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The question of the Eotriassic tetrapod genus *Wetlugasaurus* in Greenland and thoughts on the fossa coniformis entopterygoidea

Hans C. Bjerring

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Cranial specimens of Eotriassic tetrapods from central East Greenland which in the mid-1930s were assigned to the genus *Wetlugasaurus* have been re-examined and found to represent a new, capitosaur-like genus, named *Selenocara*. A cone-shaped fossa in the entopterygoid bone is the focus of particular attention. This depression appears to have engaged with the affacial process and not, as has often been maintained, with the basipterygoid process. The consequences of this re-interpretation of the fossa coniformis entopterygoidea are far-reaching, and some of them are, to an extent, discussed herein.

Key words:
Early Triassic, tetrapod, *Selenocara* n.g., cranium, jaw suspension, hearing, retroevolutionary analysis.

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Introduction

In 1930, Ryabinin (Riabinin) described a new amphibious tetrapod from the Lower Triassic of eastern European Russia, which he named *Wetlugasaurus angustifrons* (transferred to the genus *Parotosaurus* as *P. angustifrons* by Welles & Cosgriff 1965). Since then five further contemporary species of *Wetlugasaurus* have been recorded from the same region, viz., *W. cornutus* (Yefremov 1940), *W. kzilsajensis* (Ochev 1966, 1972), *W. samarensis* (Sennikov 1981), *W. vjatkensis* (Gubin 1987), and *W. malachovi* (Novikov 1990, 1994).

In addition to these Russian species, *W. groenlandicus* (Säve-Söderbergh 1935) has been described from Greenland, *W. milloti* (Lehman 1961) from Madagascar and *W. magnus* (Watson 1962) from South Africa. Each of these are also from early Triassic deposits. It is also worth noting that Sennikov (1981) found little to distinguish the Lower Triassic *W. kzilsajensis* from the similarly aged *Sassenisaurus spitzbergensis* (cf. Wiman 1914 and Nilsson 1942). This suggested to him that they are congeneric. However, it should be observed that Welles & Cosgriff (1965) consider *Sassenisaurus spitsbergensis* (Wiman) Nilsson, 1942, a nomen vanum.

The early Triassic genus *Wetlugasaurus* thus appears to occur in various areas of both the northern and the southern hemisphere. However, such a widespread distribution is unparalleled among other Triassic anamniote tetrapods, and one may therefore reasonably suspect that at least some of the above-mentioned taxa are misidentified.

Sennikov (1981) has already demurred at the alleged occurrence of South African and Malagasy wetlugasaurs. In the following account it will be shown that the presence of wetlugasaurs in East Greenland is similarly exceptionable.

Systematic section

***Selenocara*, novum genus.**

Holotypus: At.2 in Säve-Söderbergh 1935, p. 122.

Hypodigma: Holotype and specimen At.17 in Säve-Söderbergh 1935, p. 122; Säve-Söderbergh refers to the latter specimen as the cotypus.

Species typica: *Wetlugasaurus groenlandicus* Säve-Söderbergh, 1935.

Contentum: *Selenocara groenlandica* (Säve-Söderbergh) Bjerring by monotypy.

Diagnosis (for genus and species): Extinct amphibious anamniote tetrapod with greatly flattened skull. Two distinct occipital condyles. Sutural contacts between the osseous rear of the endocranium and the dermal skull roof. Conspicuous exoskeletal embayment (incisura auditiva or "otic notch") intervening the posterolateral margin of the skull table and the posteromesial margin of the cheek. Sutural union between each of the entopterygoid bones and the corpus of the crepidine bone ("parasphenoid bone"; for the term os crepidinum see p. 16). Large orbitopalatine openings ("interpterygoid vacuities") separated in the midline by the crepidine cultriform process and bounded laterally by the entopterygoid and dermopalatine bones. Medium-sized orbitofacial openings lie above the posterior halfs of each of the ipsilateral orbitopalatine openings. Jaw articulations are about level with the occipital condyles both transversally and horizontally.

Derivatio nominis: The generic name honors the late Dr. Eigil Nielsen of Copenhagen – dexterous collector and describer of Triassic fish – who among contemporary Greenland explorers went by the sobriquet of månen (the Danish word for the moon). Greek *selene*, moon + *kara*, head.

Stratum typicum: Stegocephalian or *Myalina* horizon of the *Anodontophora fassaensis* zone, Wordie Creek Formation; Lower Scythian (cf. Nielsen 1935, Spath 1935, Birkelund & Perch-Nielsen 1976).

Locus typicus: The coast southeast of Kap Stosch, Hold-with-Hope, central East Greenland, on ridge 8-9 of the northeastern slope of Stensiö Plateau.

Repositorium: Geological Museum of Copenhagen University, Denmark, where At.2 is catalogued as MGUH VP 3339 and At.17 as MGUH VP 3340.

Redescription of the holotype

General features

This specimen is mostly an internal mold of an undeformed skull, lacking the snout. Accordingly, the presence of rugose dermal ornament and grooves for the neuromast system, as in other Eotriassic tetrapods, is unknown. Sutures and centers of ossification, however, are clearly visible. Only two bones of the cranial endoskeleton are preserved, lying in the rear, respectively, of the braincase and the right palatoquadrate.

The holotype has undergone further mechanical preparation since Säve-Söderbergh's (1935) original description. Moreover, a skull fragment, collected by Eigil Nielsen in 1946 at the type locality, has turned out to be part of the holotype. Owing to this find, a smaller portion of the skull anterior to the dextral orbitofacial opening is now also available for study (cf. Fig. 1).

Although the snout is unknown, the contour of the cheek and the construction of the palatal surface suggest that the shape of the skull, in dorsal view, was parabolic in outline with a rounded muzzle (Fig. 2).

The aditus orbitarum faciales (orbitofacial openings, *aof*, Figs 1, 6) mostly face dorsally. They are of moderate size and subcircular outline, with the long axes directed anteromesially. These openings lie closer to the mediosagittal plane than to the cheek margins, and probably within the rear half of the skull.

The foramen neuro-epiphysiale (*fne*, Figs 1, 6) is small and circular. It lies intrasuturally in the dorsal midline, close behind the orbitofacial openings and level with the centers of ossification of the two bones that form its margin. Whether this foramen served a parapineal or a pineal organ remains unresolved.

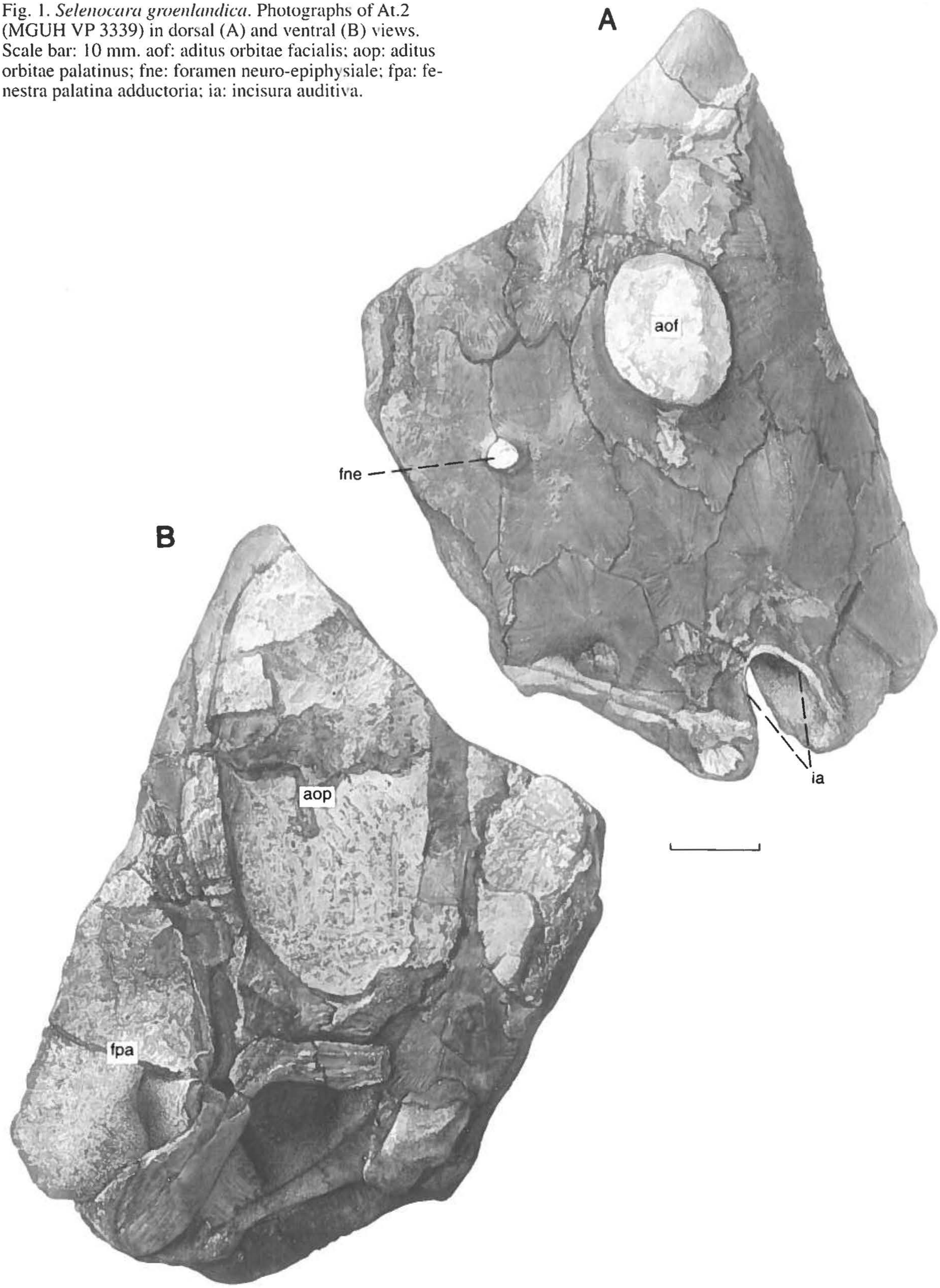
The aditus orbitarum palatini (orbitopalatine openings, *aop*, Fig. 1), known variously as the interpterygoid vacuities or fenestrae (cf. Case 1946, Nilsson 1946), occupy the greater part of the hard palate behind the snout (Fig. 3). They are significantly wider anteriorly than posteriorly. The ipsilateral orbitofacial opening lies dorsal to each of them. Viewed ventrally, the former aditus can be seen in its entirety within the rear half of the latter aditus.

The fenestra palatina adductoria (*fpa*, Fig. 1), also called the infratemporal fenestra (Bystrov & Yefremov 1940) or subtemporal vacuity (Welles & Cosgriff 1965), occupies most of the posterolateral part of the hard palate (Fig. 3). Lying mostly horizontally, this aperture is subtriangular in shape and extends forward to the transverse level of the rear of the orbitofacial aditus of the same side. Its inner margin is not indented anteriorly by an entopterygoid bulge, unlike those of many other Triassic tetrapods (cf. Welles & Cosgriff 1965).

The ostium occipitale antri supra-auditualis is the posterior entrance to a skeletal cavity situated above the membranous labyrinth. This cavity is referred to by Säve-Söderbergh (1936) as the fossa Bridgei, by Chowdhury (1965) as the fossa supraotica, and by Sawin (1941) and others as the fossa posttemporalis (for these terms see Bjerring 1984). The occipital opening of the antrum supra-audituale is frequently regarded as a window and usually designated the fenestra posttemporalis (but fenestra subtabularis in Bystrov & Yefremov 1940). In the holotype described here, the ostium in question (*os.asa*, Fig. 4) is fairly large. Facing posteromesially, it has an elongate triangular shape, whose base is directed mesially and apex dorsolaterally, The ostial margin is mostly exoskeletal, with only a small ventromesial endoskeletal part.

The foramen magnum (*f.m*, Fig. 4) is directed posteriorly. In outline, it resembles an equilateral triangle the apex of which is above in the mediosagittal plane.

Fig. 1. *Selenocara groenlandica*. Photographs of At.2 (MGUH VP 3339) in dorsal (A) and ventral (B) views. Scale bar: 10 mm. aof: aditus orbitae facialis; aop: aditus orbitae palatinus; fne: foramen neuro-epiphysiale; fpa: fenestra palatina adductoria; ia: incisura auditiva.



