MEDDELELSER OM GRØNLAND

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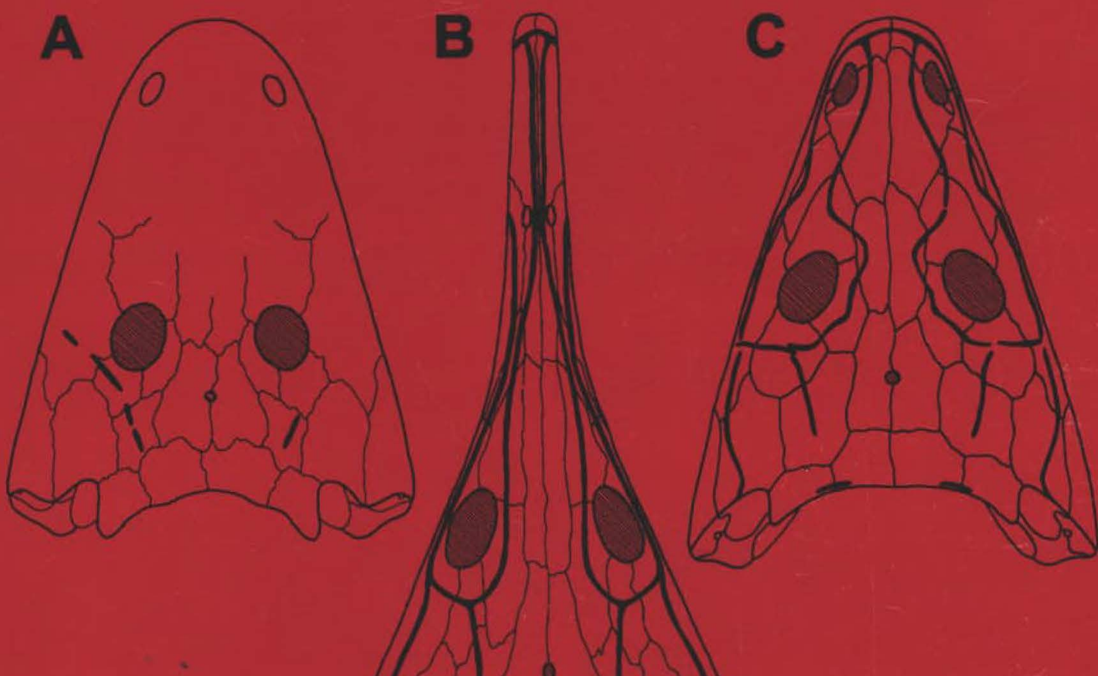

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Abstract

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The cranial anatomy, especially the allostotic parts, of a new tetrapod genus, *Aquiloniferus*, is described on the basis of four specimens from the Lower Triassic of central East Greenland at Kap Stosch. These specimens were studied briefly in the mid-1930s and assigned to four species of the trematosaur genus *Lyrocephalus* WIMAN. Herein it is suggested that only a single species, *A. kochi*, existed in this region, belonging to the Capitosauroidea.

Keywords: Aquiloniferus n.g., cranium, capitosaur, Lower Triassic, East Greenland

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Introduction

In central East Greenland, marine deposits of early Triassic age – the Wordie Creek Formation (cf. Birkelund & Perch-Nielsen 1976) – have produced comparatively large amounts of skull material of amphibious tetrapods said to belong to the complex and presumedly artificial group of craniates known variously as stegocephalians, labyrinthodonts or temnospondyls. In 1935, Säve-Söderbergh reported on 40 of these skulls, and, to an extent, described 13 of them. Of the described specimens, four, which are long-snouted, were placed in a genus of their own, *Stoschiosaurus* SÄVE-SÖDERBERGH, 1935; another four were identified with the genus *Lyrocephalus* WIMAN, 1914, from the marine Lower Triassic of Spitzbergen; and two were assigned to the genus *Wetlugasaurus* RYABININ, 1930, from the Eotriassic of eastern European Russia. The generic name *Lyrocephaliscus* was proposed by Kuhn (1961) as a replacement for *Lyrocephalus* WIMAN, 1914 (see also 1913), because the latter name has been used for an Asian agamid (cf. Merrem 1820 and Wagler 1830). This nomenclatural change is generally accepted (cf. Schultze 1969, Mazin & Janvier 1983, Carroll 1988), though it is not justifiable (cf. p. 37). Moreover, the genus *Wetlugasaurus* RYABININ, 1930, was transferred by Welles & Cosgriff (1965) to the genus *Parotosaurus* JAEKEL, 1922 (cf. Warren 1980). This reassignment, however, is not generally accepted.

Of the three assignments referred to above, the last has recently been shown to be incorrect and the two skulls (MGUH VP 3339 and MGUH VP 3340 in the Geological Museum of Copenhagen University) are now placed in the genus *Selenocara* BJERRING, 1997. The second, as will be demonstrated below, is incorrect too. Moreover, some writers (Yefremov 1940, Romer 1947) have even doubted that the genus *Lyrocephalus* (*Lyrocephaliscus*) occurred in Greenland. As time went on, also Säve-Söderbergh seems to have been doubtful of this occurrence (cf. the lists of references in his papers of 1946 and 1947 where he cited a manuscript in progress planned for publication in Palaeozoologica Groenlandica). However, Säve-Söderbergh died in 1948 at the age of 38 and did not finish this manuscript on Triassic amphibious tetrapods.

In 1980, Shishkin erected the genus *Luzocephalus* for a tetrapod skull from the Lower Triassic of eastern European Russia, and as recently as 1996 (Shishkin *et al.*) he assigned this genus to the lydekkerinids. Shishkin compared this skull with those from East Greenland that Säve-Söderbergh in the mid-1930s partially described and assigned to the genus *Lyrocephalus* (*Lyrocephaliscus*). From these comparisons it was concluded that the skulls from Greenland are generically identical with *Luzocephalus* SHISHKIN, 1980. However, as will be shown below, more detailed knowledge of the cranial morphology of these Greenlandic specimens leads to a different conclusion.

Materials and methods

All the material examined belongs to the Geological Museum of the University of Copenhagen, Denmark, and will ultimately be housed there (MGUH VP collection). It comprises four tetrapod skulls which bear the labels At. 1, At. 3. At. 28, and At. 29 in Säve-Söderbergh's paper of 1935. Of these skulls, At. 1 is nearly complete; At. 28 consists of a little more that the anterior half; At. 29 lacks the right posterolateral part; and At. 3 is a natural mold of middle and posterior parts of the external surface of the skull roof. The specimens mentioned have been partly prepared mechanically and partly cast in latex.

Systematic section

Superfamilia: Capitosauroidea WATSON, 1919.
Familia: undetermined
Genus: *Aquiloniferus* gen. nov.
Holotypus: Specimen At. 1 in Säve-Söderbergh 1935 (p. 150).
Hypodigma: Holotype plus specimens At. 28, At. 29, At. 3 in Säve-Söderbergh 1935 (pp. 164, 170, 177). and probably At. 39, in Säve-Söderbergh 1944.
Species typica: *Lyrocephalus kochi* SÄVE-SÖDERBERGH, 1935.
Contentum: *Aquiloniferus kochi* (SÄVE-SÖDERBERGH) BJERRING.
Synonyma: *Lyrocephalus kochi*, in Säve-Söderbergh 1935: 150. *Lyrocephalus johanssoni*, in Säve-Söderbergh 1935: 164. *Lyrocephalus rapax*, in Säve-Söderbergh 1935: 170. *Lyrocephalus* sp., in Säve-Söderbergh 1935: 177. *Lyrocephaliscus* cf. *johanssoni*, in Schultze 1969: pl. 14, figs 3, 4. *Lyrocephaliscus johanssoni*, Schultze 1969: pl. 15, fig. 2. *Luzocephalus kochi*, in Shishkin 1980: 91. *Luzocephalus johanssoni*, in Shishkin 1980: 91. *Luzocephalus rapax*, in Shishkin 1980: 91.

Diagnosis (for genus and species): Extinct amphibious anamniote tetrapod with shallow, triangular skull. Paired occipital condyles, widely separated, far behind the posterior edges of the iniacopluteal bones, and on level with the distal ends of the trachelic bones. Sutural contacts between the autostotic rear of the endocranium and the allostotic skull roof. Auditive incisures widely open, their deepest parts on the level of the posterior midpoint of the skull roof; the distance between these incisures is more than 50 percent of the skull roof midline length. The orbitofacial openings lie immediately behind the sagittal midpoint of the skull roof; each is oval and its long axis points outside the ipsilateral rear corner of the skull, as does the long exis of each of the exonarial fenestrae. The frontomelonic bone forms about the same proportion of the border of the orbitofacial opening as the ipsilateral melonicozygamatic bone; this also holds for the adjacent frontolacrimal and peripheral frontal bones. The groove for the supraorbital neuromast canal passes over the maxillulary bone of the same side. The fossa apicalis is ovoid, with cordiform rostropalatine vacuity. Each exoforial fenestra is oval; its long axis, if continued backwards, will pass laterally to the ipsilateral posterior corner of the skull. Large orbitopalatine openings having their greatest width posteriorly and an anteroposterior extent that is less than 50 percent of the median length of the skull roof. The cultriform process of the crepidine bone is flat and comparatively broad. The corpus ossis crepidini is much broader than long and lacks muscle crests; it extends farther backwards than the iniacopluteal bones but does not underplate the occipital condyles. The length of the body of each entopterygoid bone is less than one-third of the breadth across the entopterygoid bones. The entopterygoid bones reach forward to the dermopalatine bones. The ascending lamina of the entopterygoid bone

