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# *Acanthostega gunnari*, a Devonian tetrapod from Greenland; the snout, palate and ventral parts of the braincase, with a discussion of their significance

*J. A. Clack*

Geoscience

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J. A. CLACK

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The snout, including the naris and choana, and the palate, ventral parts of the braincase and suspensorium of *Acanthostega gunnari* are described from three-dimensional specimens and sections. The naris is low on the snout, and the choana and vomerine dentition resemble those of osteolepiform fishes. The braincase is ossified in two portions in ventral view, with the ventral cranial fissure still evident. Dorsally, however, the otic region and sphenethmoid are co-ossified, so there was no movement possible between them. The palate is "closed" as in osteolepiforms and primitive tetrapods, and the parasphenoid is grooved as in some osteolepiforms. It is argued that the low naris and divided braincase represent the primitive condition for tetrapods, and that the condition of the naris and choana most closely resemble those of panderichthyid fishes among sarcopterygians.

Key words:
Devonian, tetrapod, *Acanthostega*, snout, palate, braincase, choana, naris.

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## Introduction

Our knowledge of the earliest tetrapods has until recently been confined to a limited number of taxa of which the best known is *Ichthyostega*, from the Upper Devonian of East Greenland. This genus was described by Säve-Söderbergh (1932) and Jarvik (1952, 1955a, 1955b, 1980). A second genus from East Greenland was recognised by Jarvik (1952) and named *Acanthostega gunnari*. It was described from two partial skull roofs, also from the Upper Devonian of East Greenland. They were characterised by a tabular bearing a unique horn and embayment, and the taxon was clearly distinguishable from *Ichthyostega*. *Ichthyostega* remained the best known Devonian tetrapod for many years. However, significant details of its anatomy are still obscure and difficult to interpret. Even though several of its described features are unique, and are not those expected of a very early tetrapod, it has nevertheless been widely seen as a model for the earliest land vertebrate.

Apart from *Ichthyostega* and *Acanthostega*, the only other described Devonian tetrapod body-fossil material consists of a lower jaw described as *Metaxygnathus* (Campbell & Bell 1977) from Australia; limb and girdle elements of *Tulerpeton* (Lebedev 1984) from Russia, and fragments of newly recognised tetrapods from Scat Craig in Scotland and Latvia (Ahlberg 1991a, Ahlberg *et al.* in press). Tetrapod trackways have been reported from the Upper Devonian of Australia (Warren & Wakefield 1972), and possible tetrapod trackways from the Middle Devonian of Scotland (Rogers 1990). Trackways described by Warren *et al.* (1986) are considered unlikely to be those of a tetrapod and an isolated single footprint reported as being from the Devonian of Brazil (Leonardi 1983) is regarded here as anomalous.

Further skull and postcranial material of *Acanthostega* became available in the mid 1980's and was described by Clack (1988). It became even more clear that *Ichthyostega* and *Acanthostega*, though contemporary, were divergent in many ways other than the skull roof. That material had been discovered on Stensiö Bjerg in 1970 by an expedition from Cambridge University undertaking sedimentological studies of the Devonian deposits on Gauss Halvø (Friend *et al.* 1976, Clack 1988). Subsequently, renewed collecting at this locality by a joint expedition from Cambridge University and the Geolog-