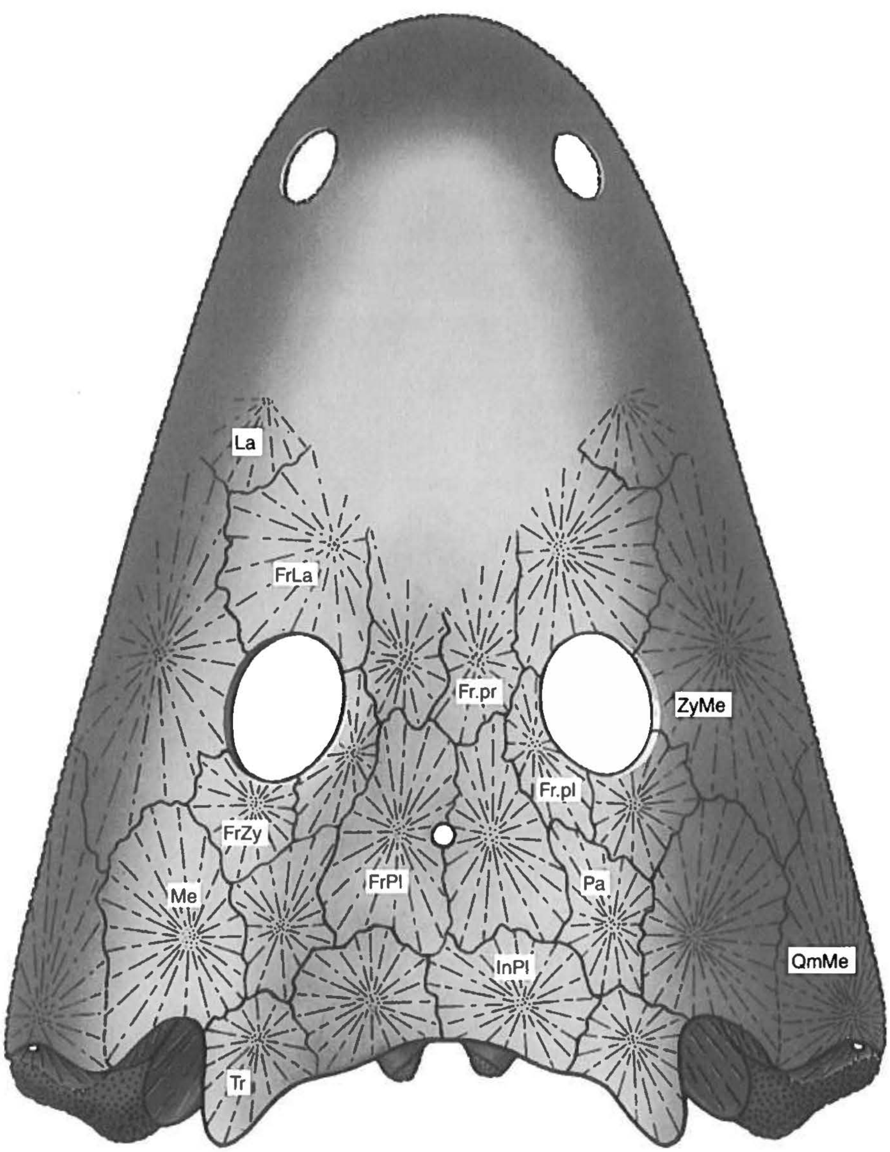


Fig. 2. *Selenocara groenlandica.* Dorsal view of skull roof, based upon At.2 (MGUH VP 3339). For terminology cf. Bjerring 1995b. FrLa: frontolacrimal bone ("prefrontal bone"); FrPl: frontopluteal bone ("parietal bone"); Fr.pl: posterolateral frontal bone ("postfrontal bone"); Fr.pr: principal frontal bone ("frontal bone"); FrZy: frontozygomatic bone ("postorbital bone"); InPl: iniacopluteal bone ("postparietal bone"); La: lacrimal bone; Me: melonic bone ("squamosal bone"); Pa: parietal bone ("supratemporal bone"); QmMe: quadratomaxillomelonic bone ("quadratojugal bone", a term coined by Nitzsch in 1815); Tr: trachelic bone ("tabular bone"); ZyMe: zygomaticomelonic bone ("jugal bone").

Its margin is bony except middorsally and midventrally.

The incisura auditiva (otic notch of Säve-Söderbergh 1935; *ia,* Figs 1, 6), probably containing the ear-drum, interrupts the posterior margin of the skull on either side. This indentation is comparatively wide and moderately deep. Its margin, shaped like an inverted letter U, is mostly horizontal, and formed by two exoskeletal bones.

Skull roof exoskeleton

Although the bones are almost completely absent the pattern of the exoskeletal elements of the posterior and middle parts of the skull roof is clearly visible. This roof pattern consists of twelve paired elements united by squamous sutures. The shape, positional relation and ossification center of each of these bones are presented in figure 2, and need no further description.

Palatal exoskeleton

The preserved posterior and middle parts of the palatal surface of the skull include three paired elements, and one which is single (Fig. 3). This palatal complex is partly represented by molds (Fig. 1B).

The single bone (*Cr,* Figs 3, 4) is the so-called parasphenoid lying beneath the endocranium. This median element will henceforth be referred to as the crepidine bone (cf. p. 16). It consists of two portions, a body and an elongate cultriform process extending anteriorly.

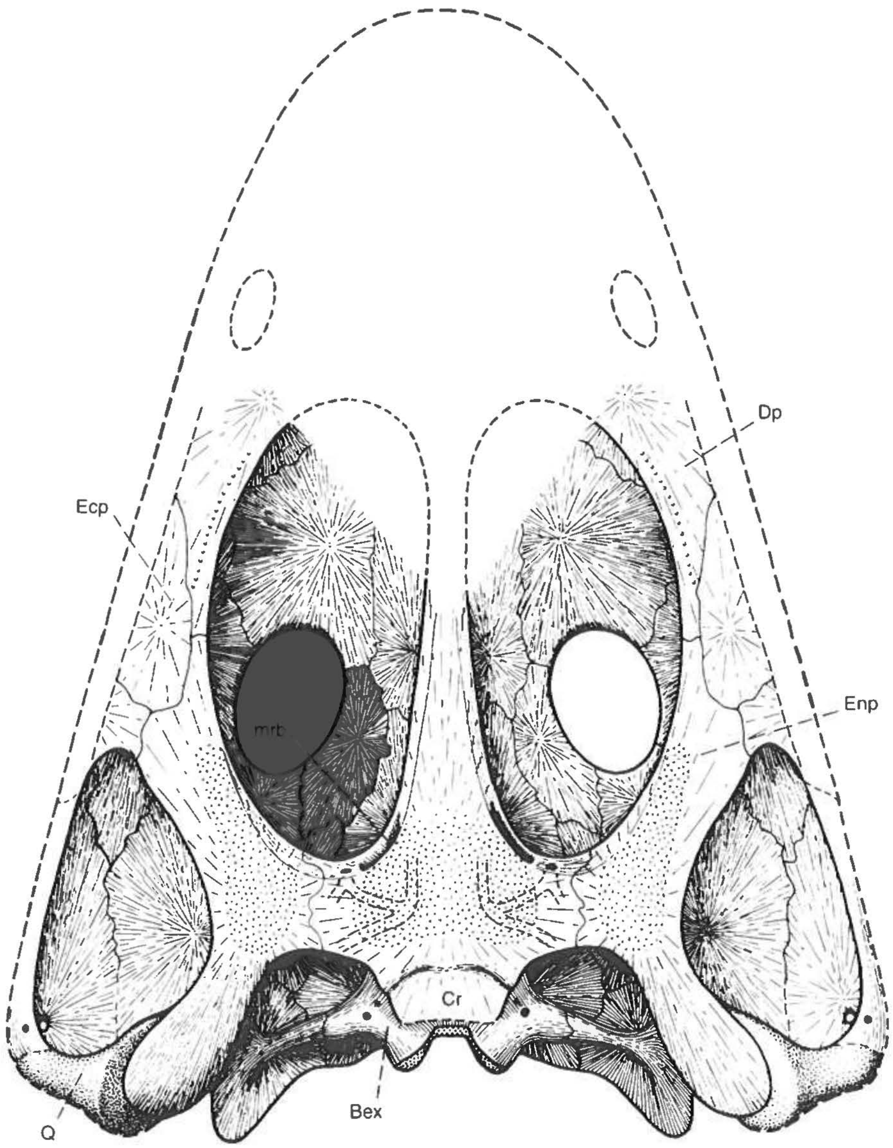


Fig. 3. *Selenocara groenlandica*. Palatal view of skull, based upon At.2 (MGUH VP 3339). Canals within the crepidine bone indicated by broken lines. Bex: basi-exoccipital bone; Cr: crepidine bone ("parasphenoid bone"); Dp: dermopalatine bone; Ecp: ectopterygoid bone; Enp: entopterygoid bone; mrb: retractor bulbi myodome; Q: quadrate bone.

The corpus ossis crepidini is significantly wider than long. It sutures laterally with the entopterygoid bone, and abuts with a compound bone (*Bex*, Figs 3,4) of the rear of the endocranium posteriorly and posterolaterally. The posterior opening of the canal for the internal carotid artery (*c.aci*, Fig. 4) lies immediately mesial to the posterior end of the sutural union just mentioned. This canal passes anteromesially for some distance within the crepidine body, and then continues to its endocranial opening dorsal to the base of the cultriform process. Within the crepidine bone the carotid canal gives off a lateral branch which opens close to the anterior end of the crepidine-entopterygoid suture. Presumably, this canal transmitted the palatine artery. A third, short canal runs downwards from the dorsal surface of the crepidine body to the anterior end of the canal interpreted as a passageway for the palatine artery; it probably conveyed the palatine ramus of the facial nerve to the mouth roof. According to Säve-Söderbergh (1936) *Lyrocephaliscus euri* (Wiman 1914) Kuhn 1961 has a similar canal.

A pocket-like depression (*mrb*, Fig. 3) lies mesial to the common opening of the two last-mentioned crepidine canals, within the margin of the crepidine bone, and at the transition between its corpus and cultriform process. This depression is probably a myodomus retractricis bulbi and might have its counterpart in what Nilsson (1946: fig. 6; *Peltostega erici*) has designated *fa* and Watson (1962: fig. 11; *Wetlugasaurus magnus*) *?Bl.Ves* (see also Säve-Söderbergh 1936: figs 5 and 21).

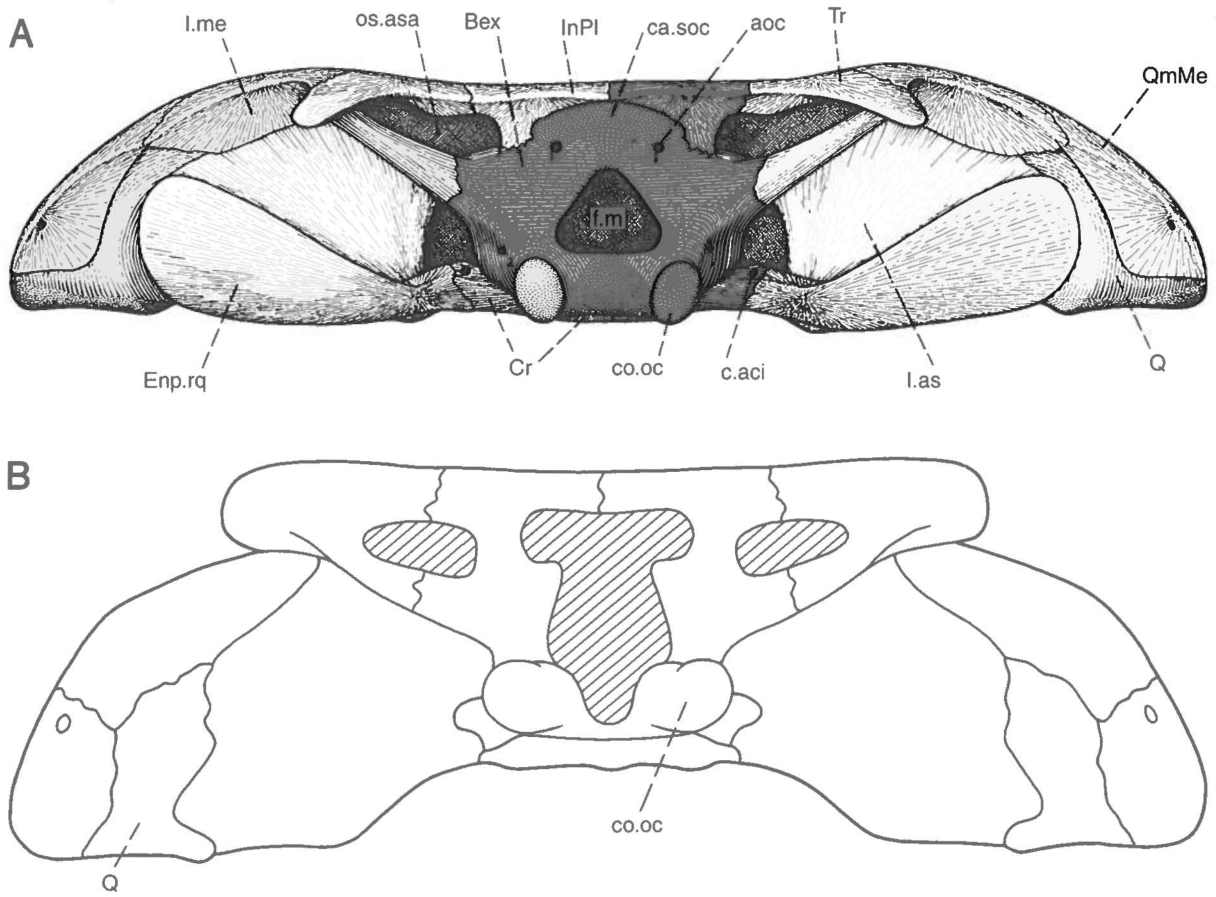


Fig. 4. A: *Selenocara groenlandica*. Occipital view of skull, based upon At.2 (MGUH VP 3339). B: *Wetlugasaurus angustifrons*. Sketch of occiput to show that, in contrast to *Selenocara groenlandica*, the jaw joints are not level with the occipital condyles. After Ryabinin 1930. Cf. Novikov 1990: fig. 1. aoc: opening for occipital artery; Bex: basi-exoccipital bone; c.aci: canal for internal carotid artery; ca.soc: supraoccipital cartilage; co.oc: occipital condyle; Cr: crepidine bone ("parasphenoid bone"); Enp.rq: ramus quadratus ossis entopterygoidis; f.m: foramen magnum; InPl: iniacopluteal bone ("postparietal bone"); l.as: lamina ascendens ossis entopterygoidis; l.me: descending lamina of melonic bone; os.asa: ostium occipitale antri supra-auditualis; Q: quadrate bone; QmMe: quadratomaxillomelonic bone ("quadratojugal bone"); Tr: trachelic bone ("tabular bone").