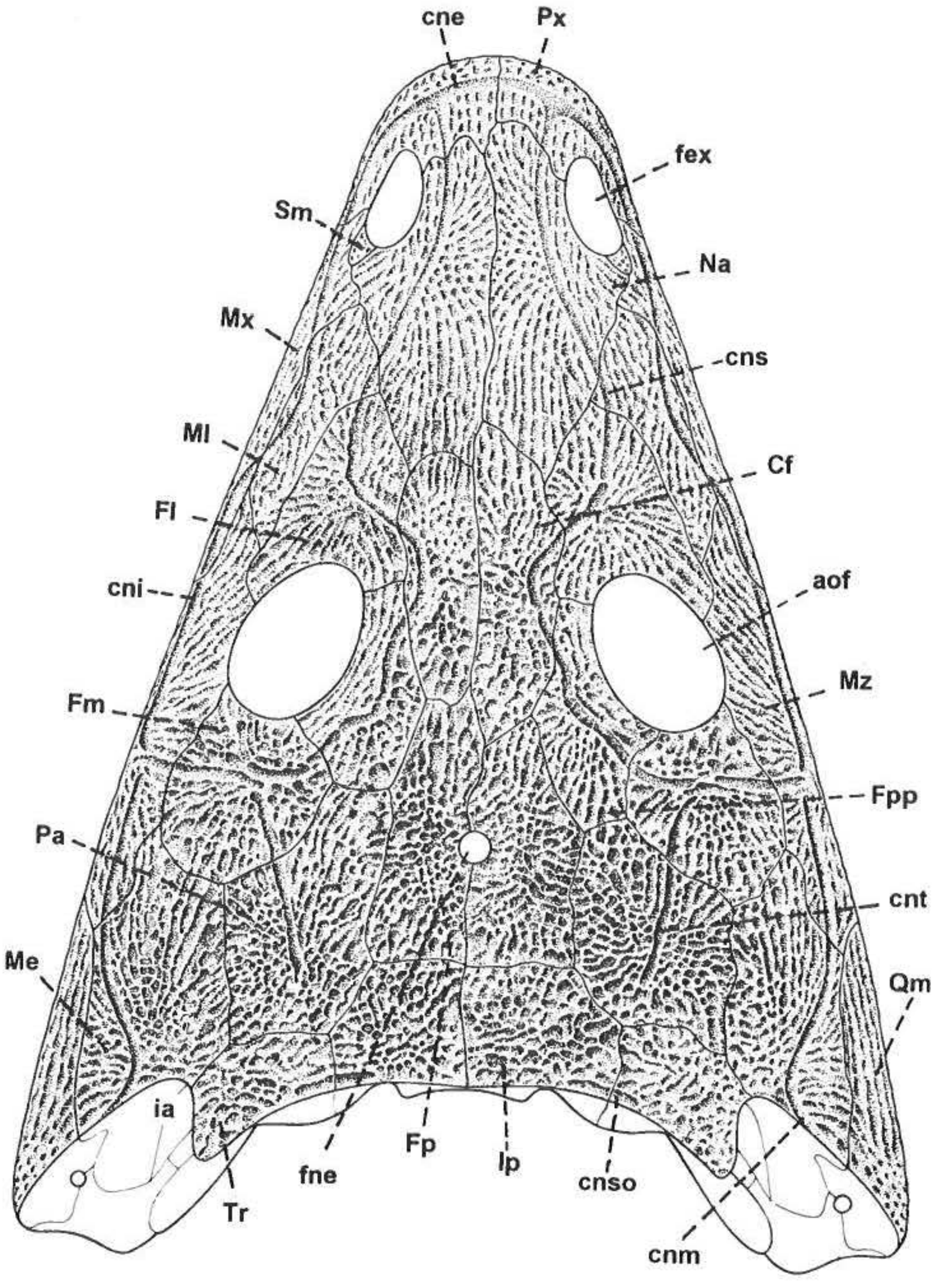


Fig. 1. Aquiloniferus kochi. Reconstruction of skull roof in dorsal view. Based on MGUH VP 3357 and MGUH VP 3358. Magnification ca. x1.2. aof: aditus orbitae facialis; Cf: os frontale centrale; cne: groove for ethmoidal neuromast commissural canal; cni: groove for infraorbital neuromast canal; cnm: groove for mandibular neuromast canal; cns: groove for supraorbital neuromast canal; cnso: groove for supraoccipital neuromast commissural canal; cnt: groove for temporotic neuromast canal; fex: fenestra exonarialis; Fl: os frontolacrimale; Fm: os frontomelonicum; fne: foramen neuro-epiphysiale; Fp: os frontopluteale; Fpp: os frontale peripherale; ia: incisura auditiva; Ip: os iniacopluteale; Me: os melonicum; Ml: os maxillulare; Mx: os maxillare; Mz: os melonicozygomaticum; Na: os nasale; Pa: os parietale; Px: os praemaxillare; Qm: os quadrato-maxillare; Sm: os septomaxillare; Tr: os trachelicum.

does not reach the descending lamina of the ipsilateral melonic bone. The jaw articulations are slightly behind the level of the occipital condyles.
Derivatio nominis: From Latin *aquilonius*, of the north + *ferus*, wild beast.
Stratum typicum: The *Ophiceras* and *Proptychites* zones of the Wordie Creek Formation; Lower Scythian (cf. Nielsen 1935, 1961, Spath 1935, Birkelund & Perch-Nielsen 1976).
Locus typicus: Stensiö Plateau and Spath Plateau on the coast southeast of Kap Stosch, Hold-with-Hope, central East Greenland.
Repositorium: Geological Museum of Copenhagen University, Denmark, where At. 1 is catalogued as MGUH VP 3357, At. 28 as MGUH VP 3359, At. 29 as MGUH VP 3360, At. 3. as MGUH VP 3358, and At. 39 as MGUH VP 3361.

Descriptive section

The skull roof

The skull is triangular in dorsal view with a rounded snout (fig. 1). Its lateral edges are slightly convex from about the level of the orbitofacial openings to the posterolateral corners, and the median roof part of its posterior border is moderately concave. Viewed in profile (fig. 3), the dorsal line of the skull roof is distinctly concave between the orbitofacial openings and the exonarial fenestrae. The skull is lowest at the snout tip and gradually increases in height back to the auditive incisures. Between and behind the orbitofacial openings the skull table is a little depressed as is the corresponding skull area in piscine osteolepipods (cf. Jarvik 1980).

The sculpture on the external surface of the skull roof (figs 1, 3) is of the type commonly encountered in Triassic amphibious tetrapods. Fine in texture and low in relief, it consists of shallow pits and short grooves separated by narrow anastomosing ridges with rounded crests. Because of this surface configuration the overlying skin was presumably not freely movable on the head.

The sculpture pattern radiates from the center of ossification of the individual bones. Some of the bones display a pattern in which the pits form the most prominent part of the sculpture and the general effect is that of a reticulate surface. Others have a pattern of ridges and grooves radiating from the pitted regions. Areas dominated by this pattern are found on the skull table in front of the orbitofacial openings and on the cheeks. These areas, as pointed out by Bystrov (1935) and Säve-Söderbergh (1937), quite likely represent the loci of most intensive skull growth.

The external surface of the skull roof also bears shorter and longer grooves that were occupied by the neuromast system, whose position is presented in fig. 1. Their presence and degree of development indicate aquatic habits.

The terminology of the bones of the skull roof used herein is in some respects unlike that currently employed by palaeohepetologists. It is a consequence of the writer's interpretation of the evolutionary origins of the human parietal and temporal bones (cf. Bjerring 1995, 1998).

Fenestra exonarialis (*fex*, fig. 1) - The paired exonarial fenestra faces upward, forward and outward. It lies a significant distance anterior to the ipsilateral exoforial fenestra (*fef*, fig. 2) and mainly behind the premaxillary-nasal suture. Moreover, it lies lateral to the fossa apicalis (see p. 24) and much closer to the margin of the skull than to the dorsal midline. It is slightly fabiform in outline and at least twice as long as broad. Its mesial border is convex and its lateral border is nearly straight. The major axis of the exonarial fenestra makes an angle of about 20 degrees with the mediosagittal plane, and the rearward extension of this axis runs laterally both to the orbitofacial opening and to the ipsilateral rear corner of the skull. The rim of the exonarial fenestra is formed

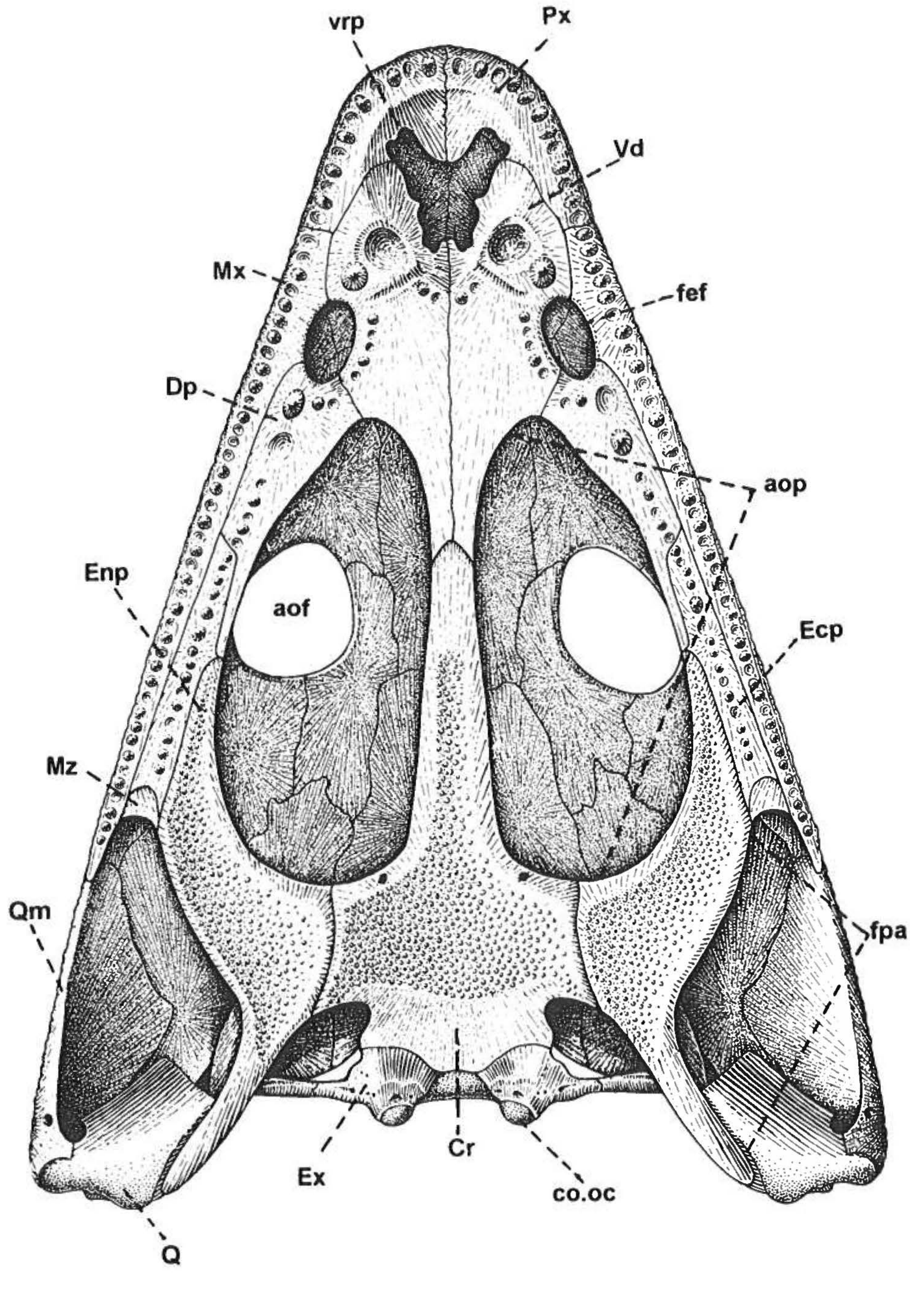


Fig. 2. Aquiloniferus kochi. Reconstruction of bony palate in ventral view. Based on MGUH VP 3357. Magnification ca. x1.2. aof: aditus orbitae facialis: aop: aditus orbitae palatinus; co.oc: occipital condyle; Cr: os crepidinum; Dp: os dermopalatinum; Ecp: os ectopterygoides; Enp: os entopterygoides; Ex: os exoccipitale; fef: fenestra exoforialis; fpa: fenestra palatina adductoria; Mx: os maxillare; Mz: os melonicozygomaticum; Px: os praemaxillare; Q: os quadratum; Qm: os quadratomaxillare; Vd: os vomerodacnile; vrp: vacuitas rostropalatina.

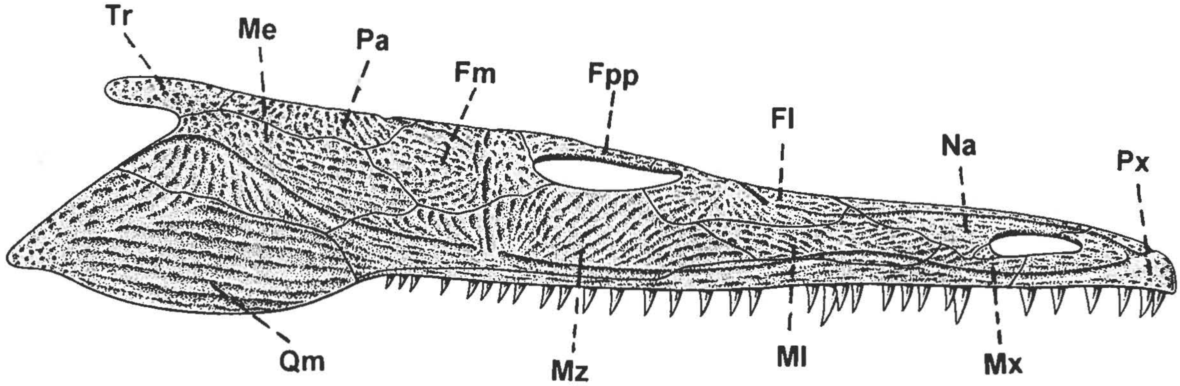


Fig. 3. Aquiloniferus kochi. Reconstruction of skull roof in dextral view. Based on MGUH VP 3357. Magnification ca. x1.2. Fl: os frontolacrimale; Fm: os frontomelonicum; Fpp: os frontale peripherale; Me: os melonicum; Ml: os maxillulare; Mx: os maxillare; Mz: os melonicozygomaticum; Na: os nasale, Pa: os parietale; Px: os praemaxillare; Qm: os quadratomaxillare; Tr: os trachelicum.

by the premaxillary, maxillary, septomaxillary and nasal bones of the same side, and it is not raised above the surrounding surfaces.