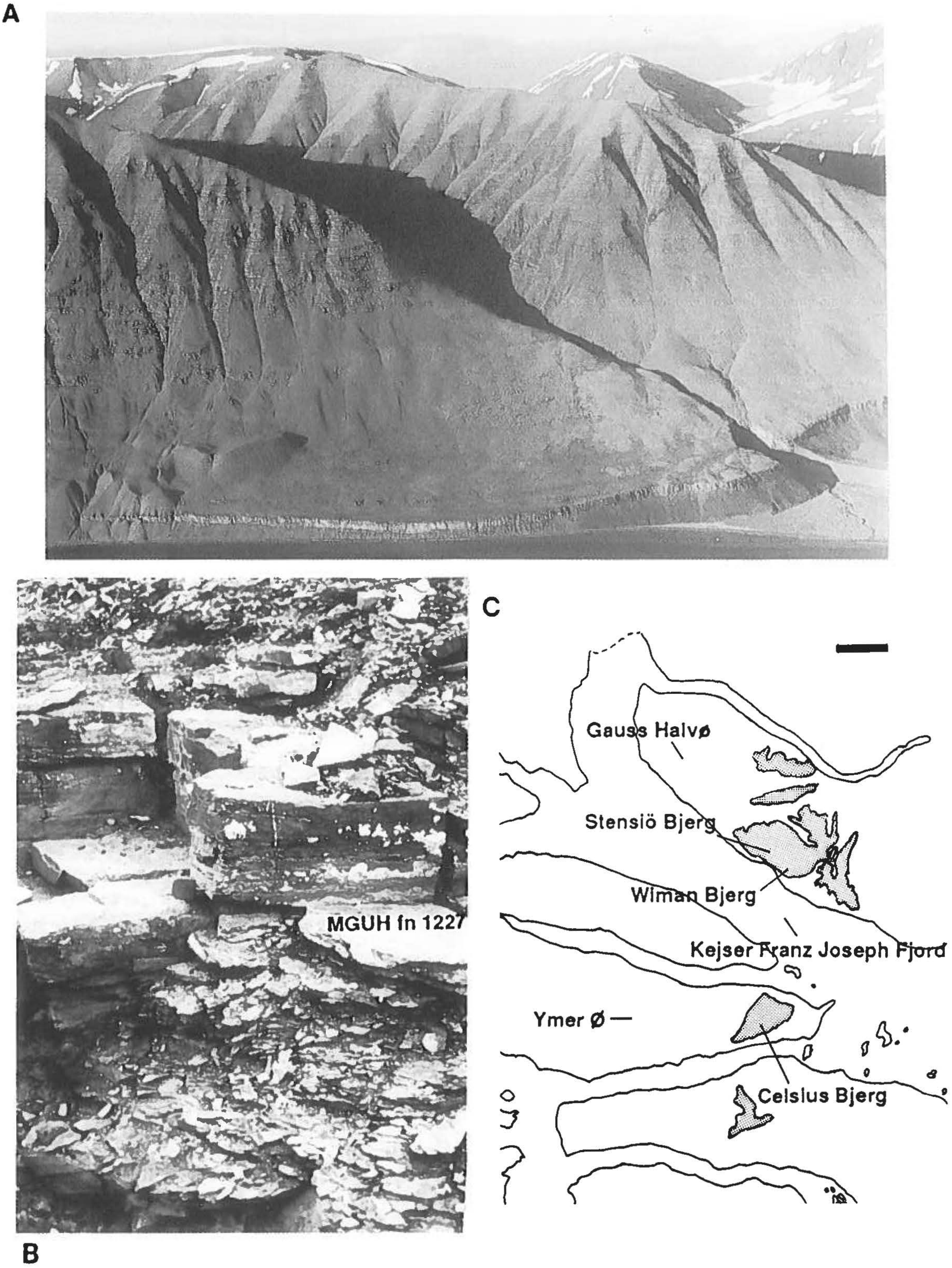


Fig. 1 A. Photograph of Stensiö Bjerg from the Southwest, showing Aina Dal Formation (shoreline cliffs) and Britta Dal Formation (above a fault running diagonally centre left to upper right). B. Photograph of exposure yielding *Acanthostega* remains from Britta Dal Formation of Stensiö Bjerg. Loose block in centre right foreground (MGUH f.n. 1227), and other blocks at that level contained the articulated specimens. C. Map showing Mount Celsius Supergroup outcrops around Kejser Franz Joseph Fjord (from Nicholson & Friend 1976). Scale bar: 10 Km.

ical Museum, Copenhagen, in 1987 (Bendix-Almgreen *et al.* 1988, 1990) provided more complete material.

Many new characters of *Acanthostega* have come to light (Clack 1989, 1992, Clack & Coates 1993, Coates 1991, Coates & Clack 1990, 1991), which have shown *Acanthostega* to be fish-like and primitive in many respects. These include retention of lepidotrichia in the tail as in *Ichthyostega*, the proportions of the radius and ulna, possession of a fish-like gill skeleton and retention of an anocleithrum and postbranchial lamina of the cleithrum. Some aspects, such as its possession of eight digits on the manus, were completely unexpected. This taxon appears to have been almost completely aquatic (Bendix-Almgreen *et al.* 1990, Coates & Clack 1990), but also to resemble other tetrapods in some features of the braincase (Clack 1992). It should provide further insight into the origin, relationships and palaeobiology of early tetrapods. It will also provide important comparisons by which to evaluate more recently recognised Devonian tetrapod material such as that from Scat Craig and Latvia (Ahlberg 1991a, Ahlberg *et al.* in press), and new material from the Tula region in Russia (Lebedev & Clack 1993) and to be described by O. A. Lebedev and M. I. Coates.

This is the first of a series of papers planned to describe the anatomy of *Acanthostega* in detail, and covers aspects of the snout, naris, choana, palate and ventral parts of the braincase, including the parasphenoid, basisphenoid and basioccipital, both from surface prepared material and from sections. It will be followed by descriptions of the skull roof, the rest of the braincase, and the axial and appendicular skeleton.

## Geological setting, palaeoenvironment and palaeoecology

The *Acanthostega* material described here derives from an outcrop on Stensiö Bjerg (Fig. 1) of the Britta Dal Formation of the *Remigolepis* Group *sensu* Nicholson & Friend (1976, see also Friend *et al.* 1983). It is regarded as Famennian in age (Bendix-Almgreen 1976) on the basis of the typical Famennian vertebrate fauna and correlation with more securely dated deposits. Precise dating by spore analysis has not so far proved possible because of the absence of suitable material.

The *Remigolepis* Group forms part of an extensive sequence of deposits from the Upper Devonian of East Greenland representing an intramontane basin. According to Nicholson & Friend (1976), the *Remigolepis* Group forms part of the Mount Celsius Supergroup and comprises the Aina Dal, Wiman Bjerg and Britta Dal Formations. Of these, the Aina Dal and Britta Dal Formations are richly fossiliferous, yielding the tetrapods *Ichthyostega* and *Acanthostega* and fishes such as the osteolepiform *Eusthenodon*, the porolepiform *Holoptychius*, the dipnoan *Soederberghia* and the placoderm *Remigolepis* (Bendix-Almgreen 1976). Associated with the *Acanthostega* material collected in 1987 were a small number of ctenacanth shark spines (J. A. Long personal communication 1992). These represent a new record for the Upper Devonian of East Greenland, but are consistent with a freshwater environment. The Britta Dal Formation deposits were formed by low-gradient rivers with meandering, vegetation-lined channels in which the above genera lived (Bendix-Almgreen *et al.* 1990).

*Acanthostega* has also been discovered on Wiman Bjerg (holotype specimen MGUH A33 Jarvik 1952, MGUH A90, MGUH f.n. 1400 Bendix-Almgreen *et al.*1988) and Celsius Bjerg (MGUH A85 Jarvik 1952). All are talus-derived specimens, but MGUH A33, A85 and MGUH f.n. 1400 may be from the Aina Dal Formation, while MGUH A90 appears from the matrix to be from the Britta Dal Formation. One specimen was also found in the Aina Dal Formation deposits on Stensiö Bjerg in 1987 (MGUH f.n.1330).

*Acanthostega* was the first Devonian tetrapod to be described in a sedimentological context (Bendix-Almgreen *et. al.* 1988, 1990). Abundant material was found in a small channel deposit on Stensiö Bjerg, preserved in point bar sediments. Other similar outcrops at this horizon also contained *Acanthostega* remains. The best articulated material is now known to derive from one small lens in this deposit, with largely isolated elements above and below it (Fig. 1). Bendix-Almgreen *et al.* (1990) interpreted the preservation as showing that the animals, primarily aquatic, lived in actively flowing rather than abandoned channels, and the articulated nature and fine preservation of some of the specimens suggested that they had not been transported far. Since their report, more articulated specimens have been discovered through preparation of the material, including limbs with digits, vertebral columns still attached to their respective skulls, and skulls to which braincase material, stapes and branchial arch elements remain connected. Further evidence of the aquatic nature of *Acanthostega* has also come to light (Clack & Coates 1993, Coates 1991, Coates & Clack 1990, 1991), adding support to Bendix-Almgreen's *et al.* (1990) interpretation of the setting.