The posterior part of the crepidine body is only preserved laterally. In the living subject, it was presumably a fairly thin sheet of bone below the midventral portion of the occipital region of the endocranium. Since the middle and anterior parts of the crepidine body are considerably thicker than its posterior part appears to have been, it is not entirely unreasonable that "pockets" for muscular attachments similar to those mentioned by Watson (1962) were present ("tubera basisphenoidales" of Romer, 1930).

The cultriform process is preserved as a mold of its dorsal surface from the crepidine body to a transverse level a little in front of the orbitofacial openings. This mold shows that the process was relatively broad and had a plane contact with the overlying part of the endocranium. Moreover, the cultriform process was probably not just a thin sheet of bone; rather, as indicated by the thickness of the crepidine body at the retractor bulbi myodome, it might have been trapezoidal in cross section, at least posteriorly.

A patch of denticles lying beneath the retractor bulbi myodome deserves mention. Apparently, the denticulation of the crepidine bone was not restricted to this small area but probably covered a large part of the palatal surface, as in *Benthosuchus sushkini* (Bystrov & Yefremov 1940).

The entopterygoid bone (*Enp*, Fig. 3) is the largest of the paired elements of the hard palate. It is triradiate in ventral view and divisible into a body, two rami, and an ascending lamina.

The corpus entopterygoidis is an almost square plate enclosing the ossification center. It sutures with the crepidine bone mesially and contributes to the margin of the fenestra palatina adductoria laterally. The ventral surface lies horizontally and was probably mostly covered by minute teeth.

The ramus palatalis (*vel* anterior) ossis entopterygoidis, which is the longer of the two entopterygoid rami, projects anterolaterally from the corpus until level with the anterior margin of the ipsilateral orbitofacial opening. It contributes to the rim of the aditus orbitae palatinus mesially and that of the fenestra palatina adductoria laterally. Anteriorly it sutures with the ipsilateral dermopalatine and ectopterygoid bones, as well as with the palatal wing of a cheek bone of the same side. Like the corpus of the bone, this ramus is horizontal and partly covered ventrally by a shagreen of denticles.

The ramus quadratus (*vel* posterior) ossis entopterygoidis is lamelliform and directed posteriorly, laterally and somewhat dorsally from the corpus of the bone, to which it is connected by a slightly constricted neck. It abuts on the mesial surface of the quadrate bone posteriorly and its lower border contributes to the rim of the fenestra palatina adductoria. The ventromesial surface of this ramus is smooth and toothless.

The lamina ascendens ossis entopterygoidis (*l.as*, Fig. 4A) is triangular and distinctly deflected toward the mediosagittal plane anteriorly. It has two surfaces and three borders. The lower border is attached to the morphologically internal surface of the quadrate ramus and corpus of the bone. This border extends from the quadrate bone to the entopterygoid ossification center and diverges forwardly from the upper border of the quadrate ramus of the entopterygoid bone. The latter border may thus be considered a longitudinal entopterygoid crest or shelf corresponding to what Shishkin (1980) calls the crista posterior entopterygoidea. The upper border of the ascending entopterygoid lamina inclines dorsally and terminates beneath the middle of the parietal bone. It is free except for a short articulation with a low descending lamina (*l.me*, Fig. 4A) of the skull roof lateral to the incisura auditiva. The anterior border is nearly vertical and directed mesially. Its ventral part, neighboring the entopterygoid ossification center and the sutural contact between the corpora of the crepidine and entopterygoid bones, is conspicuously thicker than its dorsal part. At the transition from this thick part of the border to the subjacent entopterygoid corpus, there is a cone-shaped depression which probably received a laterally projecting endocranial process, namely the processus affacialis (see below). This depression is customarily referred to as the conical recess but will henceforth be termed the fossa coniformis entopterygoidea. Of the two surfaces of the ascending lamina of the entopterygoid bone only the mesial one is available for study. This surface is smooth and, as far as can be seen, lacks the oblique ridge reported in some other Triassic tetrapods (cf. Nilsson 1946, Ingavat & Janvier 1981).

The dermopalatine bone (*Dp*, Fig. 3) is mainly preserved as a natural mold of the posterior half of its dorsal surface. It demarcates the anterolateral part of the orbitopalatine opening, and joins the ectopterygoid bone posterolaterally and the anteriormost tip of the entopterygoid bone posteriorly. Mesially, alongside the orbitopalatine opening, the little that is left of the bone presents a longitudinal row of comparatively small teeth. The lateral border of the dermopalatine bone, which articulated in life with the maxilla, was apparently somewhat thickened and raised to a narrow crest. A groove on the lateral side of the mold indicates that this crest expanded dorsomesially in a postero-anterior direction. Consequently, it appears that the dermopalatine bone abutted anteriorly with the overlying skull roof by means of a process corresponding to the spina sublacrimalis of *Benthosuchus sushkini* (Bystrov & Yefremov 1940).

The ectopterygoid bone (*Ecp*, Fig. 3) is the smallest of the preserved paired elements of the hard palate. Only a natural mold of its dorsal surface is available for study. The bone lies between the maxillary, dermopalatine and entopterygoid bones of the same side. Posteriorly, it is excluded from the boundary of the fenestra palatina adductoria by a winglike inward extension of a cheek bone (processus alaris ossis jugularis of Bystrov & Yefremov 1940).

Palatal endoskeleton

The quadrate bone (*Q*, Figs 3, 4A) is short and massive. It lies ventrolateral to the incisura auditiva and contributes to the margin of the fenestra palatina adductoria. Its condylar part is lost. The bone has three surfaces. Of these, the inner surface is convex and partly covered by the rear of the ipsilateral entopterygoid bone and a descending lamina of the skull roof. The upper surface is plane and abuts with two adjacent cheek bones. The outer surface, formed by compact bone, is concave and not covered by exoskeleton. The anterior border, situated level with the deepest part of the incisura auditiva, consists of spongy bone and in life apparently merged into a cartilaginous part of the palatoquadrate.

Endocranial bone

All that remains of the endocranium is a bony structure which rings the foramen magnum almost completely, and extends forward to contribute to the otic capsules. This posteriormost endocranial component consists of a median ventral, or basilar, part and lateral parts, flanking right and left sides. It is presumably a compound structure formed by the fusion of three embryonic ossifications; this is identified as the basiexoccipital bone (*Bex*, Figs 3, 4A).

The midventral part of the basi-exoccipital bone is an endochondrally ossified, dorsoventrally flattened lamina, which contributes to the base of the endocranium. Quadrilateral in outline and somewhat longer than broad, it extends forward from the anterior extremities of the occipital condyles to about the transverse level of the posterior openings of the crepidine canals for the internal carotid arteries. Its ventral surface rests directly on the corpus ossis crepidini; its dorsal surface as well as its anterior and posterior borders appear to have been covered by cartilage in life. Thus, in the intact skull this basicranial component is not directly visible.

The lateral parts of the basi-exoccipital bone demarcate most of the foramen magnum (*f.m*, Fig. 4A) and connect the skull roof with the hard palate. Only the external surface of the right side is available for study. This consists mostly of compact bone. Ventrally, however, it is formed of spongy bone and abuts with the corpus ossis crepidini. The lateral portion of this surface is smooth and concave anteroposteriorly and dorsoventrally. It expands anteriorly and also curves outwardly. Its ventral boundary contributes to the suture between the basi-exoccipital and crepidine bones, and its dorsal boundary to the suture between the basi-exoccipital and trachelic bones. Posteriorly there are two openings, an upper larger one and a lower smaller one, lying relatively close to each other. The former probably transmitted the vagus nerve and the latter the hypoglossal nerve.

The posterior portion of the external surface of the lateral part of the basi-exoccipital bone is mainly smooth and very nearly vertical. The occipital condyle (*co.oc*, Fig. 4A) lies ventrally, at the transition to the basilar part of the bone. This condyle is oval, and devoid of compact bone distally. Thus, in life, the articular surface of the condyle was probably cartilaginous, convex and directed posteromesially. Adjacent to the occipital condyle and in a postvagal position there is an inwardly directed projection, usually called the submedullary process (but processus basalis of Welles & Cosgriff, 1965 and of Cosgriff, 1974). This projection approaches the mediosagittal plane and overlies the space that presumably was occupied by the basilar cartilage mentioned earlier. It partially deliminates the foramen magnum ventrally. Dorsal to the foramen magnum lies another inwardly directed projection known as the supramedullary or lamellose process. Larger than the submedullary one, this projection is plate-like and probably formed a part of the surface layer of the cartilaginous supraoccipital segment of the occiput (*ca.soc*, Fig. 4A). Its upper margin presents a small notch which continues ventrally as a short, shallow groove (see Fig. 4A). This groove and notch may indicate the course of the occipital artery (cf. Jarvik 1975). Immediately lateral to the projection just described lies the suture between the basi-exoccipital and iniacopluteal bones. A small anterodorsally directed lamelliform projection of the bone under consideration neighbors this suture. The projection extends laterally to the suture between the basi-exoccipital and trachelic bones. It probably formed a superficial part of the otic capsule and contributed to the floor of the antrum supra-audituale. A correspond-

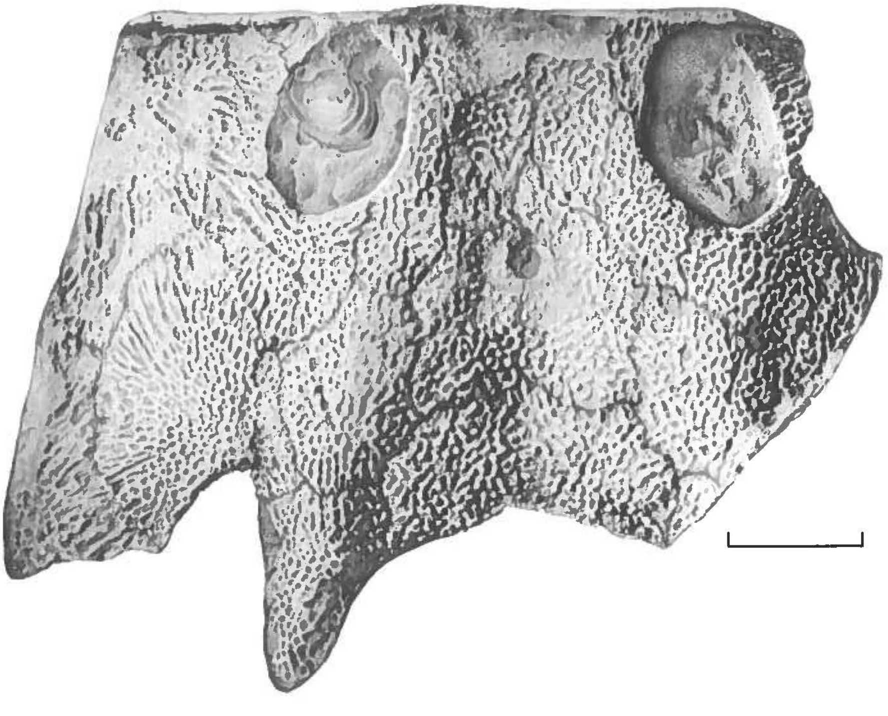


Fig. 5. *Selenocara groenlandica.* Photograph of a cast of At.17 (MGUH VP 3340) made in latex. Scale bar: 10 mm.

ing perichondral lamina has previously been recorded in *Aphaneramma rostratum* (cf. Säve-Söderbergh 1936: p. 102).

Redescription of Säve-Söderbergh's cotype

This specimen (Fig. 5) is a natural mold of the external surface of middle and posterior parts of a skull roof belonging to a cranium of approximately the same size as that of the holotype. The sculpture on the external surfaces of the bones consists of a series of anastomosing closely arranged ridges with rounded crests. In places, however, there are a few tubercles, which flank small irregular pits and short grooves. Between and behind the orbitofacial openings the median part of the skull roof is somewhat depressed as is the corresponding area in osteolepiform fishes (cf. Jarvik 1948).