Aditus orbitae facialis (*aof*, fig. 1) - The orbitofacial opening is shaped like an ellipse, the major axis of which is about 50 percent longer than the minor one. Facing dorsally and slightly laterally, this paired opening is situated most anteriorly in the posterior half of the skull roof and directly above the midlateral part of the ipsilateral orbitopalatine opening (*aop*, fig. 2). The least distance between it and its antimere equals approximately twice the length of its minor axis, and its most lateral point lies less lateral than the auditive incisure (*ia*, fig.1) of the same side. Its major axis makes an angle of about 30 degrees with the mediosagittal plane and, if continued backwards, it will pass lateral to the ipsilateral hind corner of the skull. The rim of the orbitofacial opening is formed by the frontolacrimal, peripheral frontal, frontomelonic and melonicozygomatic bones of the same side and, like that of the exonarial fenestra, it is flush with the surrounding skull surface.

Foramen neuro-epiphysiale (*fne*, fig. 1) - The neuro-epiphysial foramen is small and circular. It lies intrasuturally in the dorsal midline of the skull, directly above the most proximal part of the cultriform process of the crepidine bone (*Cr*, fig. 2) and level with the center of ossification in the middle of each of the two bones that form its rim. Its position on the dorsal midline of the skull is just as far in front of the midpoint of the posterior margin of the skull roof as the least distance between the two orbitofacial openings, and just as far behind the transverse plane through the rearmost points of these openings as the length of each of their minor axes. Whether this median foramen served a parapineal or a pineal organ remains unresolved.

Incisura auditiva (*ia*, fig. 1) - The paired auditive incisure is situated posteriorly between the cheek and the skull table, each of which contributes a bone to its formation. It is moderately deep, has an evenly curved rim, and widens gradually backwards. Its deepest point lies level with the posterior midpoint of the skull roof, and the distance between the two auditive incisures equals approximately the breadth of the skull at the anterior termination of the orbitofacial openings. This notch probably contained an eardrum.

The skull roof is composed of 16 pairs of allostoses. Of these pairs, three contribute to the palatal makeup and two to the occiput; moreover, each bone of another two pairs has a part that is associated with the rear of the ipsilateral palatoquadrate. The 32 bones of the skull roof are joined to each other by immovable articulations.

Ossa praemaxillaria (*Px*, figs 1, 2, 3, 7) - The premaxillary bones form the anterior extremity of the skull. Each consists of two portions, a facial one (figs 1, 3) and a palatal one (figs 2, 7). Of these portions, the latter will be described below in conjunction with the ossa palati.

The facial portion of each premaxillary bone sutures with three or four bones: its antimere, one or both nasal bones, and the ipsilateral maxillary bone. Of these articulations, the interpremaxillary one lies in the mediosagittal plane. It is not continuous with the internasal suture which ends anteriorly at the posterior margin of either the left or the right premaxillary bone. The premaxillary-nasal suture continues posterolaterally from the rear of the interpremaxillary suture to the exonarial fenestra of the same side so that the premaxillary bone forms about one quarter of the mesial border of this fenestra. When the premaxillary-nasal suture meets the internasal suture, the premaxillary bone articulates with both the ipsilateral and the contralateral nasal bone. The premaxillary-maxillary suture extends ventrolaterally from the ipsilateral exonarial fenestra so that the premaxillary bone forms approximately two thirds of its lateral border.

Externally, the facial portion of each premaxillary bone is marked posteriorly by the frontmost part of the groove for the supraorbital neuromast canal (*cns*, fig. 1) and by the anterior part of the groove for the infraorbital neuromast canal (*cni*, fig. 1). These two grooves conjoin at the center of ossification of the premaxillary bone, anteromesial to the ipsilateral exonarial fenestra. The surface in question is marked by one more groove, or parts of a groove. This groove (*cne*, fig. 1) crosses the snout tip and interconnects the junction of the supraorbital-infraorbital neuromast grooves just mentioned with the corresponding junction of the opposite side of the skull.

Ossa nasalia (*Na*, figs 1, 2, 6) - The nasal bones, placed side by side, are the largest elements of the skull roof anterior to the orbitofacial openings. Each is roughly a four-sided plate in which the center of ossification lies slightly in front of its midpoint. It assists in forming the mesial border of the ipsilateral exonarial fenestra and sutures with seven, eight, or nine bones: six of the same side and three of the opposite side. The internasal suture lies in the mediosagittal plane, but its anterior end deviates to one side or the other and so occasionally does its posterior end. Because of these deviations either of the nasal bones is found to articulate anteriorly with both the premaxillary bones and posteriorly with both the principal, or central, frontal bones. Of these sutural connections, those with the central frontal bones are also seen to be due to a deviation from the midline of the skull roof of the anterior end of the interfrontal suture. Besides these five articulations each nasal bone sutures laterally with four bones: the septomaxillary bone, the maxillary bone, the maxillulary bone, and the frontolacrimal bone. Of these articulations, the maxillulary-nasal suture is crossed posteriorly by the groove for the ipsilateral supraorbital neuromast canal. This groove continues forward over the nasal bone to the premaxillary bone of the same side.

Ossa frontalia centralia (*Cf*, fig. 1) - The central frontal bones are oblong elements. They lie roughly as much between the orbitofacial openings as anterior to these openings and form the central part of the skull roof. Each sutures with five, six, or seven bones depending on how far forward or backward it extends relative to its antimere. When this extension in the anterior or the posterior direction exceeds that of its fellow of the opposite side articulations occur, respectively, with both the nasal bones and with both the frontopluteal bones. Laterally each central frontal bone sutures anteriorly with the posterior part of the mesial margin of the ipsilateral frontolacrimal bone and posteriorly with the anterior part of the mesial margin of the peripheral frontal bone of the same side. The two sutural connections just mentioned are both crossed by the groove for the ipsilateral supraorbital neuromast canal. This groove merely traverses a smaller lateral part of the central frontal bone.

Ossa frontoplutealia (*Fp*, fig. 1) - The frontopluteal bones are enclosing, and centered around, the small circular neuro-epiphysial foramen, each having its center of ossification at the same transverse level as this foramen. They have about the same length as the central frontal bones, and increase in width from before backwards. Occasionally the right frontopluteal bone extends farther backward than its antimere (see Säve-Söderbergh 1935, pl. 7), and the latter farther forward than the former. Each frontopluteal bone sutures with five or six bones: four of the same side and one or two of the opposite side. Of these articulations, that between the two frontopluteal bones lies in the mediosagittal plane. Anteriorly one of the frontopluteal bones has sutural contact with both the central frontal bones, while the other merely articulates with the central frontal bone of its own side. Posteriorly each of the two frontopluteal bones either meets the iniacopluteal bone of the same side in an essentially transverse suture or one of them articulates with both the iniacopluteal bones (see Säve-Söderbergh 1935, pl. 7). Laterally each frontopluteal bone is, from before backwards, in sutural contact with the ipsilateral peripheral frontal bone and the ipsilateral parietal bone. The former of these sutures, if continued backwards, will pass mesially to the auditive incisure of the same side.

Ossa iniacoplutealia (*Ip*, fig. 1) - The iniacopluteal bones are comparatively small, pentagonal elements forming the posteromedian part of the skull roof. Each sutures with four or five bones: the opposite iniacopluteal bone, the ipsilateral frontopluteal, parietal and trachelic bones, and occasionally the contralateral frontopluteal bone (see Säve-Söderbergh 1935, pl. 7). Of these articulations, the iniacopluteal-trachelic suture is directed anterolaterally, whereas the iniacopluteal-parietal suture is directed anteromesially. The former suture points toward the ipsilateral orbitofacial opening and the latter suture toward the neuro-epiphysial foramen. The iniacopluteal-trachelic suture is crossed most posteriorly by a short groove for the supraoccipital commissural canal of the neuromast system (*cnso*, fig. 1). This groove parallels the posterior edge of the skull roof; it disappears on the mesial half of the iniacopluteal bone and thus is widely separated from its antimere.

Ossa maxillaria (*Mx*, figs 1, 2, 3, 6, 7) - The maxillary bones are the longest elements of the skull roof, each forming most of the margin of the ipsilateral cheek. Like the premaxillary bone, each maxillary bone consists of two portions, a facial one (figs 1, 3, 6) and a palatal one (figs 2, 6, 7). Only the former portion will be dealt with under this heading.

The pars facialis ossis maxillaris extends from about the middle of the exonarial fenestra to the suture between the melonicozygomatic and quadratomaxillary bones of the same side. Its anterior half is distinctly higher than its posterior half and visible in a dorsal view of the skull. Immediately behind its sutural contact with the premaxillary bone it assists in forming the lateral border of the ipsilateral exonarial fenestra. Posterior to this fenestra it sutures with five ipsilateral bones which, from front to back, are: the septomaxillary bone, the nasal bone, the maxillulary bone, the melonicozygomatic bone, and the quadratomaxillary bone. At the level of the anterior termination of the orbitofacial openings the melonicozygomatic-maxillary suture is crossed by the groove for the infraorbital canal of the neuromast system. This groove also crosses the suture between the maxillary bone and the premaxillary bone below the exonarial fenestra. Moreover, from the former of these intersections to the latter the groove in question passes over both the posterior and the anterior part of the suture between the maxillary bone and the maxillulary bone. Thus, the anterior half of the facial portion of each maxillary bone is overpassed twice by the infraorbital neuromast canal of the same side.

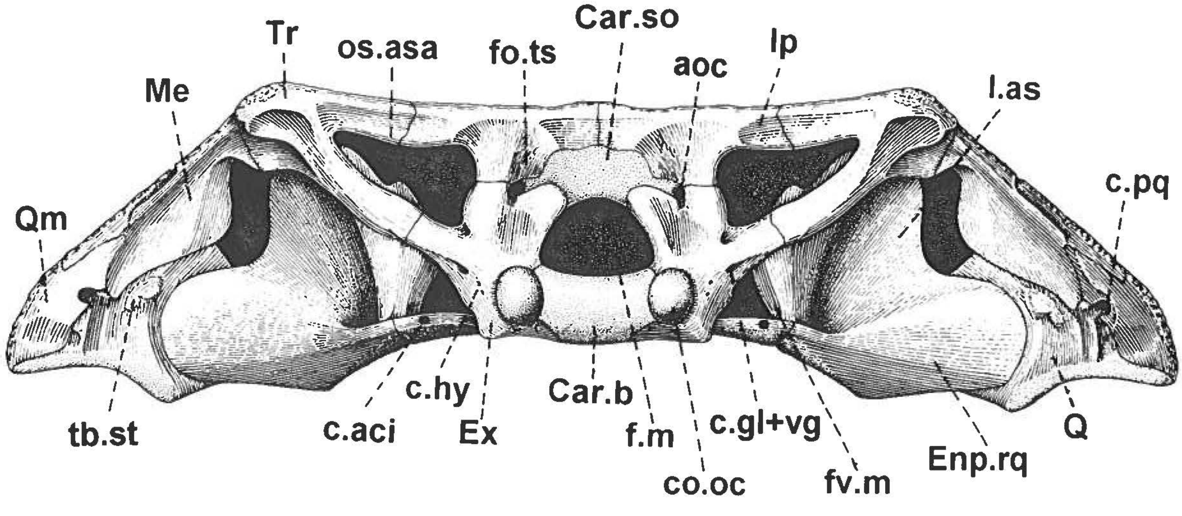
Ossa saeptomaxillaria (*Sm*, fig. 1) - The septomaxillary bones are the smallest elements of the skull roof. Each exhibits a subtriangular facial portion which is wedged in between the ipsilateral nasal and maxillary bones. Anteriorly this septomaxillary portion forms most of the posterior border of the exonarial fenestra. The portion of the septomaxillary bone which according to Säve-Söderbergh (1935, p. 167) extends into the cavity of the adjacent nasal capsule has probably been lost.