## Materials and Methods

Most of the material to be described was collected in 1987 by the Cambridge – Copenhagen expedition (Bendix-Almgreen *et al.*1988), and belongs to the Geological Museum (University of Copenhagen) and will ultimately be housed there (MGUH VP collection). Currently, it bears field numbers (MGUH f.n.). Also included is material which belongs to the University Museum of Zoology, Cambridge (UMZC), collected in 1970 (Clack 1988), bearing the prefix T. Other early tetrapod material from

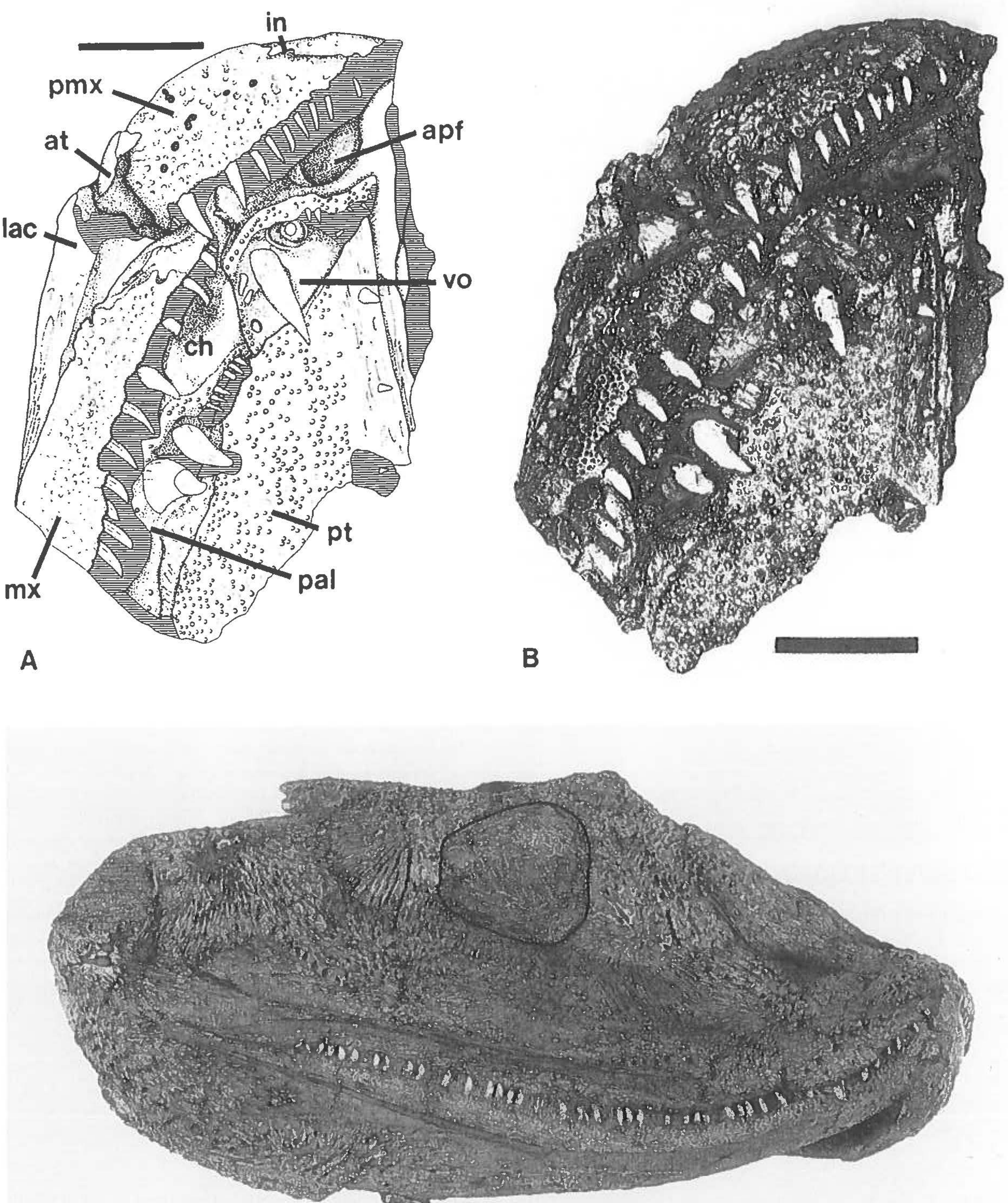


Fig. 2. *Acanthostega gunnari*. A, B: interpretive drawing and photograph of anterior palate and adjacent marginal bones of right side of MGUH f.n.1300A. C: skull of MGUH f.n.1300B in right lateral view. Scale bar: 10 mm.