Sections of the systema neuromasticum are indistinctly marked by linearly arranged pits separated through low ridges. These rows of pits show the location of the posterior part of the ductus infraorbitalis neuromasticus (*din*, Fig. 6) and most of the ductus temporalis neuromasticus (*dtn*, Fig. 6).

The roof pattern, illustrated in figure 6, is quite comparable to that of the holotype. Except that the

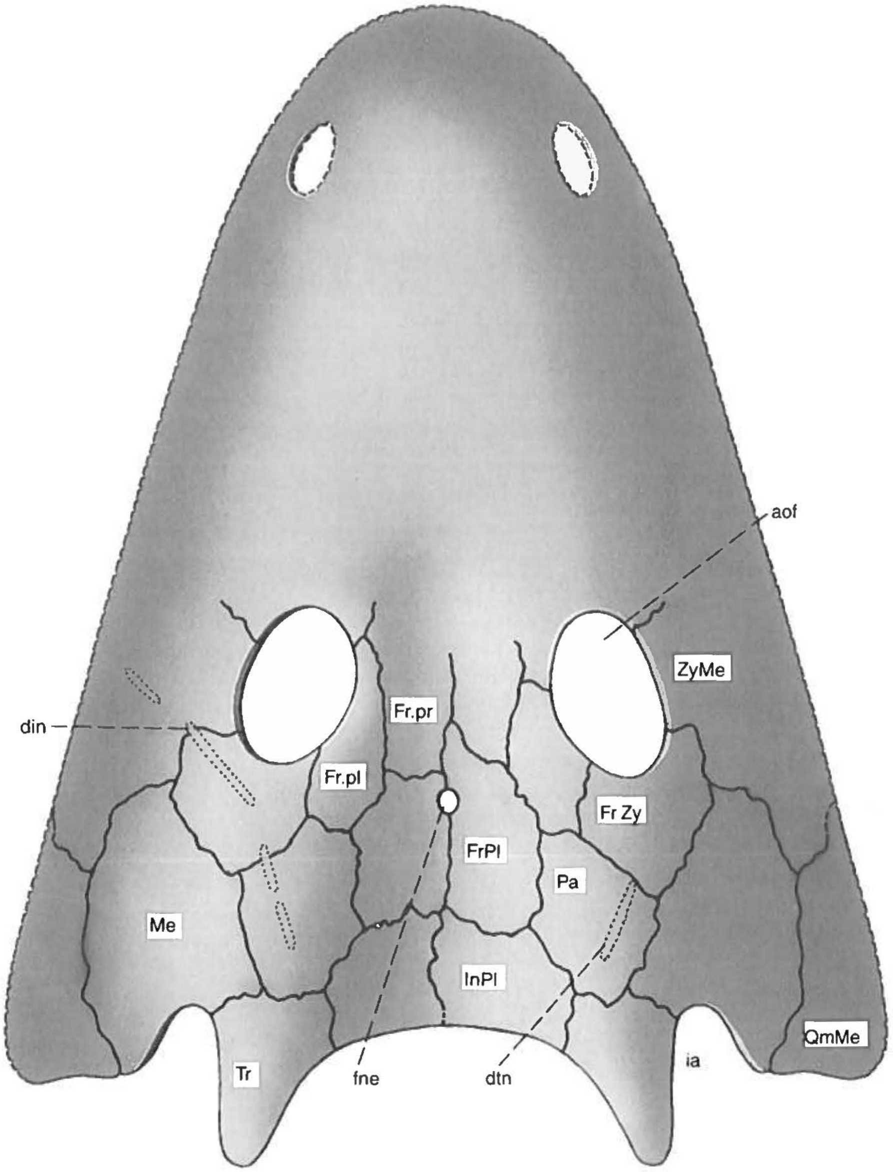


Fig. 6. *Selenocara groenlandica*. Reconstruction of skull in dorsal view, based upon At.17 (MGUH VP 3340). aof: orbitofacial opening; din: location of posterior part of ductus infraorbitalis neuromasticus; dtn: location of ductus temporalis neuromasticus; fne: neuro-epiphysial foramen; FrPl: frontopluteal bone; Fr.pl: posterolateral frontal bone; Fr.pr: principal frontal bone; FrZy: frontozygomatic bone; ia: auditive incisure; InPl: iniacopluteal bone; Me: melonic bone (os melonicum, new term from the Greek *melon* + *icus*); Pa: parietal bone; QmMe: quadratomaxillomelonic bone; Tr: trachelic bone; ZyMe: zygomaticomelonic bone.

trachelic bones are a little longer in Säve-Söderbergh's cotype than in the holotype, there is only very slight differences in the shapes and relative sizes of the roofing bones. Thus, it is reasonable to conclude that these two specimens are conspecific.

Conclusion

The flatheaded Triassic tetrapod described above cannot be allocated to the genus *Wetlugasaurus* because the quadrate condyles are about level with the occipital condyles, both transversally and horizontally (cf. Fig. 4); the orbitofacial openings are wholly visible through the orbitopalatine openings when viewed ventrally; and the long axis of each orbitofacial opening is directed towards the ipsilateral auditive incisure.

Selenocara groenlandica has a general capitosaurid appearance. Distinctive of this tetrapod is that its jaw articulations are level with its occipital condyles dorsoventrally as well as anteroposteriorly and that the length of each of its corpora ossium entopterygoidum is not more that one-fifth of the breadth across these corpora. The relationships of *Selenocara groenlandica* to other capitosaurs are not addressed within this paper.

Fossa coniformis entopterygoidea (*mihi*): origin and evolutionary significance

This skeletal depression (*fs.c.enpt*, Fig. 7), which is situated in the mesial part of the dorsal surface of the corpus ossis entopterygoidis, was discovered in the mid-1930s by the late Swedish paleozoologist Gunnar Säve-Söderbergh. In 1935, he reported its presence in the tetrapod genus *Stoschiosaurus* from the Lower Triassic of East Greenland; then, in 1936, he stated that an identical depression occurs in three further tetrapod genera, *viz*., *Lyrocephaliscus*, *Platystega* and *Aphaneramma*, all from the early Triassic of Spitzbergen.

Säve-Söderbergh referred to the depression in question as the conical recess in the corpus of the entopterygoid bone. However, he made no suggestion to account for its existence. Neither did Bystrov & Yefremov (1940) who, using the designation recessus conoideus, described and beautifully illustrated the fossa coniformis entopterygoidea in the Lower Triassic tetrapod *Benthosuchus sushkini* of eastern European Russia (Fig. 7) The cone-shaped fossa in the entopterygoid bone has more recently been recorded in several other Triassic tetrapods (cf. Lehman 1961, Chowdhury 1965, Ochev 1972, Getmanov 1989). It is worth noting that all of the fossil tetrapods known so far to possess a fossa coniformis entopterygoidea also possess a sutural connection between each of the entopterygoid bones and the crepidine bone. (For an explanation of the latter term see below.)

In 1947, Romer suggested that the fossa coniformis entopterygoidea acted as the receptacle for the laterally projecting basipterygoid process. Before long this idea gained recognition among vertebrate paleontologists and is nowadays generally accepted (cf. Panchen & Smithson 1988, Getmanov 1989). However, the relative position of the fossa coniformis entopterygoidea casts doubt on Romer's suggestion and, as will be shown later, there is an alternative explanation of this skeletal depression.

Romer (1947) considered the precursor of the immovable peg-and-socket articulation between the endoskeletal basipterygoid process and the exoskeletal cone-shaped fossa just mentioned, to be mobile, as in the Lower Permian tetrapod *Edops craigi* (cf. Romer & Witter 1942). Here, the basipterygoid process fits into a bowl-shaped depression that is occupied centrally and dorsally by an ossified mid-region of the palatoquadrate cartilage, and peripherally by a thickening of the entopterygoid bone. Thus, according to this evolutionary scenario, the immobile articulation simply arose as a result of the retreat of the palatoquadrate component from the mobile articulation and some growth of the entopterygoid bone.

The ossified mid-region of the palatoquadrate mentioned in the preceding paragraph is usually described as the epipterygoid. This term was coined by Parker (1880) to denote a columnlike endoskeletal structure in the head of the lizard *Lacerta agilis* (*Ept*, Fig. 8). It has also been described as the columelle (Cuvier

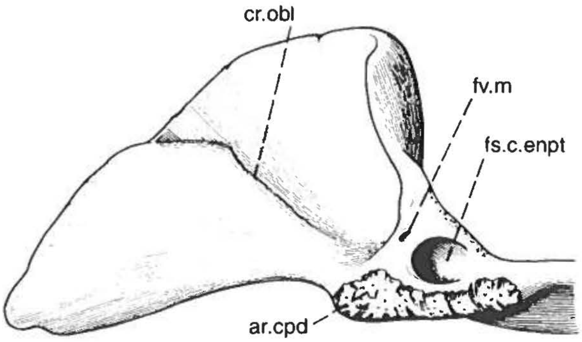


Fig. 7. *Benthosuchus sushkini*. Corpus, ramus quadratus et lamina ascendens ossis entopterygoidis of the left side in mesial view. From Bystrov & Yefremov 1940. ar.cpd: area sutured with crepidine bone; cr.obl: crista obliqua; fs.c.enpt: fossa coniformis entopterygoidea; fv.m: fovea probably for insertion of a muscle that passed backwards to stapes.

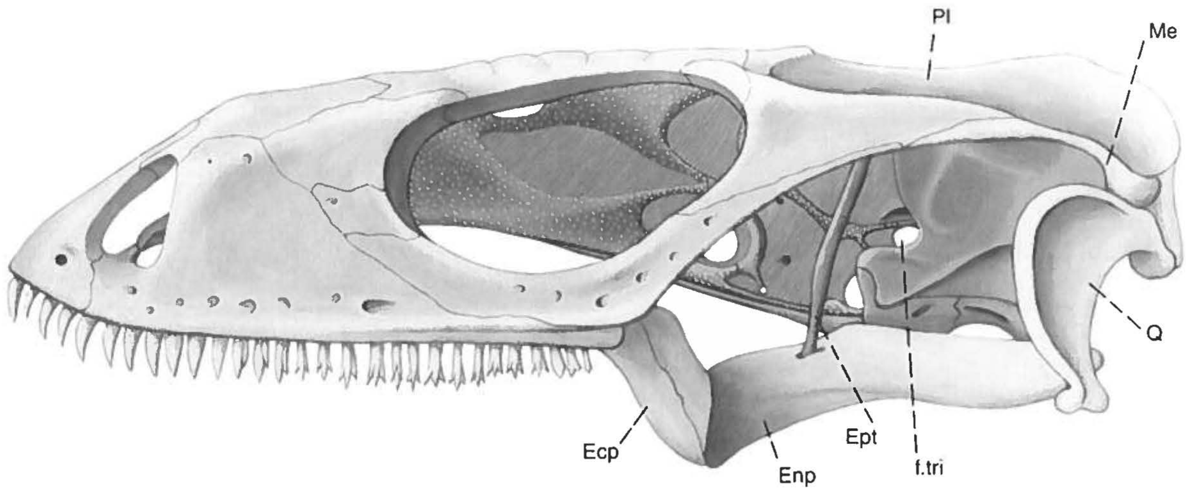


Fig. 8. *Ctenosaura pectinata*. Sinistral view of cranium to show the columnar autostosis that by definition is an os epipterygoides. Based on data obtained from Oelrich 1956. Ecp: ectopterygoid bone; Enp: entopterygoid bone; Ept: epipterygoid bone; f.tri: foramen for trigeminal nerve; Me: melonic bone; Pl: pluteal bone; Q: quadrate bone.

1825, 1837), the columella (Hallmann 1837) and the antipterygoid (Gaupp 1891). Since the so-called epipterygoid of temnospondyls (cf. Sushkin 1927, Säve-Söderbergh 1936, Wilson 1941, Sawin 1941, Romer & Witter 1942, Watson 1962) is usually a much more composite structure than that of lizards, it will be referred to as the mesopalatoquadrate bone (*Mpq*, Fig. 9).