Ossa maxillularia (*Ml*, figs 1, 3, 6) - The maxillulary bones are oblong, quadrilateral elements, lying in front of the orbitofacial openings and behind the exonarial fenestrae. The length of each bone is about five-sixths of the ipsilateral distance between two of the cranial fenestrations just referred to. On either side there are four maxillulary sutural contacts: a short nasal-maxillulary one anteromesially; a long frontolacrimal-maxillulary one posteromesially; a lower jaw. Dorsomesially, between the frontolacrimal and frontomelonic bones, the melonicozygomatic bone enters into the formation of the lateral border of the ipsilateral orbitofacial opening.

Ossa quadratomaxillaria (*Qm*, figs 1, 2, 3, 4) - The quadratomaxillary bones are comparatively large elements filling in, on either side, the far corner of the cheek region, beyond the reach of the melonic and melonicozygomatic bones. Each consists of an anterior main division which bears sculpture and a posterior division which lacks sculpture. Of these, the anterior division is quadrilateral in outline. It has a convex free margin ventrally which forms most of the lateral border of the fenestra palatina adductoria of the same side. Its sutural connections are with the ipsilateral melonic, melonicozygomatic and maxillary bones. The suture with the first of these bones is long; that with the second one is short; and that with the third one is very limited. The posterior division of each quadratomaxillary bone covers the posterior surface of the ipsilateral quadrate bone laterally. It meets a lamina of the melonic bone dorsally in a sigmoid suture. A notch in its mesial margin shows the position of the external opening of the paraquadrate canal (*c.pq*, fig. 4) which probably transmitted nerves and blood vessels to the lower jaw. There remains to mention a short quadratomaxillary lamina which covers a small part of the anterior surface of the ipsilateral quadrate bone, and a small foramen paraquadratum accessorium that lies next to this lamina.

Ossa melonica (*Me*, figs 1, 3, 4) - The melonic bones are elongate elements which, on either side, fill out the expanse of the cheek region between the

Fig. 4. Aquiloniferus kochi. Reconstruction of occiput. Based on MGUH VP 3357. Magnification ca. x1.5. aoc: opening for occipital artery; c.aci: canal for internal carotid artery; Car.b: basioccipital cartilage; Car.so: supraoccipital cartilage; c.gl+vg: canal for the glossopharyngeal and the vagus nerve; c.hy: canals for hypoglossal nerve; co.oc: occipital condyle: c.pq: paraquadrate canal; Enp.rq: ramus quadratus ossis entopterygoidis; Ex: os exoccipitale; f.m: foramen magnum; fo.ts: fossa tectosynotica: fv.m: fovea probably for insertion of a muscle that passes backwards to stapes; Ip: os iniacopluteale; l.as: lamina ascendens ossis entopterygoidis; Me: os melonicum; os.asa: ostium occipitale antri supraauditualis; Q: os quadratum; Qm: os quadratomaxillare; tb.st: tuberculum supratrochleare; Tr: os trachelicum.



parietal and trachelic bones above, the frontomelonic and melonicozygomatic bones anteriorly, and the quadratomaxillary bone below. Each is marked externally by a curved groove of the neuromast system (*cnm*, fig. 1) which has its anterior continuation on the adjacent melonicozygomatic bone. From where it crosses the melonic-melonicozygomatic suture, this groove passes backward and upward to the center of ossification of the melonic bone; it then continues posterolaterally and downward to disappear shortly before the melonic-quadratomaxillary suture. Like the quadratomaxillary bone, each melonic bone includes posteriorly a smaller unsculptured platelike part which projects in a ventromesial and posterior direction. This melonic lamina partly covers the posterior surface of the ipsilateral quadrate bone, and sutures, respectively above and below, with the trachelic and the quadratomaxillary bone of the same side.

The bony palate

The lateral edges of the palatum osseum are formed by the ventral edges of the marginal bones of the skull roof, that is, the premaxillary, maxillary, and quadratomaxillary bones. Of these, the premaxillary and maxillary bones bear the marginal teeth alongside their ventral edges, and the ventral edge of each of the quadratomaxillary bones contributes to the rim of the fenestra palatina adductoria of the same side. The palatal plate is composed of eight paired bones and a median one. It presents three paired openings and one which is unpaired.

Fenestrae exoforiales (*fef*, figs 2, 6) - The exoforial fenestrae face ventrally, and their borders are flush with the surrounding surfaces. They lie a marked distance behind the exonarial fenestrae, a short distance in front of the orbitopalatine openings, a trifle posterior to the apical fossa, and much closer to the margins of the skull than to the ventral midline. Each exoforial fenestra, which is bounded by three bones, has an elongate oval shape and is almost twice as long as broad. Like that of the exonarial fenestra, its long axis makes an angle of about 20 degrees with the mediosagittal plane and, if continued backwards, it will pass laterally to the ipsilateral rear corner of the skull.

Aditus orbitarum palatini (*aop*, fig. 2) - The orbitopalatine openings occupy the greater part of the hard palate posterior to the snout. They are almost half as long as the mediosagittal skull length, and significantly wider posterior to their centers. Each orbitopalatine opening is bounded by the vomerodacnil, dermopalatine, and entopterygoid bones of the same side as well as by the median crepidine bone. It has a deeply rounded posterior border, a very shallowly rounded mesial border, a shallowly rounded lateral border, and a slightly indented anterolateral border. The orbitofacial opening (*aof*, fig. 2) cannot be seen in its entirety through the ipsilateral orbitopalatine opening when the skull is viewed palatally. The posterior border of the former opening lies farther in front of that of the latter than the anterior border of the latter opening lies in front of that of the former.

Fenestrae palatinae adductoriae (*fpa*, fig. 2) - The adductory palatine fenestrae occupy most of the posterolateral parts of the hard palate. Each fenestra is roughly triangular with rounded corners and about twice as long as broad. Of its borders, the lateral one is slightly convex, the posteromesial one is straight, and the anteromesial one is indented in a small degree by an entopterygoid bulge. Each fenestra palatina adductoria is bounded by five ipsilateral bones, *viz.*, the quadratomaxillary bone, the maxillary bone, a winglike inward extension of the melonicozygomatic bone, the entopterygoid bone, and the quadrate autostosis of the palatoquadrate. Its forward extent is the transverse level that passes through the neuro-epiphysial foramen.

Vacuitas rostropalatina (*vrp*, fig. 2) - The rostropalatine, or anterior palatal, vacuity is the unossified deep part of the apical fossa (see p. 24). It is bounded anteriorly by the palatal laminae of the premaxillary bones and laterally and posteriorly by the vomerodacnil bones. A median premaxillary identation gives it a somewhat cordiform shape. Laterally and posteriorly it may be invaded by poorly ossified projections of the vomerodacnil bones indicating that, in life, the rostropalatine vacuity was occluded by ethmoidal endoskeleton as was the corresponding vacuity in osteolepiforms (cf. Jarvik 1942) and ichthyostegids (cf. Jarvik 1996).

Partes palatales ossium praemaxillarium (*Px*, fig. 2) - The premaxillary bones form the anterior extremity of the skull and each of them has, as already noted, both a facial and a palatal exposure. Of these, the former is described above in conjunction with the bones of the skull roof (p. 13). The palatal portion is well developed and divisible, when viewed ventrally, into an outer dental zone and an inner palatine zone. It sutures with its antimere in the ventral midline. Moreover, it meets the ipsilateral vomerodacnil bone in a suture that, beneath the exonarial fenestra, continues posterolaterally from the anterolateral part of the rostropalatine vacuity. Posterolaterally, at the same transverse level as the rear of the exonarial fenestra, it meets the palatal portion of the ipsilateral maxillary bone in a nearly transverse suture. The zona dentalis bears from eleven to fifteen teeth or tooth sockets. The zona palatina lies mainly in the apical fossa. Mesially it presents a posteriorly directed process which together with that of the opposite side divides the front part of the rostopalatine vacuity into right and left halves.

Partes palatales ossium maxillarium (*Mx*, figs 2, 6, 7) - The maxillary bones account for almost two-thirds of the lateral margins of the hard palate. Each, like the premaxillary bones, consists of a facial and a palatal portion, the former of which has been described above along with the bones of the skull roof (p. 15). Moreover, like either of the premaxillary palatal portions, each maxillary palatal portion is divisible, when viewed ventrally, into a dental zone and a palatine zone. Of these, the zona dentalis extends the entire length of the palatal exposure of the maxillary bone and bears about forty teeth or tooth sockets which decrease in size from front to rear. The zona palatine, on the other hand, is confined to the anterior half of the maxillary bone. It is very narrow except anteriorly where it extends inward to form the lateral border of the ipsilateral exoforial fenestra. The palatal portion of the maxillary bone sutures with six bones on the same side which, from rear to front, are: the quadratomaxillary bone, the melonicozygomatic bone, the ectopterygoid bone, the dermopalatine bone, the vomerodacnil bone, and the premaxillary bone. There remains to mention that the posterior edge of the maxillary bone forms part of the lateral border of the ipsilateral fenestra palatina adductoria.

Ossa vomerodacnilia (*Vd*, figs 2, 6,7) - The vomerodacnil bones form the central part of the anterior half of the hard palate. Each sutures laterally with three ipsilateral bones, *viz.*, the premaxillary, maxillary, and dermopalatine bones. Moreover, each meets its antimere in a mediosagittal suture and is covered along this suture by the anterior half of the cultriform process of the crepidine bone. Together with its fellow of the opposite side it forms the lateral and posterior borders of the rostropalatine vacuity. Laterally it forms the anterior and mesial borders of the ipsilateral exoforial fenestra. And posteriorly it forms the anteromesial border of the orbitopalatine opening of the same side. Anteriorly, between the exoforial fenestra and the apical fossa, there is a tusk and a tusk pit. At the ventral midline just behind the apical fossa there are one or two small teeth. And along the mesial border of the exoforial fenestra there are two to five teeth or tooth sockets. Immediately posterior to the tusk and the tusk pit each vomerodacnil bone presents a shallow and narrow groove which, for a short distance, continues posterolaterally from the apical fossa (cf. p. 24).

Ossa dermopalatina (*Dp*, figs 2, 6) - The dermopalatine bones are relatively slender elements lying, on either side, between the anterior half of the orbitopalatine opening and the ipsilateral maxillary bone. They are broader anteriorly than posterorly and thicker laterally than mesially. Each forms the posterior border of the ipsilateral exoforial fenestra and the anterolateral border of the orbitopalatine opening of the same side. It meets four ipsilateral bones in sutures. Anteromesially it joins the vomerodacnil bone in an oblique suture that interconnects the exoforial fenestra and the orbitopalatine opening of the same side. Anterolaterally, for about three-fifths of its length, it sutures with the maxillary bone. Posteriorly it meets the anterior end of the entopterygoid bone in a very short suture which mesially ends in the middle of the orbitopalatine opening. Posterolaterally it touches the ectopterygoid bone in a suture which first extends inwards from the maxillary bone and then backwards mesially to the ectopterygoid tooth row until it reaches the anterior extremity of the entopterygoid bone. The ventral surface of the dermopalatine bone presents a tusk and a tusk pit lying in tandem immediately posterior to the exoforial fenestra. Between these dental structures and the dermopalatine-vomerodacnil suture there is a row of two or three small teeth. And back of the dermopalatine tusk or tusk pit there is a longitudinal row of five teeth or tooh sockets at the most. The relatively thick lateral margin of the dermopalatine bone expands immediately behind the ipsilateral exoforial fenestra and forms an upwardly directed process which abuts on the overlying maxillulary bone and probably corresponds to the spina sublacrimalis of Bystrov & Yefremov (1940). Besides giving stoutness to the skull, this process forms part of the hind wall of the ipsilateral nasal capsule.

Ossa ectopterygoida (*Ecp*, fig. 2) - The ectopterygoid bones are the simplest elements of the hard palate. They are about ten times as long as broad. Anteriorly they are bounded by the dermopalatine bones, and posteriorly they are excluded from the boundaries of the adductory palatine fenestrae by inward extensions of the melonicozygomatic bones. Moreover, they intervene between the maxillary and entopterygoid bones of their own side and meet them in sutures. Throughout the length of its ventral surface each entopterygoid bone bears a row of about fifteen small teeth or tooth sockets.