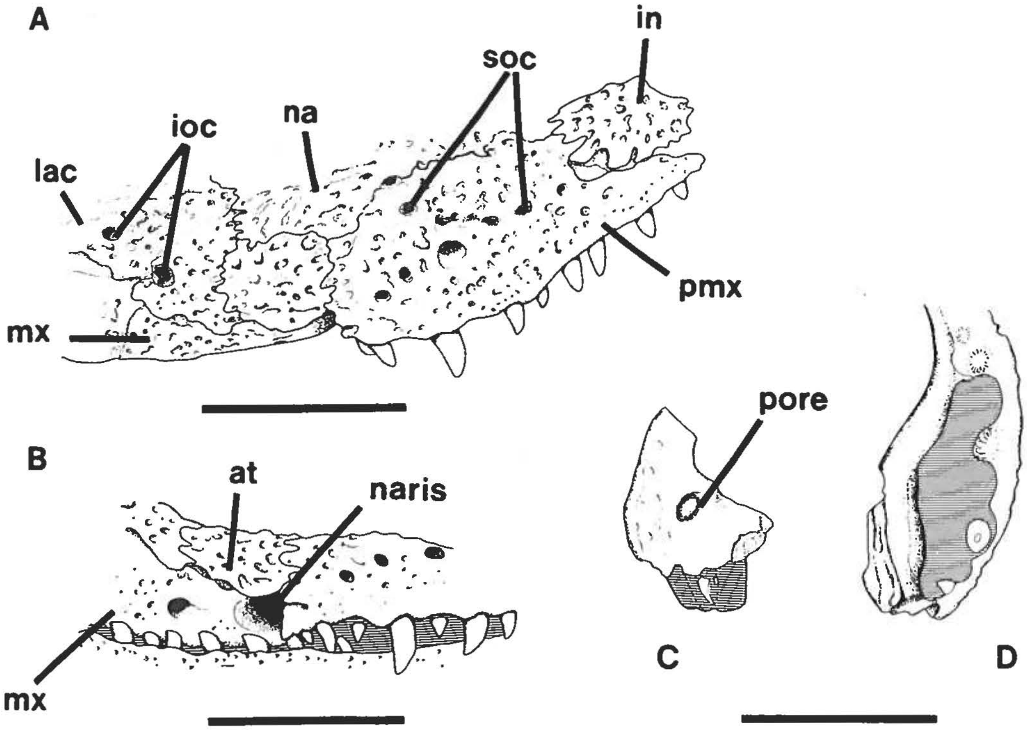


Fig. 3. *Acanthostega gunnari*. A, B: drawings of right naris of MGUH f.n.1300B in lateral and ventrolateral views. C,D: isolated premaxilla MGUH f.n.1258 (part) in posterior and ventral views. Scale bar: 10 mm.

the Natural History Museum, London, is also referred to, prefixed BMNH.

The material has been prepared by mechanical means, using pneumatic pen, dental mallet and mounted needles, or sectioned into approximately 1.5 mm slices using a Well diamond-wire saw with 0.3mm diameter wire, or a Lastec diamond-wire saw with 0.12mm diameter wire. Information comes chiefly from MGUH f.n.1227, 1300, 1305 and 1604. MGUH 1227 consists of an almost complete articulated individual (Clack 1989, 1992, Coates & Clack 1990) the skull of which has been prepared out on both sides. MGUH f.n.1300 is a complex specimen consisting of two skulls and scattered cranial and postcranial remains. The right hand side of the snout of one skull (A) has been prepared out completely to yield good information on the palate and naris, the posterior part is exposed in ventral view. The second skull (B) is preserved in three dimensions, though it is laterally compressed and a little distorted, and it lacks the otic capsules. MGUH f.n.1305 and 1604 each consist of incomplete skulls which nevertheless include braincase material. MGUH f.n. 1305 lacks the posterior part of the skull; part of it has been sectioned longitudinally, part transversely and part has been prepared in the round. MGUH f.n. 1604 lacks the snout; it has also been sectioned transversely.

# Description

## Snout and marginal bones

In this and the following sections the nomenclature is generally that which has become conventionally used to describe the skulls of early tetrapods, rather than that used for fishes. An exception is the anterior tectal, whose homology with the septomaxilla is disputed (see discussion). Included in this section are the premaxillae, maxillae, internasals (=median rostrals) and anterior tectals (?=septomaxillae).

The premaxilla, missing from the holotype, was described by Clack (1988) from an isolated element. Further specimens have now yielded more information on the dentition and sutural attachments to surrounding bones, and on the lateral line pores (Figs 2, 3). The ornament consists of deep pits of varying sizes. The lateral line canals open to the surface by a series of pores which are not easily distinguishable from ornament. The supraorbital and infraorbital canals meet in a Y-shape on the premaxilla, a condition similar to that in most sarcopterygians. In some individuals, the pits of the supraorbital canal coalesce into grooves, though separate pores are still distinguishable within them. The posterior face of the premaxilla also bore a pore, probably in the sensory canal series, present in all the specimens examined (Fig. 3C).