Smithson (1982) suggests a variation of the previously described Romerian evolutionary scenario. This starts with the osteolepiform condition, where a convex facet on the posterior surface of the processus palatobasalis palatoquadrati is received by a concave facet on the anterior surface of the processus basipterygoideus. A deep depression, described as the conical recess, is thought to have arisen immediately behind the processus palatobasalis palatoquadrati and, concomitantly, the processus basipterygoideus grew

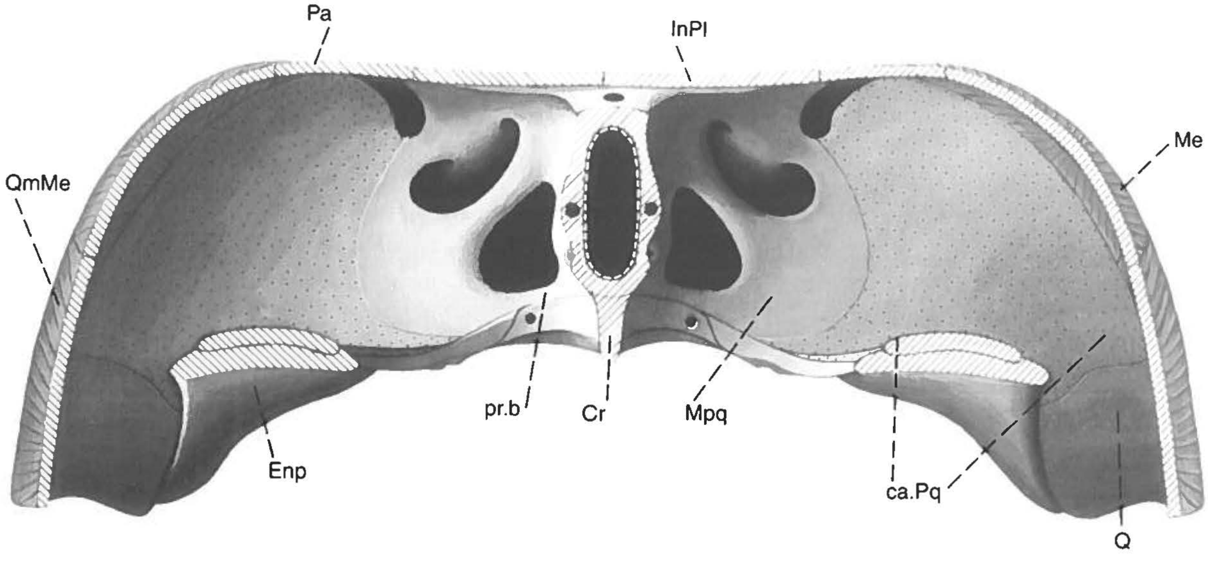


Fig. 9. *Lyrocephaliscus euri*. Reconstruction of posterior part of skull in anterior view. Based on data obtained from Säve-Söderbergh 1936, 1945.
ca.Pq: cartilaginous part of palatoquadrate; Cr: crepidine bone; Enp: entopterygoid bone; InPl: iniacopluteal bone; Me: melonic bone; Mpq: mesopalatoquadrate bone; Pa: parietal bone; pr.b: processus basalis; Q: quadrate bone; QmMe: quadratomaxillomelonic bone.

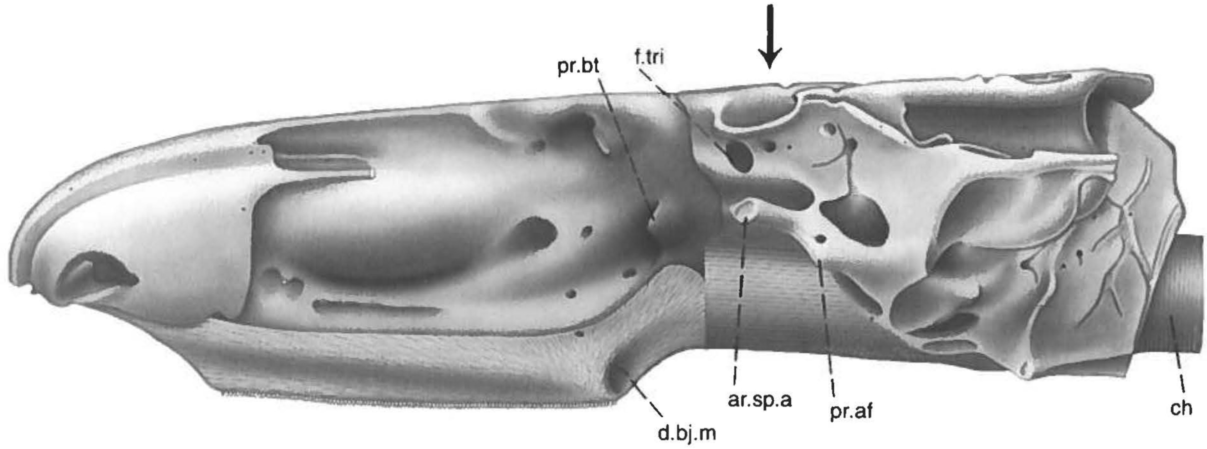


Fig. 10. *Eusthenopteron foordi*. Left-side view of endocranium with crepidine bone. From Bjerring 1995a. The arrow indicates the location of the section appearing as figure 11. ar.sp.a: endocranial area participating in anterior sanidiopalatoquadrate articulation; ch: notochord; d.bj.m: depression in posterior part of crepidine bone that gave attachment to the basijunctorial muscle; f.tri: foramen for trigeminal nerve; pr.af: affacial process; pr.bt: basipterygoid process.

outwards into this depression. In the anthracosaur lineage this new basal articulation remained mobile whereas in the temnospondyl lineage it became an immobile peg-and-socket junction that served to anchor the endocranium into the skull.

Thus, students of temnospondyls subscribe to the notion that many of these fossil tetrapods have a basipterygoid process fitting into a cone-shaped depression in the entopterygoid bone. However, current opinions sometimes turn out to be untenable. As will be shown below that of Romer (1947) on the fossa coniformis entopterygoidea is one of those which does not hold.

Osteolepiform fishes have anatomical qualifications which place them in the key position as progenitors of tetrapods. The Upper Devonian species *Eusthenopteron foordi* from Miguasha is the only example in which the articulations between the palatoquadrates and other parts of the cephalic skeleton are fully known (cf. Jarvik 1980, Bjerring 1995a). Here, each palatoquadrate articulates at nine points with the endocranial skeleton. Details of three of these articulations are relevant to the following discussion, *viz.*, the basitrabecular and the two sanidiopalatoquadrate articulations (Figs 10, 11). The basitrabecular articulation is situated in the hypophysial neighborhood and was probably a synchondrosis between the palatobasal process of the pterygoquadrate component of the palatoquadrate and the basipterygoid (basitrabecular) process of the endocranium. This articulation lies behind the canal for the internal carotid artery which connects with the hypophysial fossa and above the palatine ramus of the facial nerve. The anterior sanidiopalatoquadrate articulation was probably a synchondrosis too because its contiguous bony surfaces are devoid of periosteal lining. One of these surfaces lies on a small, low eminence that protrudes mesially from the pterygoquadrate component of the palatoquadrate. This eminence is located at the anteroventral corner of the juxtaspiracular process of the palatoquadrate. It is situated below an incisure in the upper margin of the palatoquadrate, which apparently served for passage of the maxillary branch of the trigeminal nerve. The other bony surface of the anterior sanidiopalatoquadrate articulation is placed near the anterior end of the jugular sanidium (for this term see Bjerring 1993a) and thus not far behind the hypophysial fossa. The articulation lies dorsal to the internal carotid artery and the palatine ramus of the facial nerve, and anterior to the anteroventral part of a deltoid field of spiracular dental plates (*cat*, Fig. 14). Finally, the posterior sanidiopalatoquadrate articulation was probably a syndesmosis (*art.sp.p*, Fig. 11). It lies immediately behind the anterior sanidiopalatoquadrate articulation, and is formed between a short, broad, and shallow groove ventrally on the mesial surface of the juxtaspiracular process of the palatoquadrate and the jugular sanidium. Like the two synchondroses previously mentioned, this syndesmosis is situated dorsal to the internal carotid artery and the palatine ramus of the facial nerve.

Another structure of relevance to this issue is the affacial process. This (*pr.af*, Fig. 10) is a ventrolaterally directed protrusion of the jugular sanidium situated below and immediately behind the outer opening of the endocranial canal for the palatine ramus of the facial nerve. The affacial process (or parotic process, Säve-Söderbergh 1936) is well-developed in the osteolepiform *Rhizodopsis sauroides*. It is somewhat less developed, however, in *Eusthenopteron foordi*. In osteolepiforms, this process probably served for attachment of the musculus abductor hyomandibularis

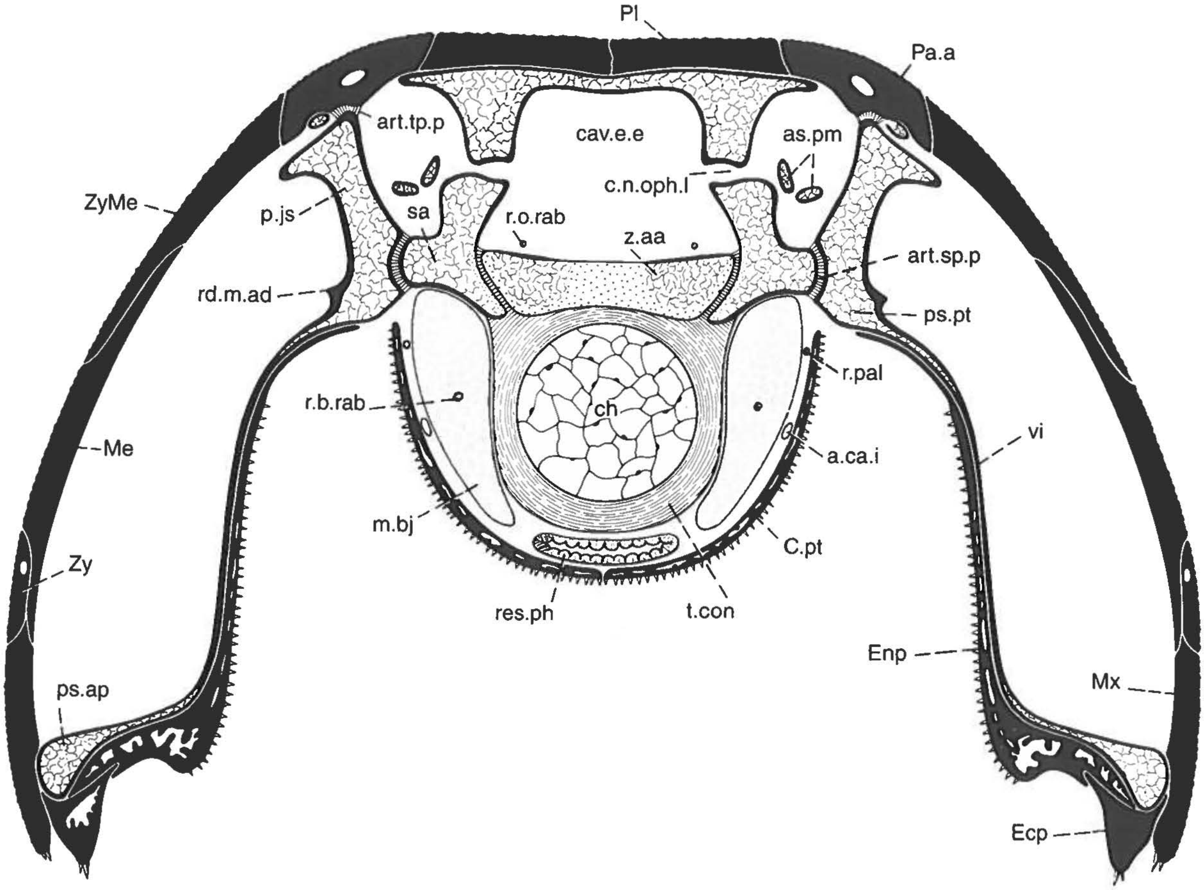


Fig. 11. *Eusthenopteron foordi*. Transverse section through the temporal region showing the syndesmotic posterior sanidiopalatoquadrate articulation and some reconstructed nonskeletal parts. Based on a series of ground sections of specimen P222 in the Swedish Museum of Natural History and a wax-plate model made from these sections. Cf. Bjerring 1993b: figs 4 & 5. a.ca.i: internal carotid artery; art.sp p: posterior sanidiopalatoquadrate articulation; art.tp.p: posterior tectopalatoquadrate articulation; as.pm: postmandibular autostoses ("prespiracular cartilage bones"); cav.e.e: cavitas encephalica endocranii; ch: notochord; c.n.oph.l: canal for ophthalmic nerve of neuromast system; C.pt: crepidinulum parabasale temporale ("paraotic dental plate"); Enp: entopterygoid bone; Ecp: ectopterygoid bone; m.bj: basijunctorial muscle ("subcranial muscle"); Me: melonic bone ("squamosal bone"); Mx: maxillary bone; Pa.a: anterior parietal bone ("intertemporal or supratemporal bone"); p.js: juxtaspiracular process of palatoquadrate (cf. Bjerring 1995a); Pl: pluteal bone (cf. Bjerring 1995b); ps.ap: autopalatine part of palatoquadrate; ps.pt: pterygoquadrate part of palatoquadrate; rd.m.ad: ridge for attachment of mandibular adductor musculature; res.ph: recessus pharyngeus; r.b.rab: basicranial branch of rarabdual nerve (cf. Bjerring 1993b); r.o.rab: orbital branch of rarabdual nerve (enters orbita via gap between infracerebral and supracerebral divisions of intracranial juncture apparatus); r.pal: palatine ramus of facial nerve; sa: jugular sanidium ("otical shelf"); t.con: connective tissue; vi: vincular part of palatoquadrate; z.aa: anterior prootic anazygal element (cf. Bjerring 1971); Zy: zygomatic bone ("jugal bone"); ZyMe: zygomaticomelonic bone ("postorbital bone").