Partes palatales ossium melonicozygomaticorum (*Mz*, fig. 2) - For want of a better place, the palatal portion of each of the two melonicozygomatic bones (cf. p. 17) may be described here. It is a winglike, inwardly directed, horizontal projection overlying the posterior end of the ipsilateral ectopterygoid bone as well as a small adjacent part of the entopterygoid bone. Laterally it sutures with the maxillary bone of the same side. Posteriorly it forms the anterior border of the ipsilateral fenestra palatina adductoria. Between this fenestra and the adjacent parts of the ectopterygoid, entopterygoid, and maxillary bones the palatal portion of the ipsilateral melonicozygomatic bone is partly visible when the skull is viewed ventrally.

Ossa entopterygoida (*Enp*, fig. 2) - The entopterygoid bones are interjacent to the orbitopalatine openings and the adductory palatine fenestrae. Each is triradiate in ventral view and divisible into a body, two rami, and an ascending lamina.

The corpus ossis entopterygoidis encloses the ossification center of the bone. It joins the crepidine bone mesially in a suture that extends posterolaterally from the midpoint of the posterior border of the orbitopalatine opening. Laterally it contributes to the formation of the mesial border of the adductory palatine fenestra and anteriorly to the posterior border of the orbitopalatine opening. The ventral surface is nearly plane anteroposteriorly but concave transversely; it faces ventromesially and carries a shagreen of denticles.

The ramus anterior ossis entopterygoidis, which is the longer of the two entopterygoid rami, extends anterolaterally from the corpus up to a transverse level through the middle of the orbitopalatine openings. Anteriorly it sutures with the ipsilateral dermopalatine and ectopterygoid bones, as well as with the pars palatalis of the melonicozygomatic bone of the same side. It contributes to the border of the orbitopalatine opening mesially and that of the adductory palatine fenestra laterally. Like the corpus of the bone, its ventral surface is slightly concave transversely and to a large extent covered by a shagreen of denticles.

The ramus posterior (quadratus) ossis entopterygoidis (*Enp.rq*, fig. 4) extends backwards, outwards and somewhat upwards from the entopterygoid corpus as a relatively thin sheet of bone. It abuts on the mesial surface of the ipsilateral quadrate bone and its lower margin contributes to the border of the adductory palatine fenestra of the same side. In contrast to the corpus and anterior ramus of the bone, this ramus is smooth and toothless.

The lamina ascendens ossis entopterygoidis (*l.as*, fig. 4) is triangular in form and distinctly thickened and deflected toward the mediosagittal plane anteriorly. Reaching nearly to the skull roof, especially beneath the ipsilateral parietal bone, it arises from the internal surface of the entopterygoid bone along a line which extends between the center of ossification within the corpus and the rear of the posterior ramus and which concomitantly converges towards the upper margin of this ramus. Posteriorly the ascending entopterygoid lamina abuts on the quadrate bone of the same side. At its anteroventral thickened part there is a fossa coniformis entopterygoidea which very likely acted as the receptacle for the ipsilateral affacial process of the endocranium (cf. Bjerring 1997). Close behind this fossa there is a small fovea (*fv.m*, fig. 4). Probably, as suggested elsewhere (Bjerring 1997), a muscle that passed backwards to the stapes originated from this depression.

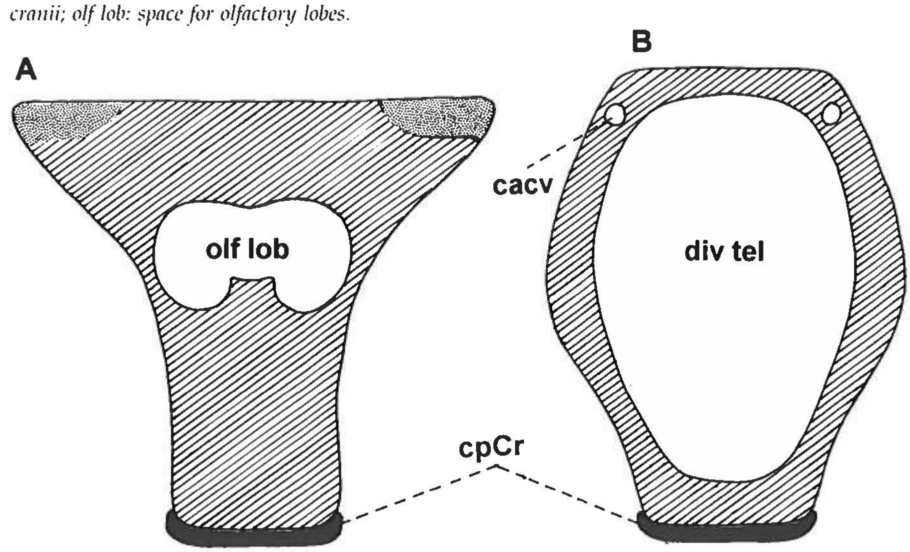
Ossa quadrata (*Q*, figs 2, 4) - The quadrate bones are the articular elements for the two jaw rami and the only preserved parts of the palatoquadrates. Each of these autostoses is interjacent to the entopterygoid and quadratomaxillary bones of the same side, and forms the posterior border of the ipsilateral adductory palatine fenestra. Posteroventrally it bears the upper part of the jaw joint which consists of a large inner condyle orientated about 45 degrees anteromesially, a small lateral condyle, and an intercondylar depression. Postero-externally, above this intercondylar depression, lies a small distinct protuberance, the tuberculum supratrochleare (*tb.st*, fig. 4), which probably gave attachment to musculature that opened the jaw. The quadrate bone continues a short distance upward and forward beyond this protuberance and is here in contact with the ascending entopterygoid lamina mesially and the descending melonic lamina laterally. Its anterior border, situated below the auditive incisure, consists of spongy bone and in life apparently merged into a cartilaginous part of the ipsilateral palatoquadrate.

Os crepidinum (*Cr.* fig. 2; see also figs 4, 5, 6) - The crepidine bone is the only median element of the hard palate. It extends from the apical fossa to the occipital region of the endocranium and thus represents an NEHTA-crepidine bone (cf. Bjerring 1997). The posterior part of the bone, the corpus ossis crepidini or the basal crepidine plate, is somewhat wider than long. It meets the corpus of the entopterygoid bone laterally in a suture continuing posterolaterally from the orbitopalatine opening, and abuts posteriorly on the exoccipital bones of the endocranium. The greatest width of the basal crepidine plate is about two-thirds of the least distance between the adductory palatine fenestrae. The anterior part of the crepidine bone is the cultriform process (*cpCr.* figs 5, 6) which separates the orbitopalatine openings and projects forward above the vomerodacnil bones at least as far as the transverse level of the anterior borders of the exoforial fenestrae. This process is flat and comparatively broad. It is exposed ventrally as far forward as the transverse level of the anterior borders of the orbitofacial openings. A shagreen of denticles covers most of the middle and anterior parts of the ventral surface of the basal crepidine plate and continues forwards to cover also the median part of the posterior third of the ventral surface of the cultriform process. There is no muscular crest at the back of the crepidine bone.

Immediately mesial to the posterior end of each of the crepidine-entopterygoid sutures lies the posterior opening of the canal for the internal carotid artery (*c.aci*, fig. 4). This canal curves anteromesially within the crepidine body and opens anteriorly on its dorsal surface, at the transition to the cultriform process. A short distance behind its anterior opening the intracrepidine carotid canal gives off a lateral branch which continues obliquely upwards to open on the dorsal surface of the basal crepidine plate, near the anterior end of the crepidine-entopterygoid suture. Presumably, this canal transmitted the palatine artery (cf. Shishkin 1968). Slightly closer to the mediosagittal plane than the canal for the palatine artery the crepidine body is pierced by a very short canal, the outer opening of which is visible when the skull is viewed palatally (cf. fig. 2). This canal quite likely conveyed the palatine ramus of the facial nerve to the mouth roof.

Fossa apicalis - The apical fossa lies on the ventral surface of the hard palate near its front end. It is ovoid in outline and formed by the premaxillary bones anteriorly and the vomerodacnil bones posteriorly. Its central part is unossified. Thus, in the fossil, the fossa apicalis exhibits a median opening, the rostropalatine vacuity (*vrp*, fig. 2). However, in the living animal, this open-

Fig. 5. Aquiloniferus kochi. Sections through the orbitonasal autostosis (hatched). Reconstructed cartilage, dotted. Specimen MGUH VP 3357. Magnification ca. x4.5 cacv: canal for anterior cerebral vein; cpCr: cultriform process of os crepidinum; div tel: telencephalic division of cavitas encephalica endocranii; olf lob: space for olfactory lobes.



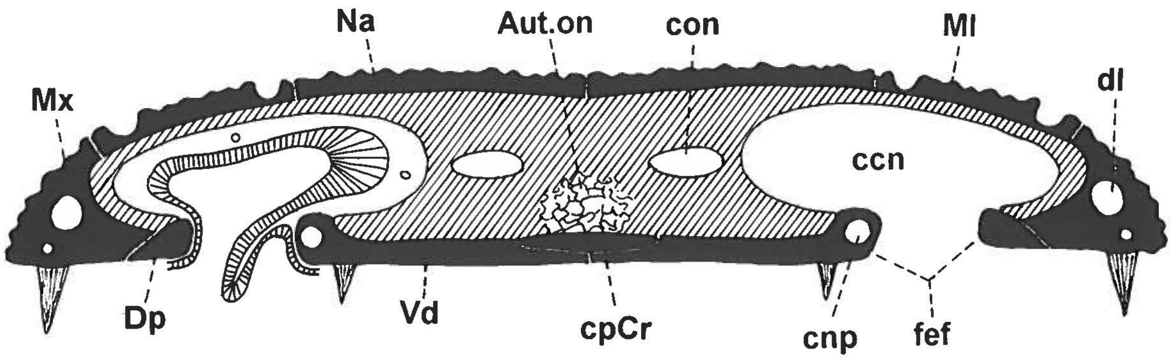


Fig. 6. Aquiloniferus kochi. Section through nasal region. Reconstructed cartilage, hatched. Specimen MGUH VP 3357. Magnification ca. x3.3. Aut.on: orbitonasal autostosis; ccn: cavitas capsilae nasalis; cnp: canal for palatine branch of facial nerve; con: canalis olfactorius; cpCr: cultriform process of os crepidinum; dl: canal for tear duct; Dp: os dermopalatinum; fef: fenestra exoforialis; Ml: os maxillulare; Mx: os maxilare; Na: os nasale; Vd: os vomerodacnile.

ing was quite likely occluded by ethmoidal endoskeleton as was the corresponding opening in *Eusthenopteron* and *Ichthyostega* (cf. Jarvik 1942, 1996). Immediately posterior to the vomerodacnil tusks there is on either side a shallow, narrow groove. From the back part of the apical fossa, this groove continues posterolaterally the better part of the distance to the adjacent exoforial fenestra. By comparison with frogs (cf. Wiedersheim 1876, Gaupp 1904, Duellman & Trueb "1986" [1985]) it can be suggested that the apical fossa and the grooves accomodated, respectively, an intermaxillary gland and its ducts (fig. 7).

The occiput

The breadth of the back part of the skull is about four times the absolute depth of the skull and five times the height of the iniacopluteal bones above the crepidine bone. The occipital region of the endocranium is visible for most of its length when the skull is viewed from above, and the occipital condyles are as far posterior to the midpoint of the rear margin of the skull table as they are apart. These condyles are also posterior to the distal ends of the trachelic bones. The jaw articulations are located posteroventral to the occipital condyles, approximately equidistant from the transversal and horizontal planes in which these two articular projections of the endocranium lie. The major occipital openings are the median foramen magnum and a pair of ostia occipitalia antrorum supra-auditualium. The latter openings are usually designated the posttemporal fenestrae but also the subtabular fenestrae (see *i.a.* Welles & Cosgriff 1965 and Bystrov & Yefremov 1940).

Foramen magnum (*f.m*, fig. 4) - This aperture, through which the cavitas encephalica endocranii communicates with the canalis vertebralis, is directed backward and a little upward. In outline, it resembles a triangle the apex of which is above and in the mediosagittal plane. Its margin is bony except ventrally and middorsally.