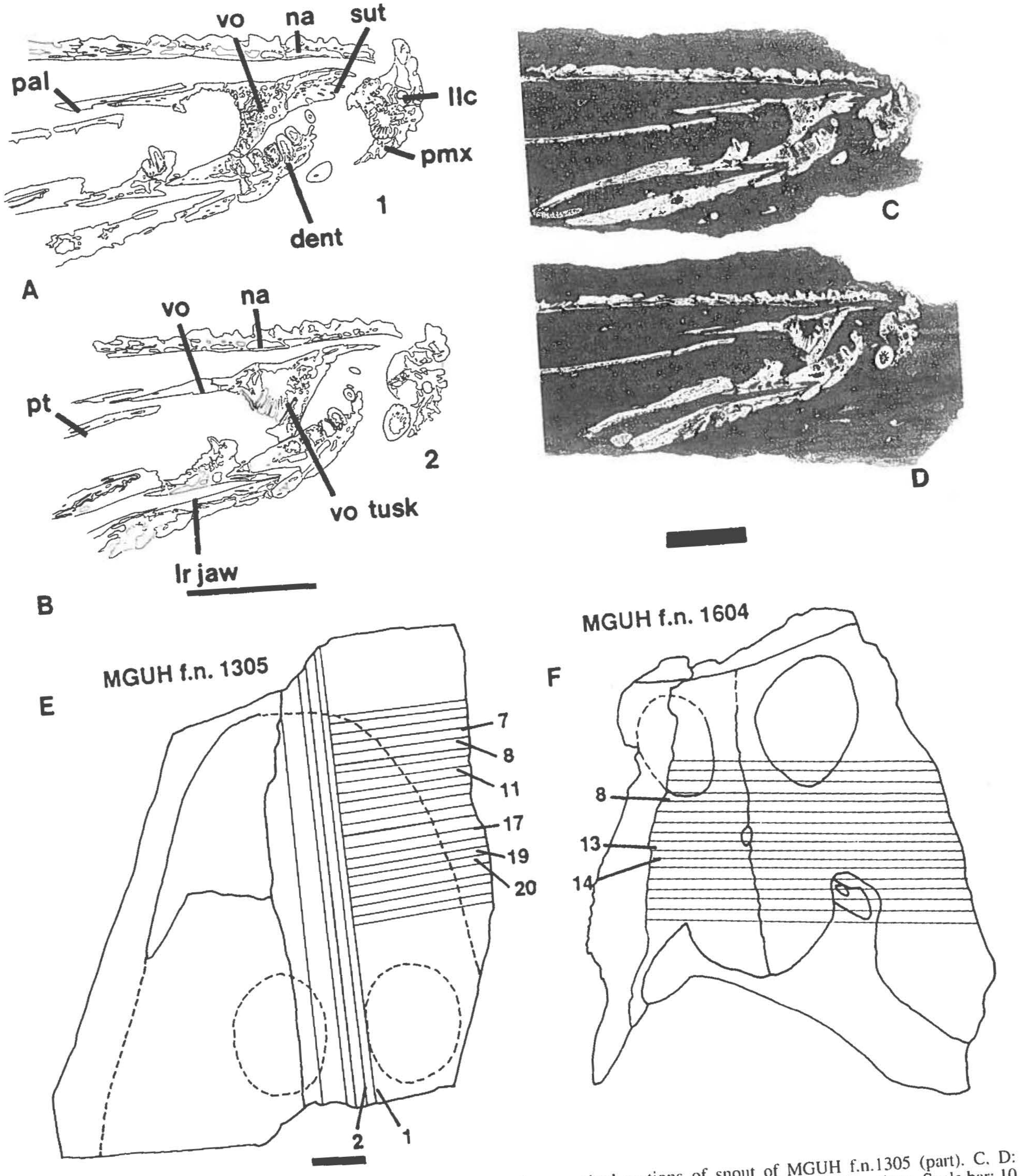


Fig. 4. *Acanthostega gunnari*. A, B: interpretive drawings of parasagittal sections of snout of MGUH f.n.1305 (part). C, D: photographs of same sections. E, F: Diagrams of MGUH f.n. 1305 and MGUH f.n. 1604 showing positions of sections. Scale bar: 10 mm.

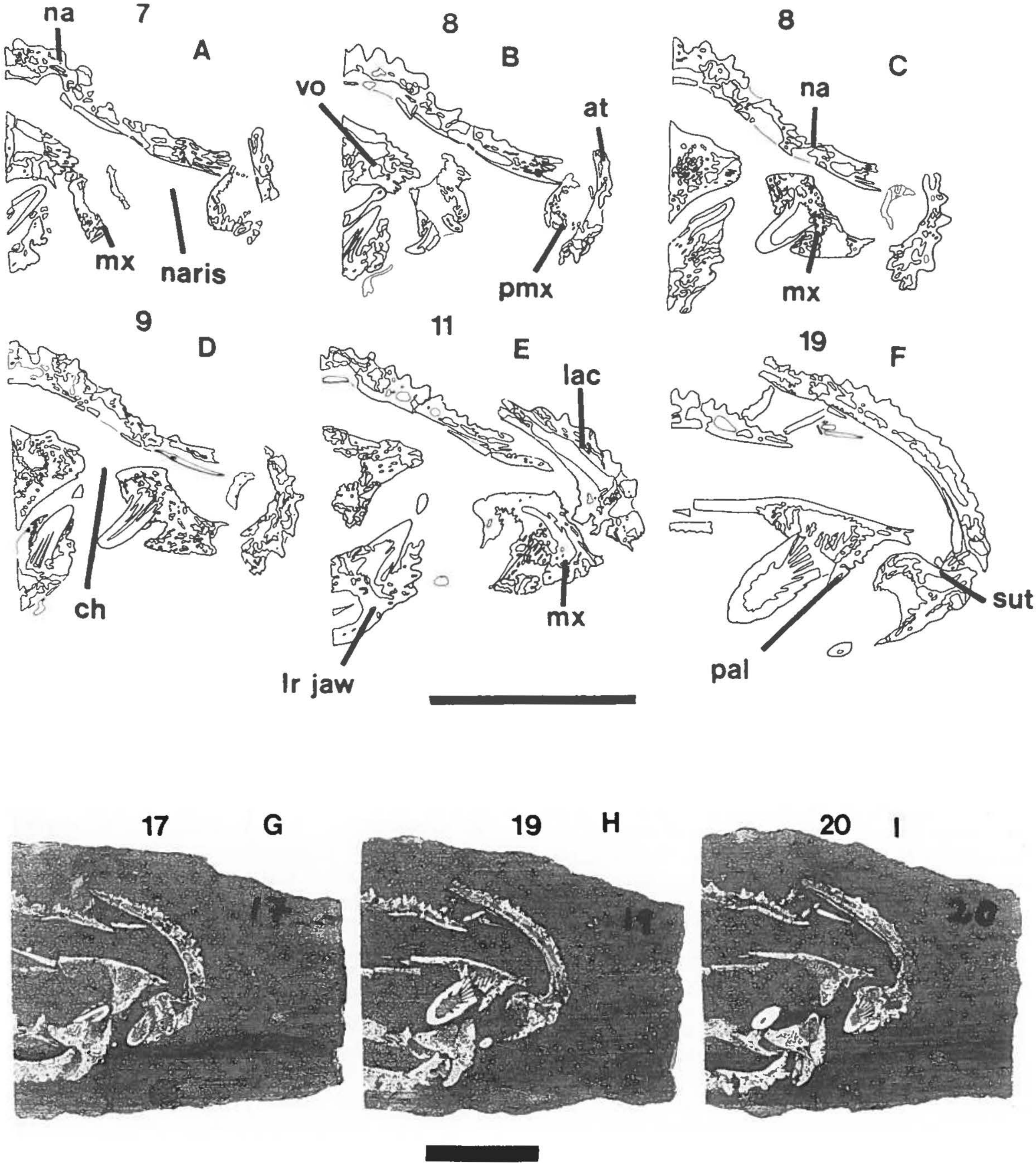


Fig. 5. *Acanthostega gunnari*. A-F: interpretive drawings of transverse sections of right side of snout of MGHU f.n.1305 (part). G-I: photographs of transverse sections of right side of snout of MGUH f.n.1305 (part). Scale bar: 10 mm

The anterior part of the bone consists of a narrow process, above which lies an embayment for one of a pair of internasal bones (Figs 2, 3, see also Clack 1988). Paired internasals are found in loxommatids, and a single one in *Ichthyostega*. Possession of internasals is a primitive character, a retention of some of the mosaic of bones which forms the snout in many early sarcopterygians. Most later tetrapods lack these bones.

The junction of the premaxilla with its fellow at the midline, and with the internasals dorsally appears smooth and uninterdigitated. The premaxilla was firmly sutured to the vomer by a process of the latter close to the midline

Fig. 6. *Acanthostega gunnari.* Isolated left vomer of MGUH f.n.1233 in dorsal view. Scale bar: 10 mm.