(*m.ab.hy*, Fig. 12), a plausible forerunner of the musculus stapedius. A well-developed affacial process also occurs in coelacanthiforms (Bjerring 1972, 1973), where its apex carries a small, curved, dental plate that is visible in the spiracular pouch (*sp.d.pl*, Fig. 13). This coelacanthiform dental plate probably corresponds to one of the comparatively large spiracular dental plates lying next to the affacial process in *Eusthenopteron foordi*. The affacial process lies below and behind the palatine ramus of the facial nerve, above the internal carotid artery and a little in front of where the ventral head of the hyomandibular bone articulates with the endocranial sidewall.

In order to provide an adequate explanation of the fossa coniformis entopterygoidea, it is also necessary to consider briefly the bone that is usually described as the parasphenoid. This term was used first by Huxley (1864) to denote the largest of the palatal bones in the northern pike, *Esox lucius* (Fig. 15). Thus, by definition, the parasphenoid bone is a median, edentate, exoskeletal element which extends along almost the entire lower part of the endocranium and in its poste-

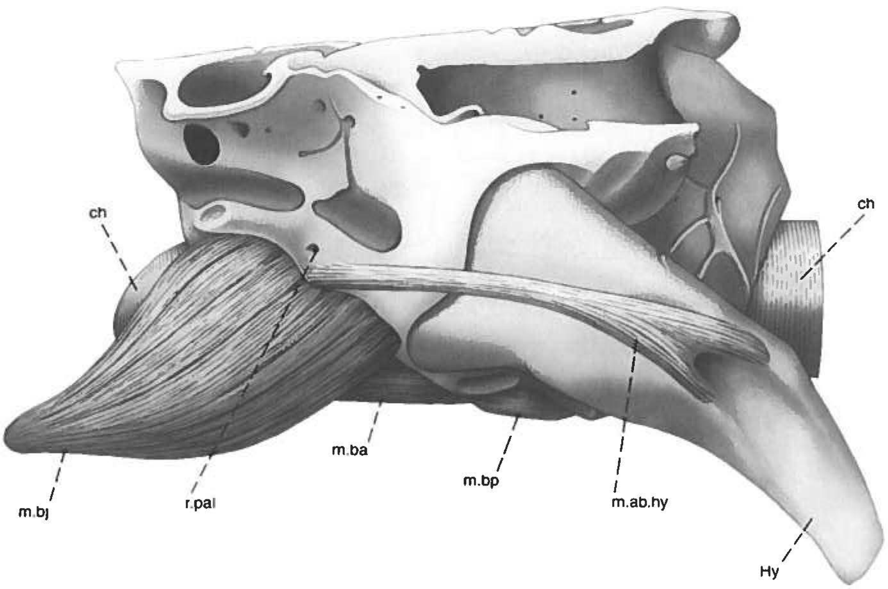


Fig. 12. *Eusthenopteron foordi*. Left lateral view of posterior endocranial moiety, hyomandibula, and some muscles. ch: notochord; Hy: hyomandibula; m.ab.hy: abductor hyomandibular muscle; m.ba: anterior basiotic muscle; m.bj: basijunctorial muscle; m.bp: posterior basiotic muscle; r.pal: canal for palatine branch of facial nerve.

rior half exhibits two ascending processes on either side. The anterior process, which lies parhypophysially, sutures with and slightly overlaps the ipsilateral posterior process, dorsal to the internal carotid foramen. This parasphenoid has been illustrated by Holmgren & Stensiö (1936: fig. 370) and by Starck (1979: fig. 145). However, it is not shown in the pioneer work on the cranial anatomy of *Esox lucius* by Arendt (1822).

Gaupp (1905; see also 1896) suggested that the term os parabasale should be used in place of Huxley's term os parasphenoides, chiefly because of the extensive anteroposterior development in *Esox lucius*. This proposal has never been popular among zoologists. Jarvik (1944), however, argued that Gaupp's term may be used for the so-called parasphenoid which in certain fishes and amphibians extends backwards to the otic region of the endocranium. It should also be mentioned that Gaupp did not abandon the word parasphenoid but, in 1908, employed it to denote a palatal bone in *Tachyglossus aculeatus* which nowadays, probably wrongly, is identified as the pterygoid bone (cf. Kuhn 1971).

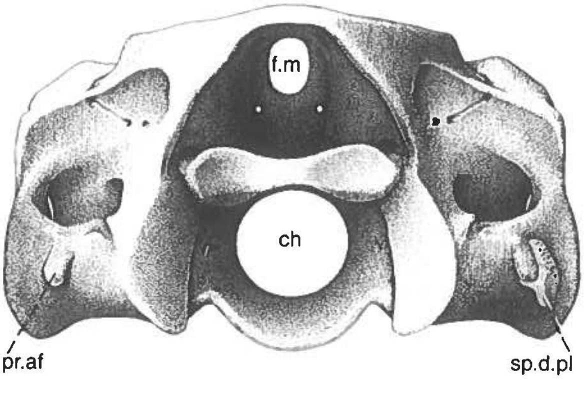
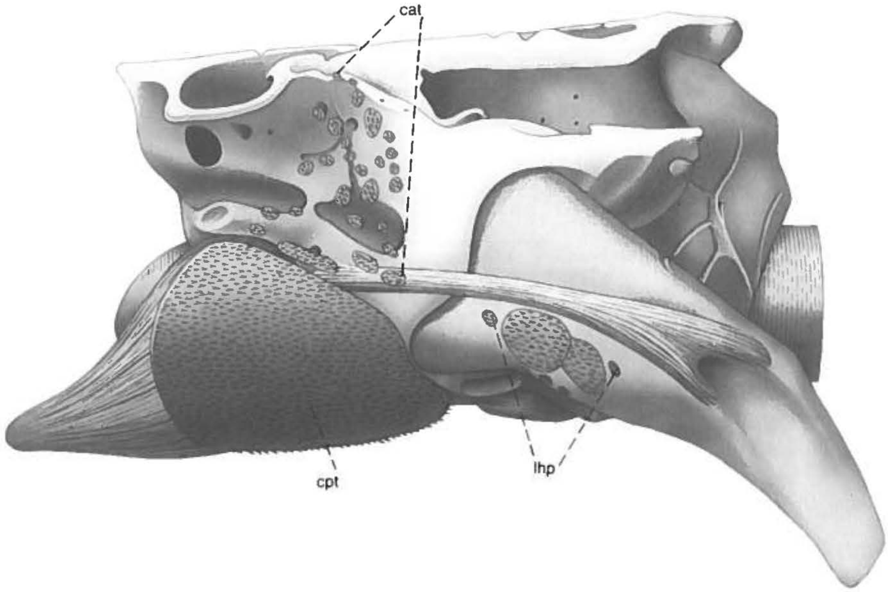


Fig. 13. *Nesides schmidti*. Posterior moiety of endocranium and right spiracular dental plate in anterior view. Cf. Bjerring 1972. ch: canal for notochord; f.m: foramen magnum; pr.af: affacial process; sp.d.pl: spiracular dental plate.

One way of remedying this muddle is to discard the term os parasphenoides as well as the term os parabasale, and to introduce a new term: os crepidinum (Latin *crepidinus*, from *crepida*, sandal). A crepidine bone is an unpaired, dentate or edentate, alate or nonalate, palatal allostosis which extends beneath one (temporal or auditory), some, or all the regions of the endocranium, and occasionally beneath the most anterior part of the vertebral column. According to this definition crepidine bones exhibit a great variety of anteroposterior development. Moreover, as evidenced by embryological and paleontological data, the variations in crepidine composition are so many that there really is no such entity as a "typical" os crepidinum. Types of crepidine bones may therefore be classified from their relation to overlying endocranial regions. This can be accomplished by abbreviations as follows: (N) regio nasalis, (E) regio orbitalis, (H) regio hypophysialis, (T) regio temporalis, (A) regio auditivus, (O) regio occipitalis, and (S) regio spinalis. Thus, among mammals, man (*Cr*, Fig. 16) has an A-crepidine bone (cf. Reinbach 1967, Grube & Reinbach 1976), whereas the camel has a T-crepidine bone (cf. Starck 1956); the Devonian tetrapod *Acanthostega gunnari* has an EH-crepidine bone (cf. Clack & Coates 1993) and the Devonian fish *Eusthenopteron foordi* has an NEH-crepidine bone (cf. Jarvik 1954); the Triassic palaeoniscid *Pteronisculus magna* has an NEHT-crepidine bone (cf. Nielsen 1942); the lepto-

Fig. 14. *Eusthenopteron foordi*. The structures seen in figure 12 plus various tooth plates. cat: crepidinula alaria temporalia or spiracular dental plates; cpt: crepidinulum parabasale temporale ("paraotic dental plate"); lhp: lateral hyomandibular tooth plates.



dactylid Chilean frog *Caudiverbera caudiverbera* has an NEHTA-crepidine bone (cf. Reinbach 1939, Lynch 1971); the northern pike, *Esox lucius*, has an NEHTAO-crepidine bone and the African brachiopterygian fish *Polypterus senegalus* has an NEHTAOS-crepidine bone (cf. Bjerring 1991).

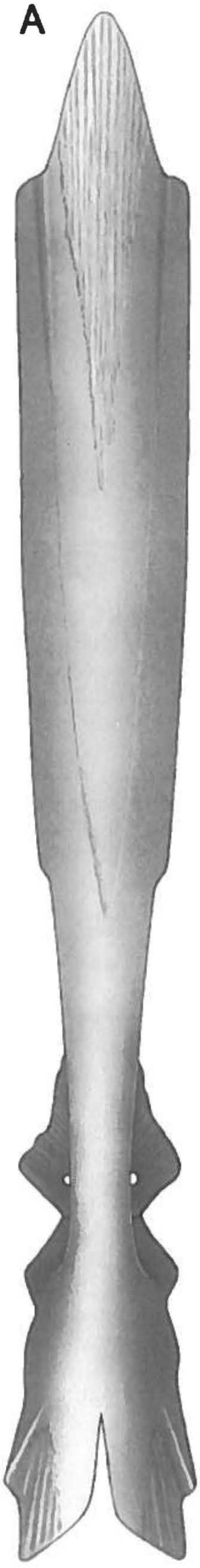
Crepidine bones may be grouped further in subtypes according to their composition. Often a crepidine bone is initiated by two or more components which unite during ontogeny (cf. de Beer 1937, Pehrson 1940, 1945, Holmgren 1943, Jollie 1957, Lebedkina 1964, 1979, Müller 1963). These embryonic components, several of which occur as separate bones in fossils (cf. Nielsen 1949, Jarvik 1972, 1980, Jessen 1980, Chang 1982, Gardiner 1984), are referred to collectively as crepidinules. They are arranged in longitudinal series which, from the mediosagittal plane outward, are called: the basal series (designated *b*), the parabasal series (designated *p*), and the alary series (designated *a*). The crepidinules of the two last-named series may well be derived from the exoskeleton of three branchial arches (cf. Jarvik 1954).

Within each of these series, a crepidinule is distinguished from other crepidinules on the basis of its relation to the neighboring region of the axial endoskeleton. This may be expressed by lower-casing the abbreviations employed above for crepidine classification. Thus, a crepidinule situated basal to the temporal region of the endocranium is a crepidinulum basitemporale and will be designated *bt*; a crepidinule situated parabasal to the hypophysial region of the endocranium is a crepidinulum parabasale hypophysiale and will be designated *ph* (see Fig. 17).

Two further abbreviations needed for crepidine characterization are D and ED. The former designates a toothed and the latter a toothless condition.

The os crepidinum of the domestic fowl may be used to illustrate this new descriptive terminology. In this bird (cf. Erdmann 1940, Jollie 1957), the edentate (ED) crepidine bone extends beneath the orbital (E), hypophysial (H), and temporal (T) regions of the endocranium and arises from seven separate bonelets. Of these bonelets, one (rostroparasphenoid of Jollie) is a crepidinulum basiorbitale (*be*), two (sellaparasphenoids of Jollie) are crepidinula basihypophysialia (*bh*), another two (basiparasphenoids of Jollie) are crepidinula basitemporalia (*bt*), and still another two (alaparasphenoids of Jollie) are crepidinula parabasalia temporalia (*pt*). Thus, the subtype of the os crepidinum of *Gallus domensticus* is EHT-crepidine-(ED:*be*, *bh*, *bt*, *pt*).