Ostia occipitalia antrorum supra-auditualium (*os.asa*, fig. 4) - Each of these openings affords entry to a skeletal cavity (the fossa Bridgei of Säve-Söderbergh (1936) and the fossa posttemporalis of Romer (1947); but see Bjerring 1984), situated above the ipsilateral membranous labyrinth. The ostium occipitale antri supra-auditualis faces posteriorly and a little mesially. It is a fairly large, triangular opening, situated between the occipital region of the endocranium and the posterolateral part of the skull table. Of its three borders, the mesial one is the shortest; it extends nearly, but not quite parallel with the mediosagittal plane, and is formed by the exoccipital bone and the superjacent iniacopluteal bone. The dorsal border is the thinnest of the three; it slightly overhangs the fenestra, and is formed by the iniacopluteal bone mesially and the trachelic bone laterally. The ventrolateral border is the longest of the three, being about twice as long as the mesial border; it is formed mainly by a descending metotic process of the trachelic bone which mesially meets a short dorsolaterally directed metotic process of the exoccipital bone of the same side.

Ossa exoccipitalia (*Ex*, figs 2, 4) - The exoccipital bones, or autostoses, are the posteriormost endocranial elements. They demarcate to an extent the foramen magnum, connect the skull roof with the hard palate, and serve to form the transistion to the vertebral column. Each presents three processes

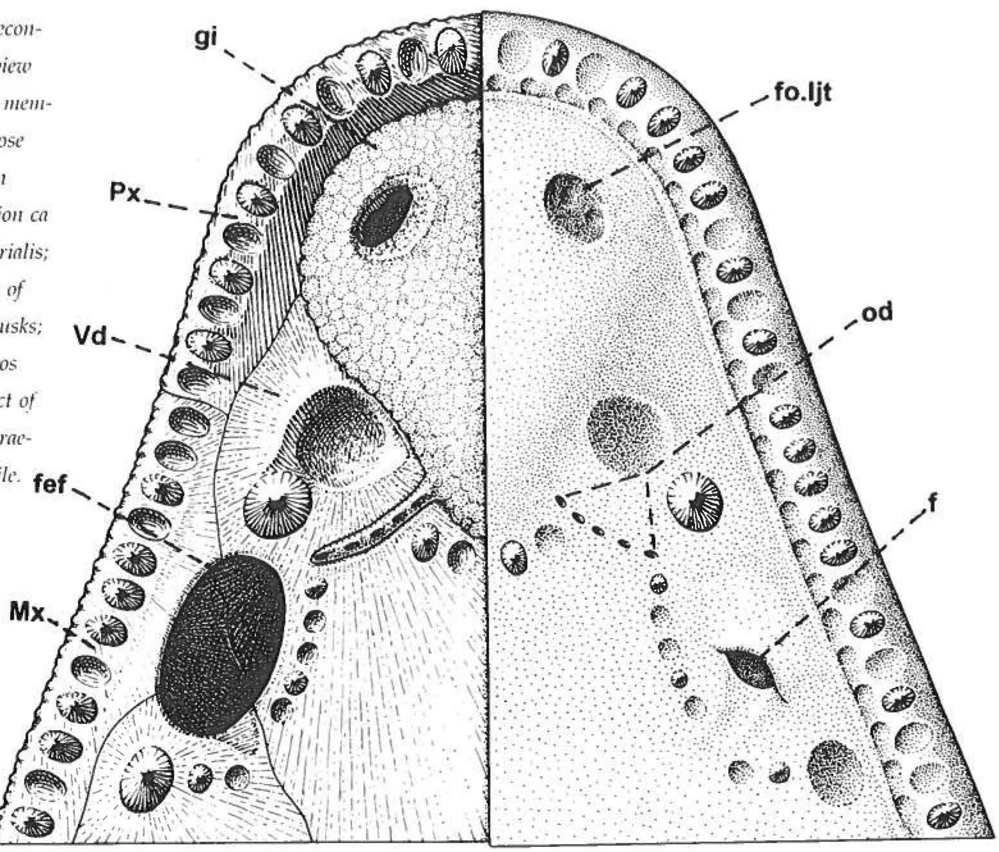


Fig. 7. Aquiloniferus kochi. Reconstruction of snout in ventral view with right half of oral mucous membrane removed in order to expose intermaxillary gland. Based on MGUH VP 3357. Magnification ca x2.8 f: foris; fef: fenestra exoforialis; fo.ljt: fossa for accommodation of tips of lower jaw symphysial tusks; gi: intermaxillary gland; Mx: os maxillare; od: openings for duct of intermaxillary gland; Px: os praemaxillare; Vd: os vomerodacnile.

(condylar, metotic, and vertical) and four surfaces (external, encephalic, mesial, and anterior). In the intact head, the two last-named surfaces were most likely contiguous to cartilage.

The processus condylaris (ossis exoccipitalis) constitutes the posteroventral part of the bone. It lies widely apart from its antimere, and is stout but very short. Its distal end is subcircular in outline and lacks a periosteal lining; this roughened area faces inward, downward, and backward, and evidently bore a cap of cartilage (*co.oc*, figs 2, 4). The processus metoticus (ossis exoccipitalis) projects dorsolaterally and slightly anteriorly to meet the similarly named process of the ipsilateral trachelic bone. It bounds the ventral part of the mesial third of the superjacent ostium occipitale antri supra-auditualis. Ventrally, close to the body of the exoccipital bone, it is pierced by a comparatively large foramen for the passage of the nervi glossopharyngeus and vagus of the same side (*c.gl+vg, fig. 4*). This foramen is continued by a groove which extends about half the length of the metotic process in question. The processus verticalis (ossis exoccipitalis) is a short, cylindric eminence which constitutes the dorsolateral part of the bone and forms part of the mesial boundary of the ispilateral ostium occipitale antri supra-auditualis. Its distal end sutures with the descending supraoccipital process of the superjacent iniacopluteal bone.

The facies externa (ossis exoccipitalis) is divisible into three parts – ventral, lateral, and posterodorsal. Of these, the pars ventralis faciei externae extends from the condylar process to the level of the anterior limit of the posterolateral crepidine notch. Thus its anterior half is underlapped by the crepidine bone. Its palatally exposed posterior half presents a shallow depression probably for the insertion of rectus capitis musculature (cf. the "pocket" of Watson, 1962). The pars lateralis faciei externae, which is concave from before backwards, lies between the condylar process, the metotic process, and the posterolateral corner of the crepidine bone. Besides facing laterally, it is directed somewhat downward and backward. Near the condylar process are two small foramina, one above the other (*c.hy*, fig. 4); these probably gave exits to branches of the ipsilateral hypoglossal nerve. The pars posterodorsalis faciei externae extends between the three processes of the exoccipital bone as well as between the ostium occipitale antri supra-auditualis of the same side and the foramen magnum. Above the condylar process it exhibits a shallow depression which probably gave attachment to neck musculature. Immediately above this depression lies a short vertical groove which ends in a notch formed by the exoccipital bone and the superjacent iniacopluteal bone. This groove and notch may indicate part of the course of the occipital artery (*aoc*, fig. 4; cf. Bjerring 1997). At the angle between the metotic process and the corpus of the exoccipital bone there is a comparatively large foramen which apparently transmitted a nerve of the neuromast system.

The facies encephalica (ossis exoccipitalis) consists of an upwardly directed, or horizontal, ventromesial part and a lateral part which faces inward and somewhat downward. Immediately inside the foramen magnum, at the tran-

Comparisons of *Aquiloniferus kochi* with Wiman's *Lyrocephalus euri* and Shishkin's *Luzocephalus blomi*.

As already mentioned, Säve-Söderbergh assigned in 1935 the above tetrapod from Greenland to the monotypic genus *Lyrocephalus* WIMAN, 1914 (= *Lyrocephaliscus* KUHN, 1961) from Spitzbergen. Since then much new information is now available concerning the cranial morphology of both these animals (cf. Mazin & Janvier 1983). Consequently, of the two tetrapods *Lyrocephalus euri* can now be distinguised from the Greenland one by the following (see figs 1, 2, 8A, 9A): The cultriform process of the crepidine bone is exceedingly high and narrow, and exposed palatally along the whole length of the orbitopalatine openings (that is, the vomerodacnil bones lack posterior processes); the corpus of the crepidine bone is broadest posteriorly, has a considerably greater length than breadth and reaches back to underplate the occipital condyles; the entopterygoid-crepidine suture is almost as long as the crepidine corpus: the quadrate ramus of the entopterygoid bone is comparatively broad and short; the orbitofacial openings lie level with the sagittal midpoint of the skull roof; the absence of an entopterygoid-dermopalatine suture; the presence of a zone of intensive growth of the skull roof both in front of the orbitofacial openings and behind these openings; the grooves for the supraorbital neuromast canals lie close together interjacent to the exonarial fenestrae; the cheek margin of either side is markedly convex in occipital view and steeply sloped down in its vertral part; the absence of an apical fossa; and the jaw articulations are close to the transverse level of the occipital condyles.

Together these differences indicate that the flatheaded East Greenland tetrapod cannot be allocated to the genus *Lyrocephalus* WIMAN, C., 1914. They also indicate that it is not a trematosaur.

But can this Greenland tetrapod be allocated to the monotypic genus *Luzocephalus* from European Russia as suggested by Shishkin in 1980? The answer is no because, of these two animals, the one from Greenland can be distinguished from *Luzocephalus blomi* SHISHKIN, M. A., 1980, by the following (see figs 1, 2, 8B, 9B): The jaw articulations lie only a relatively short distance behind the occipital condyles; the zone of intensive growth of the skull roof immediately posterior to the orbitofacial openings is lacking; the skull has relatively little depth; the palate is only slightly vaulted; the exoccipital bones are in a great measure visible when the skull is viewed from above; the auditive incisures are farther apart relative to the breadth and length of the skull roof and their deepest parts lie level with the posterior midpoint of the skull roof; the corpus ossis crepidini has a considerably greater breadth than length and does not reach back to the occipital condyles; the length of the