(Fig. 2A, B) and seen in the sections of MGUH f.n.1305 (Fig. 4).

The bone broadens posteriorly, and its posterior border is rounded. On the external, ornamented surface, there is no embayment for the naris. However, the posterior face is smooth and curved inwards, where it forms the anterior wall of the naris (Figs 2, 3C, D).

The premaxilla bears 13 teeth, increasing in size posteriorly, except for the last which is the smallest of the row. In this it resembles *Greererpeton* (Smithson 1982) and a premaxilla attributed to *Tulerpeton* from the Upper Devonian of Russia (Lebedev & Clack 1993).

A small bone, equivalent in position to the anterior tectal of *Eusthenopteron* and *Ichthyostega*, formed most of the dorsal margin of the naris. This bone is best seen in skull B of MGUH f.n.1300, but is also visible in MGUH f.n.1305. It bears no lateral-line pores (Figs 3A, B). The homologies of this bone remain in dispute. While it occupies a similar position to the anterior tectal of osteolepiforms and *Panderichthys* and may be homologous with them, its homologies with the bones of the tetrapod snout are less clear (see discussion section). Jarvik (1952, 1980) maintained that *Ichthyostega* possessed both an anterior tectal and a lateral rostral.

The maxillae found in the new material match that described by Jarvik (1952) from the holotype specimen. Ornament is generally finer on the maxilla than on other dermal skull roof bones, especially near the ventral margin. The external surface is roughly parallel-sided except anteriorly, where it meets the premaxilla via a narrow, inwardly curving process with a smooth dorsal surface, forming the ventral margin of the naris. The tip of this process is extremely thin dorsoventrally and narrow as seen in MGUH f.n.1305 and 1604d. The dorsal surface of the process may provide a contact surface for the premaxilla, but from its orientation, seems more likely to have contacted the vomer. The contact with either bone must have been minimal.

A sensory pore lies on the external surface of the process, seen in all specimens examined (e.g. MGUH f.n.1300A, Fig. 2A, B). In early tetrapods such as *Greererpeton* (Smithson 1982) and loxommatids (Beaumont 1977) the infra-orbital canal turns downwards at the anterior end of the lacrimal to run onto the anterior end of the maxilla, where it apparently terminated. This condition appears to be unique to tetrapods, and does not occur in fishes.

The sensory canal in *Acanthostega* likewise passed from the lacrimal, where it ran close to the suture with the maxilla, down posterior to the naris, onto the maxilla. Rather than terminating here as it appears to have done in later tetrapods, it may have run across below the naris to enter the premaxilla at the pore described above. There is, however, no evidence of a lateral rostral as was described by Jarvik (1980) for *Ichthyostega*.

Posterior to this, the maxilla widens to a maximum, dorsally forming a horizontal sutural surface with longitudinal striations for contact with the lacrimal. The suture with the lacrimal and jugal bones was a poorly consolidated butt joint with the result that the maxilla is frequently dislocated or missing from many skulls. This was noted by Jarvik (1980) in the holotype and second specimen. The form of this suture can also be seen in section (Figs 4, 7). Posteriorly, the maxilla sutured with the quadratojugal, contributing to the adductor fossa and preventing entry of the jugal into the jaw margin.

Its deepest point in lateral view is also its widest in ventral view. The largest teeth are found here, as is a palatal process which marks the posterior limit of the choana and sutures with the palatine. The sections of the skull of MGUH f.n.1305 (Fig. 5) show an interdigitating suture between the palatine and the maxilla at this point. On the skull of MGUH f.n.1227, there are teeth or spaces giving a total of 52, whereas on the holotype, there may be as few as 45 or as many as 49 teeth, depending on how spaces are counted. In each skull, the first three or four teeth are small and on the inwardly turned anterior process. In both, approximately the seventh to eleventh teeth are somewhat enlarged (depending whether one or two teeth were present in spaces at this point in the holotype), and the posteriormost few are very small (Fig. 11).

The naris, formed between the anterior tectal dorsally, the posterior face of the premaxilla and the anterior process of the maxilla, must have been small in life (Fig. 2C). The lacrimal made little if any contribution to its margin, and the nasal was excluded by the anterior tectal. Like that of *Ichthyostega*, the naris would have been visible in ventral view (Fig. 3, also seen crushed in section, MGUH f.n.1305, Fig. 5).