A second example is the os crepidinum of the Lower Devonian osteolepiform *Youngolepis praecursor* (Fig. 18). In this fossil fish (see Chang 1982), the dentate (D) crepidine bone extends beneath the orbital (E) and hypophysial (H) regions of the endocranium. Usually it also extends beneath the nasal (N) region and occasionally even beneath the anterior part of the temporal (T) region of the endocranium. In some specimens, the posterolateral parts of the bone are separate elements (the prespiracular dental plates: Chang 1982); moreover, in other specimens, the bone exhibits a bilateral projection which contributes to the orbital floor on the same side. Thus, the known subtypes of the os crepidinum of *Youngolepis praecursor* are four: Most specimens have an NEH-crepidine-(D: *bn*, *be*, *bh*, *pe*, *ph*); specimens with an independent crepidinulum parabasale hypophysiale have an EH-crepidine-(D: *be*, *bh*); specimens in which the bone assists in flooring the orbits have an NEH-crepidine-(D: *bn*, *be*, *bh*, *pe*, *ph*, *ae*); and specimens in which the bone extends backwards beyond the basicranial fis-



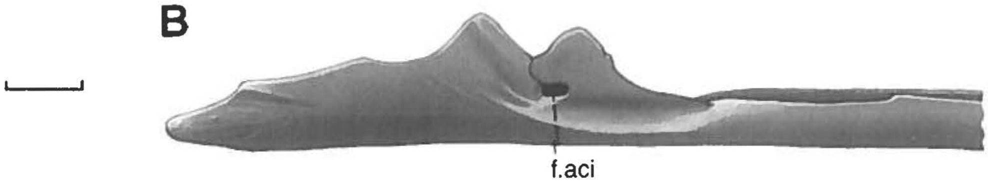


Fig. 15. *Esox lucius*. The median palatal allostosis for which Huxley (1864) coined the term os parasphenoides. According to the terminology used herein it is an NEHTAO-crepidine bone. A, ventral view of the entire bone; B, right-side view of the posterior part of the bone. Scale bar: 10 mm. f.aci: foramen for internal carotid artery.

sure have an NEHT-crepidine-(D: *bn*, *be*, *bh*, *bt*, *pe*, *ph*). Whether other crepidine subtypes such as EH-crepidine-(D: *be*, *bh*, *ph*), NEHT-crepidine-(D: *bn*, *be*, *bh*, *bt*, *pe*, *ph*, *ae*) and NEHT-crepidine-(D: *bn*, *be*, *bh*, *bt*, *pe*, *ae*) also exist in *Youngolepis praecursor* remains to be seen.

Returning to temnospondyls with a fossa coniformis entopterygoidea, their crepidine bone is, as noted already, sutured to the entopterygoid bones. Each of these connections is relatively long in *Lyrocephaliscus euri* and *Benthosuchus sushkini* and lies below the hypophysial, temporal and otic regions of the endocranium. Thus, in both these tetrapods the dentate corpus ossis crepidini very probably includes basihypophysial, basitemporal and basiotical crepidinules as well as hypophysial, temporal and otical parabasal crepidinules. Moreover, the crepidine bone of *Lyrocephaliscus euri* extends beneath the occipital region of the endocranium and that of *Benthosuchus sushkini* beneath the ethmoid region. Consequently, it would appear that the former tetrapod (Fig. 19) has an EHTAO-crepidine-(D: *be*, *bh*, *bt*, *ba*, *bo*, *ph*, *pt*, *pa*) and the latter (Fig. 20) an NEHTA-crepidine-(D: *bn*, *be*, *bh*, *bt*, *ba*, *ph*, *pt*, *pa*).

In both these tetrapods, each of the sutural connections between the crepidine bone and the entoptery-

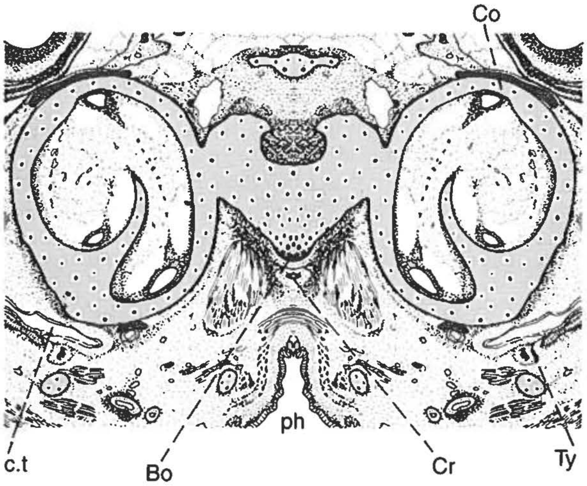


Fig. 16. *Homo sapiens*. Transverse section through the head of an 80-mm embryo to show a transient crepidine bone underneath the basioccipital autostosis. After Reinbach 1967. Bo: basioccipital autostosis; Co: cochlear part of otic capsule; Cr: A-crepidine bone; c.t: tympanic cavity; ph: pharynx; Ty: tympanic bone.

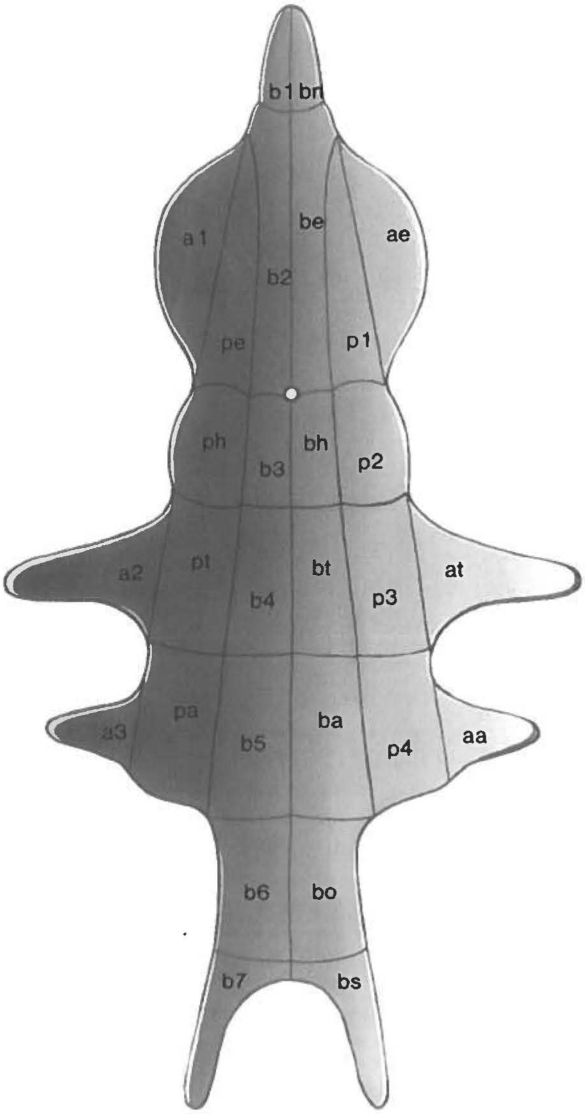


Fig. 17. Dorsal view diagram of crepidinules. b1-b7: series of seven basal crepidinules; p1-p4: series of four parabasal crepidinules; a1-a3: series of three alary crepidinules. From before backwards the crepidinules of each of these series are: bn, crepidinulum basinasale; be, crepidinulum basiorbitale; bh, crepidinulum basihypophysiale; bt, crepidinulum basitemporale; ba, crepidinulum basiauditivum; bo, crepidinulum basioccipitale; bs, crepidinulum basispinale; pe, crepidinulum parabasale orbitale; ph, crepidinulum parabasale hypophysiale; pt, crepidinulum parabasale temporale; pa, crepidinulum parabasale auditivum; ae, crepidinulum alare orbitale; at, crepidinulum alare temporale; aa, crepidinulum alare auditivum.

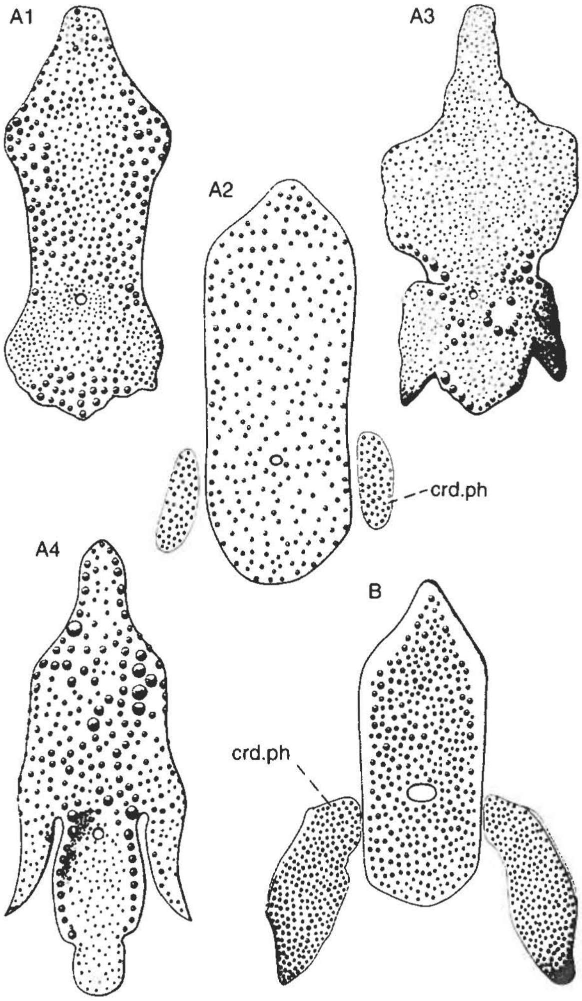


Fig. 18. *Youngolepis praecursor* (A1-A4) and *Powichthys thorsteinssoni* (B). Crepidines and crepidinules seen in ventral view. From Chang (1982) and Jessen (1980). A1 (specimen V6180 in Chang): NEH-crepidine-(D: *bn*, *be*, *bh*, *pe*, *ph*): A2 (specimen V6553 in Chang): EH-crepidine-(D: *be*, *bh*) and crepidinula parabasalia hypophysialia (prespiracular dental plates of Chang); A3 (specimen V6221 in Chang): NEH-crepidine-(D: *bn*, *be*, *bh*, *pe*, *ph*, *ae*); A4 (specimen V6234 in Chang): NEHT-crepidine-(D: *bn*, *be*, *bh*, *bt*, *pe*, *ph*); B (mainly specimen CGS33364 in Jessen): EH-crepidine-(D: *be*, *bh*) and crepidinula parabasalia hypohpysialia (parasphenotic dental plates of Jessen). crd.ph: crepidinulum parabasale hypophysiale.

giod bones to all appearances involves the hypophysial, temporal and otical parabasal crepidinule components of the corpus ossis crepidini. Lateral to either of these sutures, the entopterygoid bone has an ascending lamina which almost reaches the dermal skull roof. The mesial surface of this lamina is crossed by an oblique ridge called torus obliquus or crista obliqua (Nilsson 1946) which provided attachment for the mandibular depressor musculature (Bystrov & Yefremov 1940) or protected the stapes form pressure by this musculature (Welles & Cosgriff 1965; cf. Waren & Schroeder 1995).

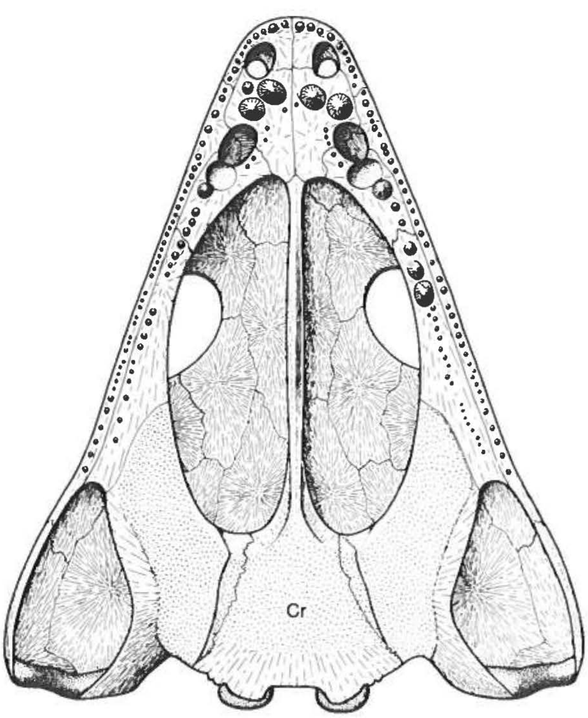


Fig. 19. *Lyrocephaliscus euri*. Cranium in palatal aspect. From Säve-Söderbergh 1936. Cr: EHTAO-crepidine- (D: *be*, *bh*, *bt*, *ba*, *bo*, *ph*, *pt*, *pa*).