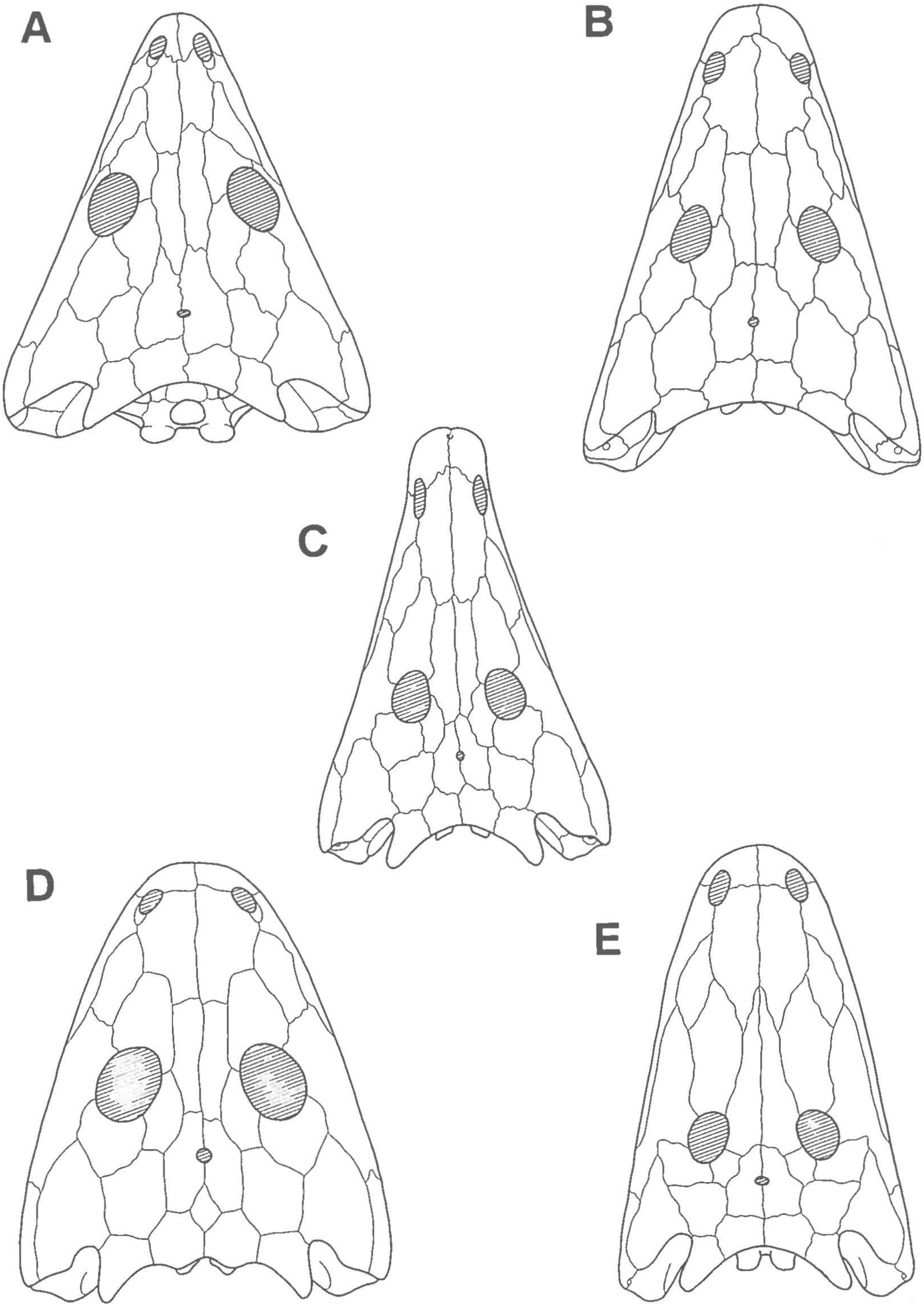


Fig. 8. Skull roofs of (A) Lyrocephalus euri *after Säve-Söderbergh (1936), (B)* Lyzocephalus blomi *after Shishkin (1980), (C)* Benthosuchus sushkini *after BystrovYefremov (1940) and Getmanov (1989), (D)* Lydekkerina huxleyi *after Shishkin* et. al. *(1996) and (E)* Parotosuchus nasatus *after Schroeder (1913) and Warren (1980). Magnifications: A and B, ca. x0.35; C, ca. x0.30; D, ca. x0.90; E, ca. x0.20.*

corpus of the entopterygoid bone behind the ipsilateral orbitopalatine opening is relatively short (only about 29 percent of the breadth across the corpora ossium entopterygoidum); the groove for the supraorbital neuromast canal passes over the ipsilateral maxillulary bone; the anterior parts of the melonicozygomatic bones are markedly farther forward that the orbitofacial openings; the cultriform process of the crepidine bone is relatively broad; and the major axes of the exonarial fenestra and orbitofacial opening will, if continued backwards, pass laterally to the ipsilateral rear corner of the skull.

These differences make the East Greenland tetrapod under consideration worthy of more than specific separation from *Luzocephalus blomi*. Hence the present writer proposes a new genus *Aquiloniferus* with *Lyrocephalus kochi* SÄVE-SÖDERBERGH, 1935, as the type.

In addition to assigning one of the tetrapod specimens from the Eotriassic deposits in East Greenland at Kap Stosch to the genus *Lyrocephalus* WIMAN as *L. kochi*, Säve-Söderbergh (1935) assigned three other specimens from these deposits to *Lyrocephalus* WIMAN as *L. johanssoni* (fig. 10), *L. rapax* (fig. 11), and *L. sp*. However, the minor differences in skull measurements used to establish these species do not seem of sufficient significance to require separation at the specific level. Thus they are here synonymized with *Aquiloniferus kochi*.

Comparison of *Aquiloniferus* with other tetrapod genera of Triassic age

Benthosuchus (figs 8C, 9C) - This amphibious tetrapod differs from *Aquiloniferus* in having a more slender and deeper skull and in being much more slender-snouted; the crepidine body underplates the exoccipital bones back to the occipital condyles and exhibits muscular crests; the cultriform process of the crepidine bone is relatively narrow; the orbitofacial openings lie above the posterior halves of the orbitopalatine openings posterior to the entopterygoid-dermopalatine sutures and the long axis of each orbitofacial opening is pointed toward the inner border of the ipsilateral auditive incisure; the auditive incisures are closer together relative to the median length of the skull; the posterior border of the skull roof is markedly more concave; vomerodacnil teeth are arranged in line posteromesially from the rostropalatine vacuity to the midline at the level of the anterior part of the exoforial fenestra of the same side; the exoforial fenestra is oval with its major axis being more than twice the length of its minor one and pointed toward the ipsilateral jaw articulation; the orbitopalatine opening is relatively narrow and broadest at its center; the jaw articulations lie only a little behind the occipital condyles.

Lydekkerina (figs 8D, 9D) - This tetrapod differs from *Aquiloniferus* in being broad-skulled and very short-snouted; the exoccipital bones are hardly visible when the skull is viewed from above; the posterior midpoint of the skull roof lies behind the rear margin of the crepidine bone; the crepidine body has muscle crests; the orbitofacial openings lie posterior to the dermopalatine-entopterygoid sutures and their long axes, if continued backwards, will pass mesially to the posterolateral corners of the skull roof; the jaw articulations are only slightly behind the occipital condyles; the orbitopalatine openings are broadest in their anterior halves; the trachelic bones extend far behind the occipital condyles and also behind the quadrate rami of the entopterygoid bones as well as the jaw articulations.

Uranocentrodon (see Broom 1930) - This tetrapod differs from *Aquiloniferus* in having a broader skull, a shorter snout and a somewhat elongated facial region; the exoccipital bones are not visible when the skull is viewed from above; the posterior midpoint of the skull roof lies behind the rear margin of the crepidine bone; the crepidine body exhibits muscle crests; the orbitofacial openings lie above the posterior parts of the orbitopalatine openings and their long axes point toward the trachelic bones; the basioccipital autostosis is present; the parietal bones assist in bordering the auditive incisures; the crepidine body underplates the exoccipital bones back to the occipital condyles.

Parotosuchus (figs 8E, 9E) - This tetrapod differs from *Aquiloniferus* in the broader and shorter snout, and a marked elongation of the facial part of the skull; the central frontal bones enter into the formation of the mesial borders

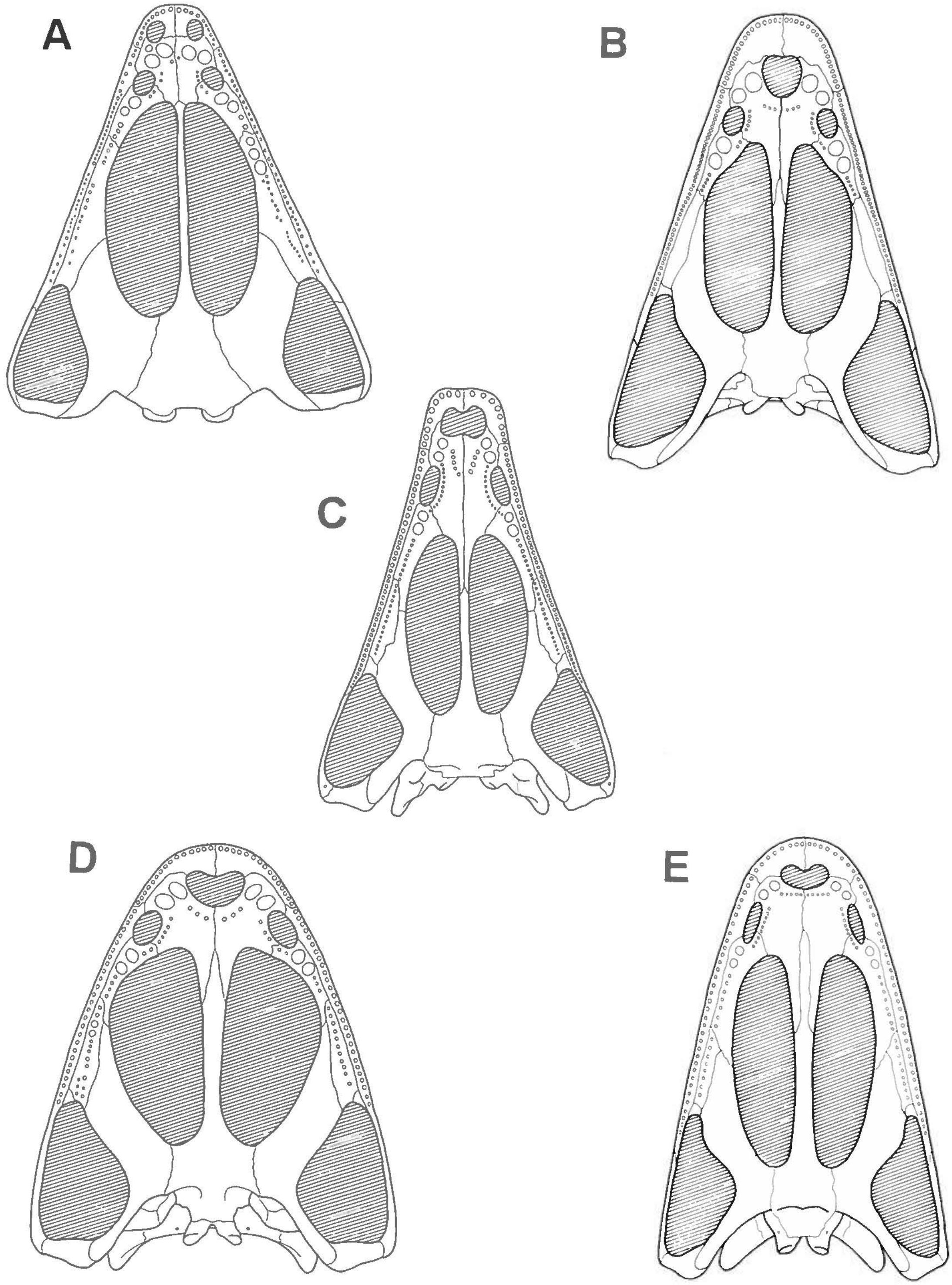


Fig. 9. Bony palates of (A) Lyrocephalus euri *after Säve-Söderbergh (1936), (B)* Luzocephalus blomi *after Shishkin (1980), (C)* Benthosuchus sushkini *after Bystrov & Yefremov (1940) and Getmanov (1989), (D)* Lydekkerina huxleyi *after Shishkin* et al. *(1996) and (E)* Parotosuchus nasatus *after Schroeder (1913) and Warren (1980). Magnifications: A and B, ca. x0.35; C, ca. x0.30; D, ca. x0.90; E, ca. x0.20.*

of the orbitofacial openings; the melonicozygomatic bones are invaded by the frontomelonic bones; relative to the length of the skull roof the orbitofacial openings are closer together, as are the auditive incisures; the orbitofacial openings are also much farther back and situated above the posterior parts of the orbitopalatine openings; the long axis of each orbitofacial opening points to the outer border of the ipsilateral auditive incisure; the exoforial fenestrae are elongate; the exoccipital bones are almost completely hidden when the skull is viewed from above; the body of the crepidine bone underplates most of the exoccipital bones and has muscle crests; an exoccipital-entopterygoid contact is present; and the distal ends of the trachelic bones are well behind the level of the occipital condyles.

From these comparisons it should be clear that *Aquiloniferus kochi* cannot be considered a benthosuchid, a uranocentrodontid, a lydekkerinid, or a capitosaurid. Nor can this Greenland tetrapod be considered a cyclotosaurid, a paracyclotosaurid, or a stenotosaurid in which the auditive incisures are closed or semi-closed, a deltocephalid in which the cheek borders are curved in occipital view, or a rhinosuchid in which, like in the uranocentrodontids, each auditive incisure is bounded by three bones. And it cannot possibly be considered a rhytidosteid in which the maxillary and maxillulary bones of the same side are united with one another.

Apart from the rhytidosteids, the groups noted above are usually considered to be members of the Capitosauroidea. According to the diagnosis of this presumedly artificial unit (cf. Shishkin *et al.* 1996), *Aquiloniferus kochi* should be classed as a capitosauroid *incertae sedis*.