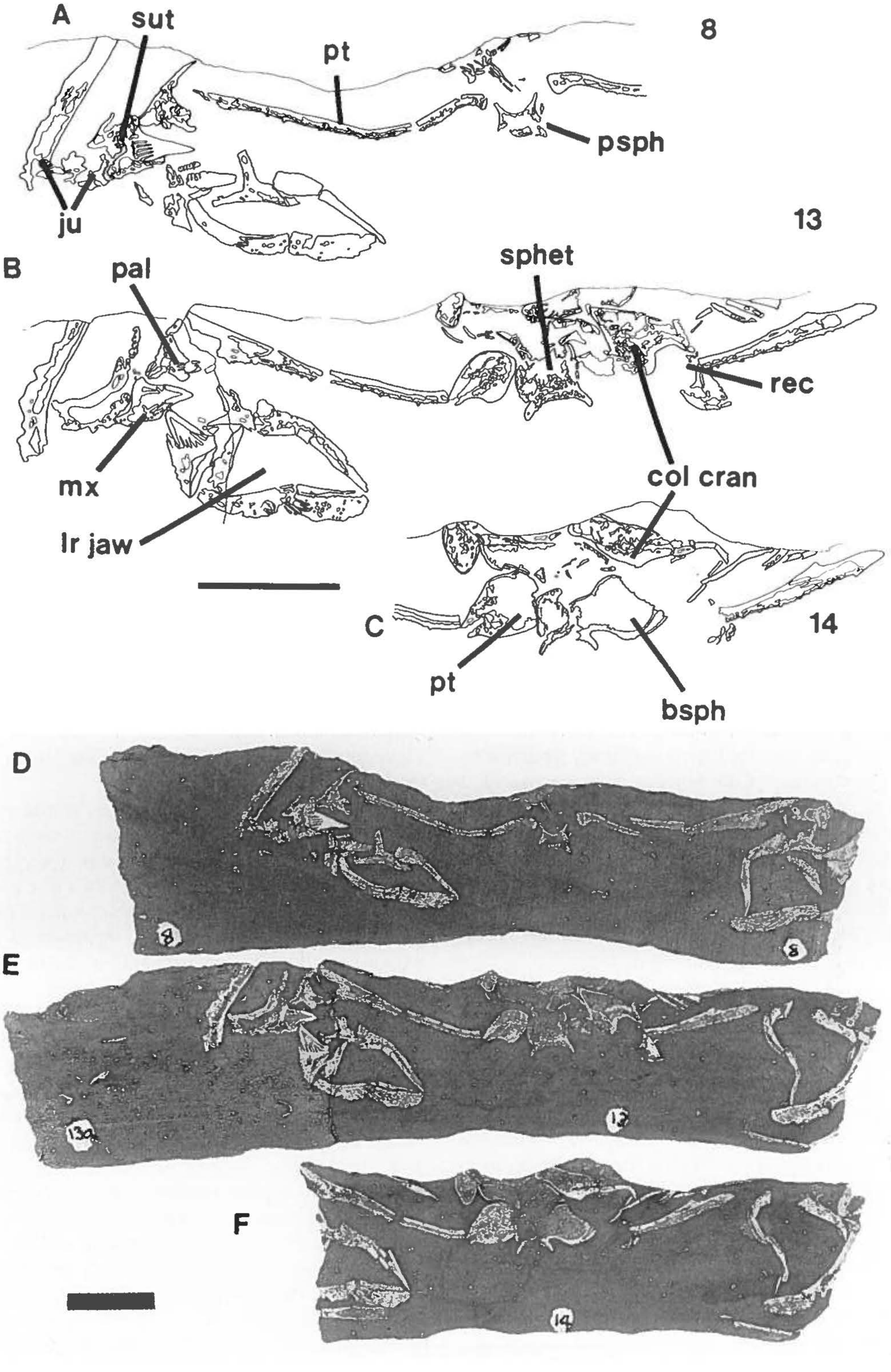


Fig. 7. *Acanthostega gunnari*. A-C: interpretive drawings of transverse sections of skull of MGUH f.n.1604. D-E: photographs of same sections. Scale bar: 10 mm.

## Palate

The ventral view of the vomer is seen in MGUH f.n.1300A (Fig. 2), the dorsal view in MGUH f.n.1233 (Fig. 6) and 1300A and in section in MGUH f.n.1305 (Figs 4, 5). Its most striking feature is the dentition, which is unlike that of other described tetrapod vomers, but resembles that of sarcopterygians such as osteolepiforms and *Panderichthys* (Vorobyeva & Schultze 1991). Laterally, a curved ridge runs around the anterior margin of the choana and passes medially, delimiting the posterior margin of an anterior palatal fossa. It bears a row of small teeth on the lingual side and a few denticles on the labial side. The row of small teeth is interrupted by a large fang and replacement pit pair. In MGUH f.n.1300A, the tip of a new tooth can just be seen in the replacement pit.

The vomer of *Acanthostega* bears an anteromedial process by which it joins the premaxilla in an interdigitating suture, seen in section and in MGUH f.n.1233 (Figs 5, 6). Posteriorly, the bone consists of a thin plate which laps over the pterygoid dorsally, forming an apparently poorly consolidated junction. Frequently, skull specimens are lacking the internasals, premaxillae and vomers, which appear to have fallen off together.

The anterior palatal fossae, formed between the vomers and the premaxillae, are paired structures separated by the midline processes of the vomers. In *Ichthyostega*, a single fossa is found here as in many sarcopterygians (e.g. *Glyptolepis* and *Eusthenopteron*, Jarvik 1980) and other early tetrapods such as loxommatids (Beaumont 1977) and *Crassigyrinus* (Panchen 1985). In *Greererpeton* (Smithson 1982), as in *Acanthostega*, the fossae are paired. They probably served to accommodate large parasymphysial fangs which lay on the dentary.

MGUH f.n.1233 shows the lateral process which sutured with the premaxilla. The sutural contact area consists of three regions, an anterolaterally facing one for the premaxilla, a more lateral one also probably for the premaxilla and a posterolaterally facing one, which may have been for the maxilla. If this interpretation is correct, *Acanthostega* would have had a maxillary – vomerine suture, as in *Ichthyostega* excluding the premaxilla from the naris. However, as mentioned above, this surface may also have contacted the premaxilla rather than the maxilla. In either case, the premaxilla would nevertheless have contributed little or nothing to the margin of the choana.

Posterior to this lies an embayed margin for the choana, bounded mesially by a series of ridges and grooves for suture with the palatine. The most mesial ridge extends forwards and mesially in an arc, gradually decreasing in height, enclosing a depression for an overlap of the palatine. The surface of this depression bears fine striations. The central part of the bone is thickened, where the teeth lie below, and many small foramina are evident. However, the surface of the bone is missing from this portion, where the bone was split prior to collection. The mesial margin where the bone overlies the pterygoid, is thin and irregular.

The tooth-bearing ridge on the vomer continues onto the palatine. It borders the choana, and passes back to run parallel to the maxilla and lateral margin of the pterygoid. As with the vomer, the row of small teeth is interrupted at the anterior end of the palatine by a large fang pair (Fig. 4). The tooth-bearing ridge of the palatine is separated from the maxilla by a conspicuous groove, seen in skull MGUH f.n.1300A.

The junction with the maxilla is achieved via a narrow overlap zone, but no strong interdigitations are evident, except at the anterior end. The junction with the pterygoid, as with the vomer, consists of a thin lamina which laps dorsally over the pterygoid without interdigitations (Figs 5, 7).

Continuing that on the vomer and palatine, a tooth-bearing ridge on the ectopterygoid runs parallel to the maxilla and pterygoid margin. As exposed ventrally, the ectopterygoid is a narrow parallel-sided bone, but like the palatine bears a medial lamina which laps dorsally over the pterygoid. Its junction with the maxilla is like that on the palatine, except that posteriorly it is contacted and overlain by a narrow lamina from the jugal (Fig. 7). At about the middle of the row of small teeth, are two somewhat larger ones, as seen in MGUH f.n. 1300A. These appear to be equivalent to the fang and pit pairs on the other marginal palatal bones.