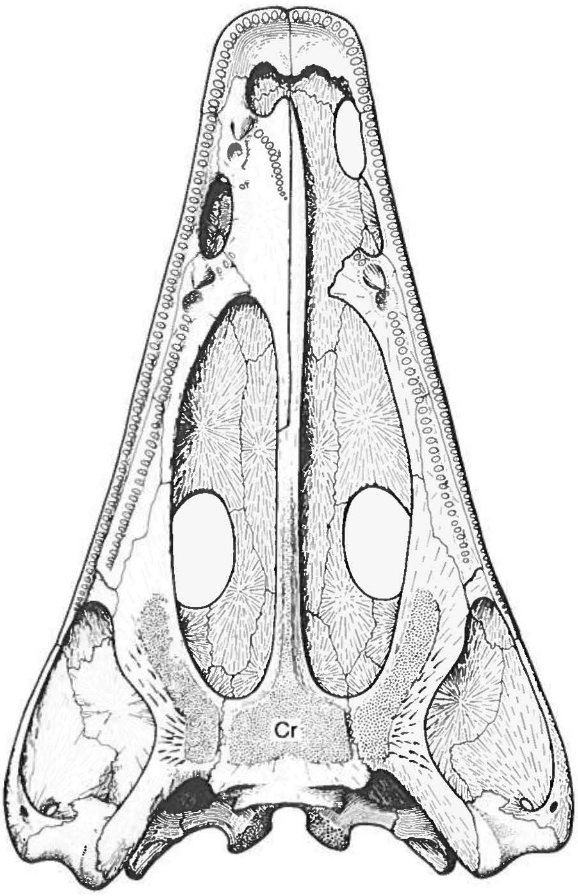


Fig. 20. *Benthosuchus sushkini*. Cranium in palatal aspect. From Bystrov & Yefremov 1940. Cr: NEHTA-crepidine- (D: *bn*, *be*, *bh*, *bt*, *ba*, *ph*, *pt*, *pa*).

Precristally, the lamina ascendens entopterygoidis is conspicuously high and, at least in *Lyrocephaliscus euri*, abuts with the ipsilateral prootic autostosis of the endocranium. This laminal part of the entopterygoid bone lies mesial to the process of the mesopalatoquadrate bone contacting the otic capsule. The same palatoquadrate process in osteolepiforms is represented by the juxtaspiracular process (*p.js*, Fig. 11, paratemporal process of Jarvik 1954; cf. Bjerring 1995a) which, in *Eusthenopteron foordi* (Jarvik 1980), extends upwards and laterally to a deltoid field of exoskeletal spiracular plates (cf. Fig. 14). The primordium of the so-called processus ascendens posterior (crepidinulum alitemporale) of the crepidine bone in *Amia calva* (Pehrson 1940) and the os obturans in *Tachyglossus aculeatus* (Kuhn 1971, Kuhn & Zeller 1987) share a relationship with adjacent nervous and vascular structures which is consistent with the hypothesis that they evolved from coalesced exoskeletal spiracular plates. It is therefore interesting to note that the os obturans arises ontogenetically through the fusion of several exoskeletal primordia (Griffiths 1978). Thus, it appears that spiracular allostoses which have united and entered into the formation of the crepidine bone (*Amia calva* and other actinopterygians), or the sidewall of the braincase (*Tachyglossus aculeatus* and *Ornithorhynchus anatinus*), or the lamina ascendens entopterygoidis (*Lyrocephaliscus euri* and other so-called temnospondyls) represent phylogenetically separate events. An indication of a separate origin of the precristal portion of the ascending entopterygoid lamina is seen in *Peltostega erici* (Nilsson 1946: fig. 10C).

If this suggestion is correct, it follows that the cone-shaped fossa in the entopterygoid bone cannot have acted as the receptacle for the basipterygoid process. Instead, when the exoskeletal spiracular plates fused with each other and with the adjacent entopterygoid bone, the endocranial affacial process became enclosed in a hollow. This exoskeletal socket is the fossa coniformis entopterygoidea.

This view is corroborated by the situation of the cone-shaped entopterygoid fossa behind the hypophysial region of the endocranium and directly in front of the fenestra ovalis. Moreover, this fossa lies posteroventrally relative to the palatine ramus of the facial nerve. And in *Benthosuchus sushkini*, a distinct small pit (fovea ovalis, Bystrov & Yefremov 1940) lies just behind the fossa coniformis entopterygoidea.

This depression (*fv.m*, Fig. 7) might have served for attachment of a muscle homologous to the musculus abductor hyomandibularis (*m.ab.hy*, Fig. 12) which in osteolepiforms, as noted earlier, probably arose from the affacial process.

The most important argument to be stated here derives from the fact that the mesopalatoquadrate bone of *Lyrocephaliscus euri* (cf. Säve-Söderbergh 1936) exhibits a processus basalis (*pr.b*, Fig. 9) which probably formed a parhypophysial connection between the palatoquadrate and the endocranium. Apparently, therefore, besides a peg-and-socket articulation between the affacial process and the fossa coniformis entopterygoidea – fittingly called the sanidio-entopterygoid articulation – this tetrapod even had a basitrabecular articulation.

To all appearances, the sanidio-entopterygoid articulation was immobile and helped to prevent endocranial dislocation during muscular contractions that lowered the head. Moreover, together with sutural connections between the entopterygoid bones and the crepidine bone as well as synchondroses between the mesopalatoquadrate elements and the endocranium, the sanidio-entopterygoid articulations participated in affixing the upper jaw complexes to the rest of the skull. Since, as suggested above, the evolution of the sanidio-entopterygoid articulation was accompanied with the incorporation of fused exoskeletal spiracular plates in the entopterygoid bone, tetrapods possessing this articulation conceivably lacked an air-filled middle ear cavity. Their stapes was rod-like and with an expanded footplate. The latter had a short sutural connection with the underlying crepidine bone (cf. Säve-Söderbergh 1936, Bystrov & Yefremov 1940) which, one can assume, restricted stapedial mobility. The distal end of the stapes lay below the incisure auditiva and was probably cartilaginous because it is devoid of periosteal lining. Presumably, as in several frogs (cf. Jaslow *et al.* 1988), this cartilaginous structure was partly embedded in unspecialized epidermis and dermis covering the exoskeletal incisure just mentioned. If so, external sound absorbed by this skin area could thence have been transmitted to the inner ear via the extrastapes and stapes.

Tetrapods with sanidio-entopterygoid articulations might have utilized one more nontympanic pathway of acoustic reception. As noted earlier, the lamina ascendens entopterygoidis of *Benthosuchus sushkini* exhibits a small depression (*fv.m*, Fig. 7) which is situated immediately behind the fossa coniformis entopterygoidea. Probably a largely tonic muscle originated from this depression and inserted into a stapedial crest. Such a tensed muscle, derived presumably from the musculus abductor hyomandibularis in osteolepiforms (cf. Fig. 14), would have acted as a taut structural connection between the strongly fenestrate palate and the near-immobile stapes. It appears that external sound can penetrate into the mouth cavity of frogs to produce motion of palatal tissues that might be relayed to the inner ear (cf. Vlaming *et al.* 1984). Thus, it can be hypothesized that the buccal cavity of *Benthsuchus sushkini* and other tetrapods possessing sanidio-entopterygoid articulations had an audio-receptive function. Sound energy absorbed by the palate could have reached the inner ear via the entopterygoid bone, the tensed muscle that connected the lamina ascendens entopterygoidis with the stapedial shaft, and the stapedial footplate as well as via the entopterygoid bone and the affacial process.

All known tetrapods with sanidio-entopterygoid articulations presumably spent a considerable amount of time in water. It is unsurprising, therefore, to find that these animals probably employed nontympanic mechanisms for reception of waterborne sound. Unrelated to a tympanic ear, these mechanisms for aquatic hearing appear to be a consequence of the evolution of the fossae coniformes entopterygoidea.

The Carboniferous tetrapod *Greererpeton burkemorani*, as it appears from the description of Smithson (1982), has an EHTAO-crepidine bone the corpus of which lacks sutural contacts with the entopterygoid bones. Dorsal to the crepidine corpus, on either side, lies a well-developed basicranial process projecting into a deep socket in the adjacent mesial surface of the fused entopterygoid and mesopalatoquadrate

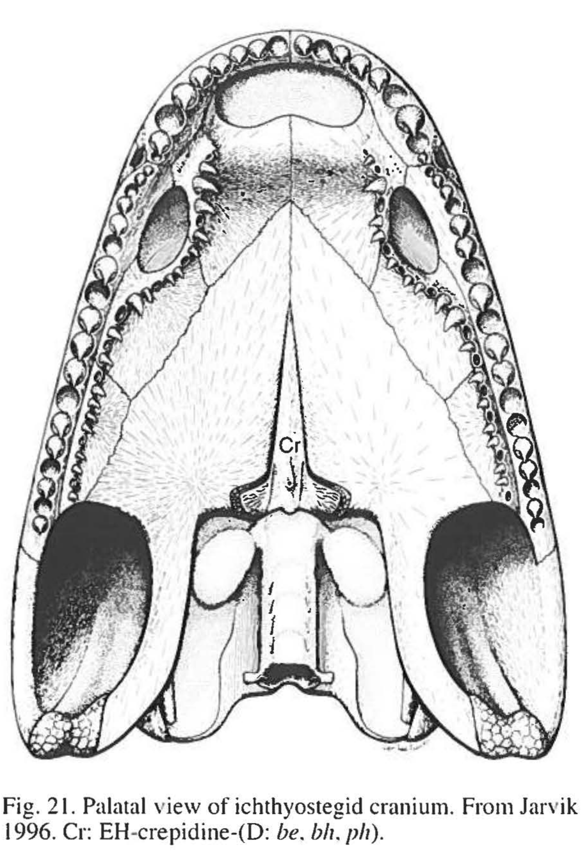


Fig. 21. Palatal view of ichthyostegid cranium. From Jarvik 1996. Cr: EH-crepidine-(D: *be*, *bh*, *ph*).

bones. This basicranial process occupies a methypophysial position, but it is farther from the fenestra ovalis than the affacial process. Its dorsal surface exhibits a shallow groove which appears to correspond with a low ridge that partially subdivides the palatal socket mentioned previously into anterior and posterior parts. Thus, the basicranial process and its palatal socket may be dual structures. Positionally, they match the parts that contribute to the formation of the contiguously-placed anterior and posterior sanidiopalatoquadrate articulations in osteolepiforms (cf. Figs 10, 11). Therefore, it is possible that the peg-and-socket articulation in the temporal region of the skull of *Greererpeton burkemorani* represents a fusion of the adjoining sanidiopalatoquadrate articulations in osteolepiforms. This interpretation differs strongly from that of Smithson (1982), which, as already emphasized, identifies the aforesaid peg-and-socket articulation as a derivative of the osteolepiform basitrabecular articulation.

There remains to be added only a brief word pertaining to the connection between the palatoquadrate and the endocranial base in ichthyostegids. These Devonian tetrapods, the anatomy of which is chiefly known from Jarvik's descriptions (1952, 1955, 1964, 1980, 1996), have a relatively small EH-crepidine bone (*Cr*, Fig. 21). Posteriorly, this palatal allostosis extends outward on either side beneath a parhypophysial basicranial process articulating synchondrotically with the ipsilateral palatoquadrate. Topographically, these lateral projections of the ichthyostegid crepidine bone correspond to the independent crepidinules (*crd.ph*, Fig. 18) that in *Powichthys thorsteinssoni* and *Youngolepis praecursor* (cf. Jessen 1980, Chang 1982) lie next to the hypophysial region of the endocranium and cover most of the ventral surface of a pair of basicranial processes. Each of these endocranial projections is reasonably identified as a basipterygoid process because, topographically, it resembles closely the lizard basicranial process for which Parker (1880) coined the term processus basipterygoideus. Clearly, then, the aforementioned ichthyostegid basicranial process, which lies above the part of the crepidine bone interpreted as the homologue of a crepidinulum parabasale hypophysiale, must be considered similarly a basipterygoid process. This implies that the ichthyostegid cranium includes a pair of basitrabecular articulations involved in the support of the upper jaws. Ichthyostegids, however, lack sanidiopalatoquadrate and sanidio-entopterygoid articulations.

In sum, the widely held belief that the upper jaw suspension on the midbasilar part of the endocranium in so-called temnospondyl tetrapods is effected entirely by the basipterygoid process, fails to account for all available data. However, it is sufficient for the Devonian ichthyostegids, which utilize one of the original articulations within the mandibular arch as a jaw support. In *Greererpeton burkemorani*, classified by Carroll (1988) as a colosteid temnospondyl, the upper jaw is not suspended by an intramandibular articulation but by an interarcual articulation corresponding to adjoining sanidiopalatoquadrate articulations in osteolepiforms. In *Benthosuchus sushkini*, which Carroll (1988) refers to as a capitosauroid temnospondyl, it is neither an intramandibular nor an interarcual articulation that functions as a jaw support, but a sanidial process that is received into a cone-shaped fossa in the entopterygoid bone. This projecting process of the sanidium is present in osteolepiforms whereas the fossa coniformis entopterygoidea is absent in these fish. In *Lyrocephaliscus euri*, identified by Carroll (1988) as a trematosauroid temnospondyl, there is support for the upper jaw both from the basitrabecular articulation and from the sanidio-entopterygoid articulation. Both these articulations were static because the underlying sutural union of the crepidine and entopterygoid bones precluded palatal kinesis.

In the light of these arguments, the monophyly of the Temnospondyli may be challenged.

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