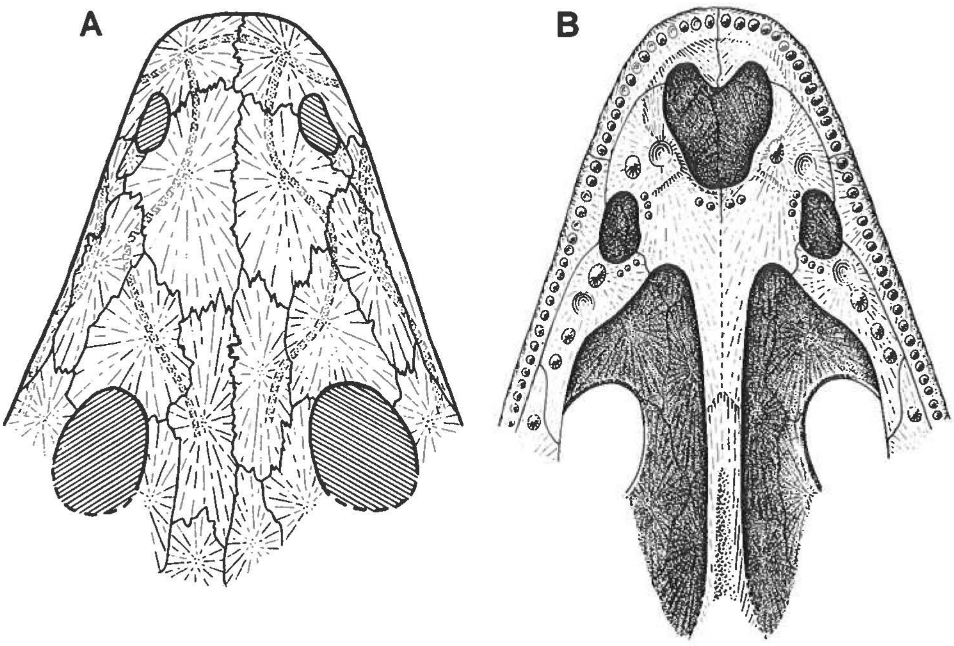


Fig. 10. Aquiloniferus kochi. Specimen MGUH VP 3359 (At. 28) in dorsal (A) and ventral (B) view. A: from Säve-Söderbergh 1935. Approx. nat. size.

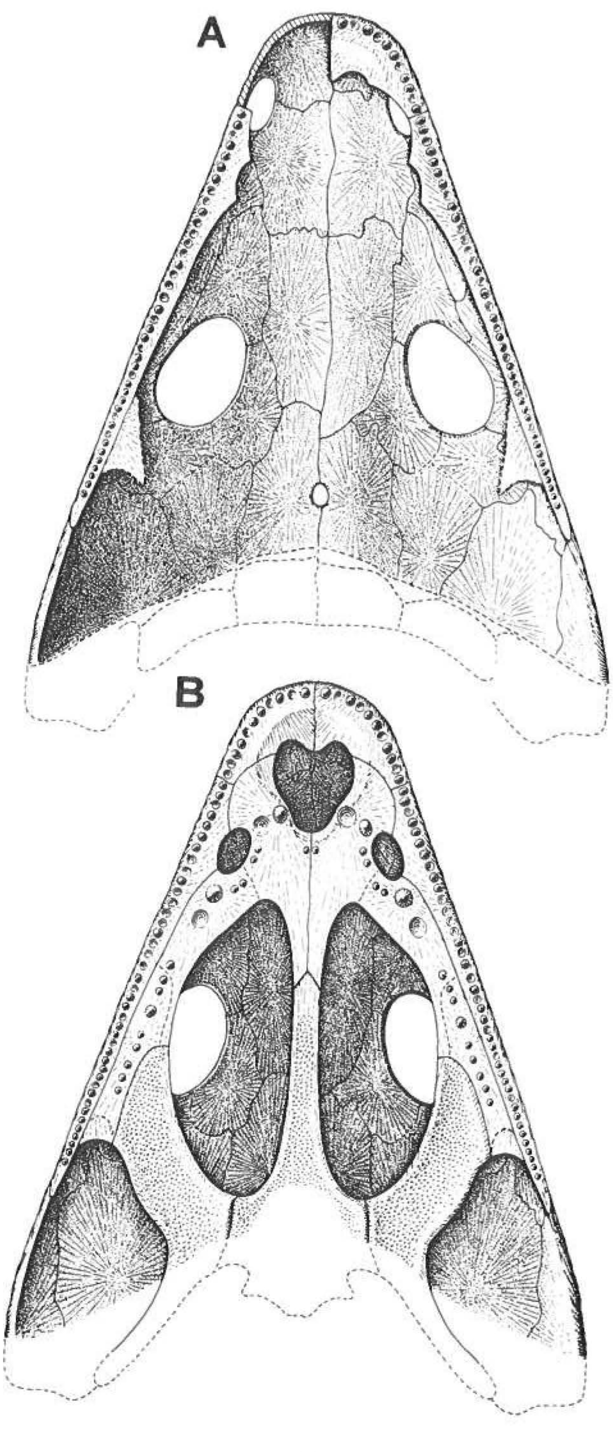


Fig. 11. Aquiloniferus kochi. Specimen MGUH VP 3360 (At. 29). Skull roof (A) and bony palate (B) in ventral view. Approx. nat. size.

Concluding remarks

In 1935, Säve-Söderbergh recorded four different tetrapods a s trematosaurs and a fifth one as a capitosaur from the Eotriassic of central East Greenland at Kap Stosch. He assigned three of these trematosaurs to the genus *Lyrocephalus* WIMAN first described from the Lower Triassic of Spitzbergen (as *L. kochi*, *L. rapax*, and *L. johanssoni*), one of them to a new genus, *Stoschiosaurus* (as *S. nielseni*) and the capitosaur to the genus *Wetlugasaurus* RYABININ from the Russian Eotriassic (as *W. groenlandicus*).

In 1830, Wagler substituted *Lyrocephalus* for the generic name *Lyriocephalus* MERREM, 1820, because he disapproved of the way it was spelt. To date, however, this orthographic change has been generally ignored, and rightly so; the generic name *Lyriocephalus* has indeed continued to be, and still is, used by herpetologists for one of the Asian agamids (cf. Underwood 1970). Clearly, then, the name *Lyrocephalus* was available nomenclaturally when Wiman in 1914 introduced it for a Triassic tetrapod from Spitzbergen. Never-

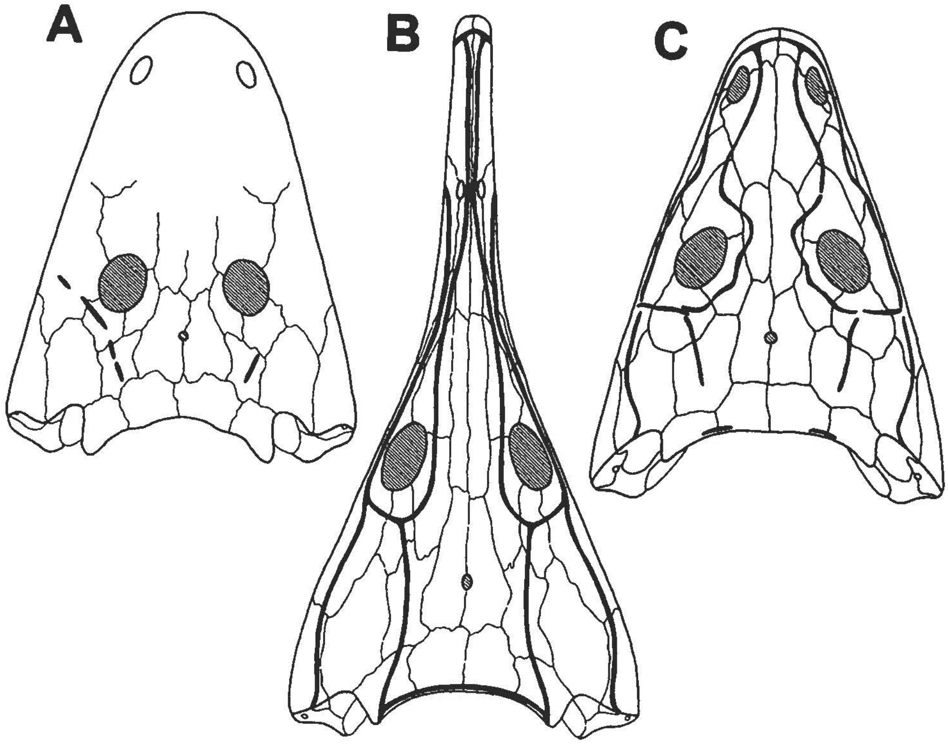


Fig. 12. Dorsal skull views of three amphibious tetrapods known from the Eotriassic of East Greenland at Kap Stosch. (A): Selenocara groenlandica; (B): Stoschiosaurus nielseni; (C): Aquiloniferus kochi. Magnifications: A and C, ca. x0.50; B, ca. x0.30.

theless, in 1961 Kuhn asserted that it was preoccupied. He therefore proposed a new name, *Lyrocephaliscus*, as a replacement for *Lyrocephalus* WIMAN. This renaming was made without any bibliographical reference. Hence, the junior synonym *Lyrocephaliscus* KUHN, 1961, is a *nomen nudum*.

In 1980, Shishkin transferred Säve-Söderbergh's three Greenland species of *Lyrocephalus* to the genus *Luzocephalus* from the Russian Eotriassic. Recently, *Wetlugasaurus groenlandicus* was transfered by Bjerring (1997) to the genus *Selenocara*, as *S. groenlandica*.

In this paper, *Lyrocephalus kochi* SÄVE-SÖDERBERGH, *Lyrocephalus rapax* SÄVE-SÖDERBERGH and *Lyrocephalus johanssoni* SÄVE-SÖDERBERGH are lumped into one species which is transferred to the genus *Aquiloniferus*, as *A. kochi*.

Consequently, instead of four trematosaurs and one capitosaur the tetrapod record from the Lower Triassic of East Greenland at Kap Stosch is now known to comprise one trematosaur (*Stoschiosaurus nielseni*) and two capitosaurs (*Selenocara groenlandica* and *Aquiloniferus kochi*) all of which are monotypic and confined to this geographic area. The skull roofs of these three animals are shown in figure 12.

Parenthetically, mention may be made also of the embolomerous tetrapod *Tupilakosaurus heilmani* NIELSEN that comes from the same Eotriassic beds near Kap Stosch. Its describer (Nielsen 1954, 1967) considered it closely related to the brachyopids (cf. Shishkin 1961, Schultze 1969). Brandtoft, a Danish student, restudied the material of this animal in the early 1970s. He found *Tupilakosaurus* to be a true brachyopid genus (pers. comm.).

Acknowledgements

This paper is dedicated to the memory of the Swedish paleozoologist Gunnar Säve-Söderbergh who in the 1930s collected a large number of Devonian and Triassic tetrapods in East Greenland and described many of them. Thanks go to the Greenland Geological Survey for funds which enabled me to visit, in 1958, the Eotriassic sediments at Kap Stosch, central East Greenland. Celso Salgueiro assisted with the illustrations, Filip Bjerring was indispensable in labeling them, Ritva Woode typed the final manuscript and Jennifer Clack checked the English. I am indeed grateful for all this help. The paper benefited from comments by Svend Erik Bendix-Almgreen and David Harper.

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In the early 1930s, a large number of Eotriassic fish and tetrapods were found in East Greenland. Of these, the fish have been thoroughly studied *i.a.* using the Sollasian grinding method. Conversely, our knowledge of the tetrapods is limited to preliminary descriptions of a few skull roofs and palates. Despite of paucity of available data, some of these skulls were assigned to a Russian genus and others to a genus known from Spitsbergen. Recently, the author demonstrated that the material allocated to the Russian genus had been misidentified (Meddelelser om Grønland, Geoscience 34). Herein he shows that the skulls allocated to the Spitsbergen genus have been misidentified, too. It is now clear that this tetrapod fauna includes only one trematosaur and two capitosaurs, instead of four trematosaurs and one capitosaur as originally believed.

Hans C. Bjerring, born 1931 in Copenhagen, obtained a Docteur ès Sciences in development biology at the Sorbonne and has for three decades been a research scientist of the Swedish Museum of Natural History. His interest is the basic composition and evolution of the vertebrate head. One of the highlights of Bjerring's retro-evolutionary analyses was the prediction and discovery of two cranial nerves that had previously been overlooked.