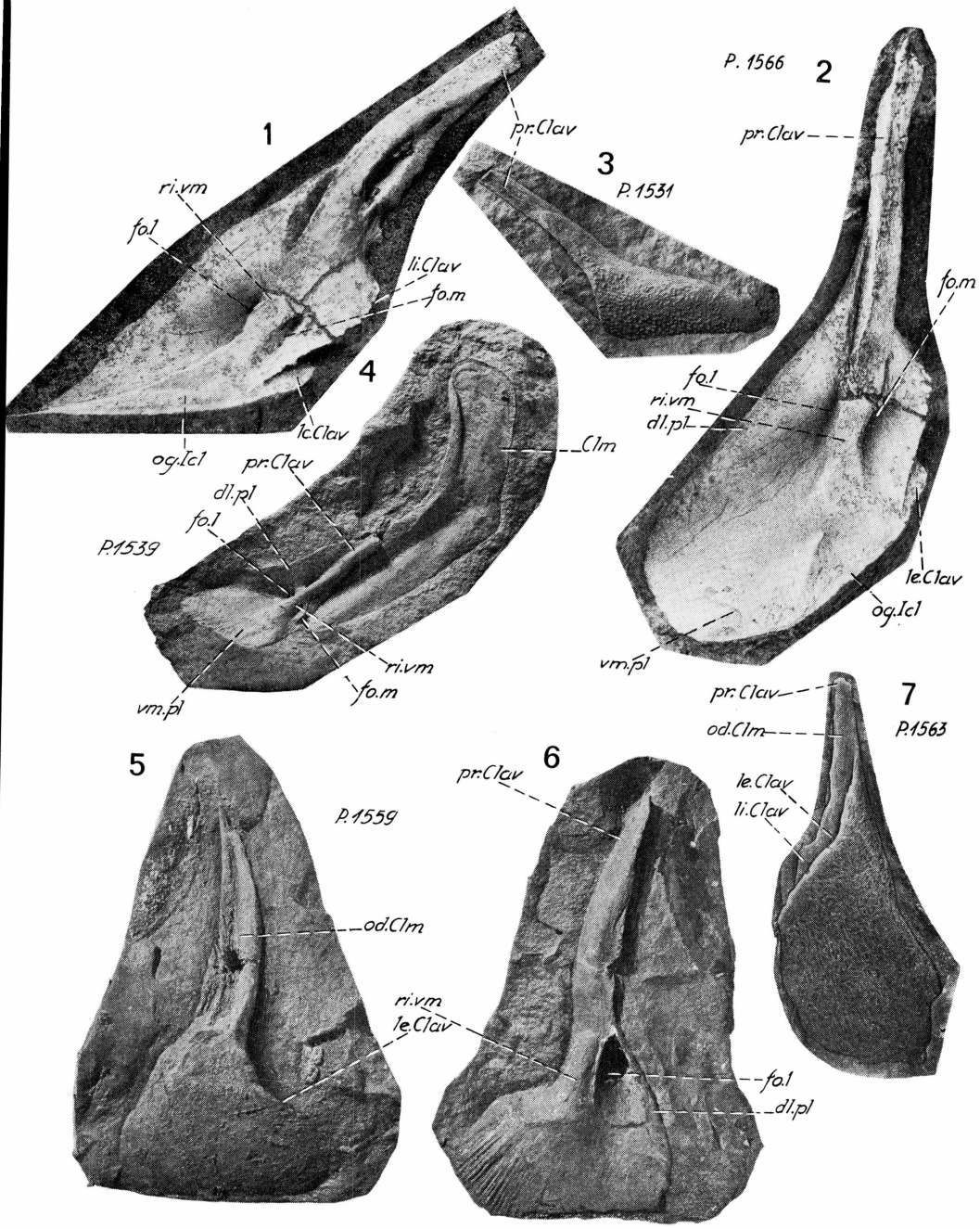
4. Right cleithrum and clavicle in medial aspect. Photograph of latex cast. Specimen No. P. 1539, Min. Mus., Copenh. Coll. 1954. N. side of Celsius Bjerg, Ymers Ø. × 3/5.

5, 6. Left clavicle in postero-ventral and antero-dorsal aspects. Photographs of latex casts. Specimen No. P. 1559, Min. Mus., Copenh. Coll. 1933, Nathorsts Bjerg, Gauss Halvø. × 3/5.

7. Right clavicle in antero-ventral aspect. Photograph of latex cast. Specimen No. P. 1563, Min. Mus., Copenh. Coll. 1932. N. side of Celsius Bjerg, Ymers Ø. × 3/5.

Clm, cleithrum.

dl. pl, dorso-lateral vertical plate of clavicle; *fo. l*, *fo. m*, lateral and medial fossa on inner side of clavicle; *le. Clav*, *li. Clav*, external and internal lamellae of clavicle; *od. Clm*, area of ascending process of clavicle overlapped by cleithrum; *og. Icl*, area overlapping interclavicle; *pr. Clav*, ascending process of clavicle; *ri. vm*, rod-like continuation of ascending process of clavicle on inner side of ventro-medial plate; *vm. pl*, ventro-medial, horizontal plate of clavicle.


1
ri.vm
fo.l
li.Clav
fo.m
lc.Clav
og.Ic1
3
pr.Clav
P. 1531
P. 1566
2
pr.Clav
fo.m
fo.l
ri.vm
dl.pl
le.Clav
og.Ic1
vm.pl
4
Clm
pr.Clav
dl.pl
fo.l
P.1539
ri.vm
fo.m
vm.pl
5
P.1559
od.Clm
ri.vm
le.Clav
6
pr.Clav
fo.l
dl.pl
7
pr.Clav
od.Clm
P.1563
le.Clav
li.Clav