The pterygoid forms most of the ventral palatal surface, and as in primitive tetrapods and in most sarcopterygian fishes there are no significant interpterygoid vacuities in the midline. The pterygoids meet closely, but without suturing, for about half the distance between their tips and the basal articulation. Posterior to that, they separate to allow the parasphenoid of the braincase to fit between them.

Almost the whole of the ventral surface of the pterygoid is denticulated, the main exception being along the midline, where anteriorly the surface is longitudinally striated, and more posteriorly where a pronounced and smooth ridge forms a rolled edge to the bone running beside the parasphenoid (Fig. 7). The denticle field continues posteriorly, tapering to a point along the quadrate ramus. The denticles bordering the adductor fossa are somewhat enlarged. In MGUH f.n.1300A the enlarged denticles on the medial margin are an artefact of preservation, and are not seen in any other specimen.

Anteriorly the pterygoid is a thin bone, less than one millimetre thick, except for the thickened edge at the midline, and the region surrounding the basal articulation (Fig. 7). As it passes posteriorly towards the adductor fossa, it thickens significantly, to form the substantial though narrow bar of the quadrate ramus. There is no descending flange to the quadrate ramus as in anthracosaurs. In this *Acanthostega* resembles *Ichthyostega*; in both, the anterior and mesial margins of the adductor fossae are characteristically rounded in outline.

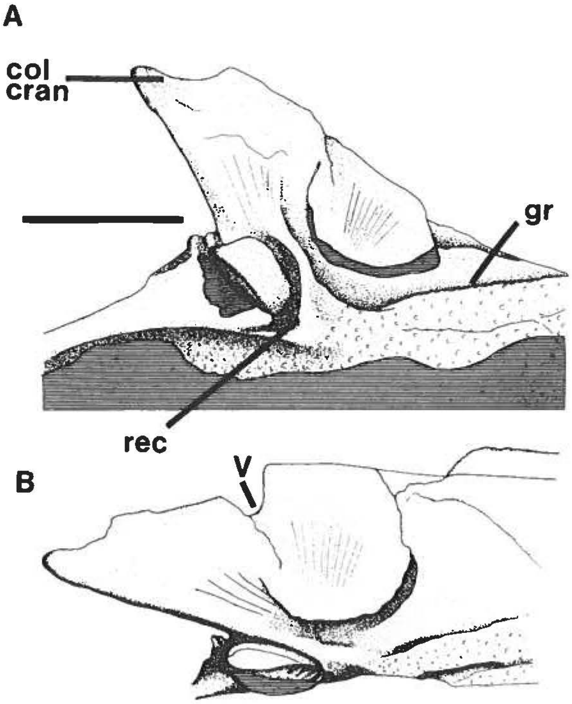


Fig. 8. *Acanthostega gunnari.* A, B: isolated (epi)pterygoid complex of MGUH f.n.1258 (part) in approximately ventral and ventrolateral views. Scale bar: 10 mm.

The dorsal surface of the pterygoid can be seen in specimen T1300j (skull C, Clack 1988). Despite the poor preservation, there appear to be no obvious muscle scars, except posteriorly where a ridge runs along the thickened quadrate ramus.

The pterygoid and the endochondral component of the palatoquadrate, the latter usually called the epipterygoid by tetrapod workers, but probably more correctly the metapterygoid (Gardiner 1984), appear co-ossified in all specimens whether viewed in the round or in section. In regions where its identity is in doubt, it will be referred to as the (epi)pterygoid. In all specimens to show the quadrate ramus, the (epi)pterygoid is marked by a strong groove and ridge on its medial surface where the thickened horizontal ramus, bearing the posterior end of the denticle field and muscle scars, is separated from the very thin vertical ramus, but this is not a sutural line (Figs 8, 10). A similar groove and ridge was described by Smithson (1982) in *Greererpeton* as supporting the ventral margin of the stapes, and as marking the boundary of the pterygoid with the epipterygoid. Both may also be true of *Acanthostega*. The vertical component also bears numerous fine striations on its mesial surface.

Parts of the complex which are clearly endochondral (the epipterygoid) form a thick, vertical columella cranii at the level of the basal articulation. It meets the skull roof in crushed specimens, though probably did not in life. Sections of specimen MGUH f.n.1604 (Fig. 7) and an isolated pterygoid from MGUH f.n.1258 (Fig. 8) show a round blunt termination to the process, covered with perichondral bone.

At the base of the columella cranii lies the socket for the basal articulation, formed at least in part by the endochondral epipterygoid. As noted above, the junction between dermal and endochondral components has been co-ossified in all specimens examined. MGUH f.n.1258 best shows the structure of the socket. The anterior part is formed where the thickened midline ridge of the pterygoid is drawn out into a cone-shaped process whose termination forms the anterior face of the socket (Fig. 8). The ventral rim of this process has been eroded away in MGUH f.n.1258, but it is represented in MGUH f.n.1227 (Fig. 9). MGUH f.n.1258 shows that this face was separated by a groove from the mesial face, shaped as a semicircle and slightly convex in profile. This in turn was separated by a groove from a buttress forming the posterior margin of the socket, both components apparently formed from the epipterygoid. MGUH f.n.1227 shows a groove which may define the ventral limit of the epipterygoid component at the base of the socket, but it is not seen in MGUH f.n.1258. The socket would have had two clearly defined surfaces, presumably matching those on the basal process of the braincase.

At the level of the articulation, the parts of the vertical ramus posterior to the columella cranii are orientated almost at right angles to the braincase, thereafter the ramus curves around to become almost parallel to it. A notch for the exit of the mandibular ramus of the Vth nerve marks the dorsal margin of the vertical ramus just posterior to the columella cranii (Fig. 8).

The dorsal margin of the vertical ramus did not suture with the dermal skull roof, though a buttress met the squamosal at its junction with the tabular. This dorsal margin can be seen in MGUH f.n.1300B, which also shows a flange running down the posterior margin of the squamosal, which the vertical ramus met but with which it did not suture (Fig. 10, Clack 1992).

No specimen shows the quadrate clearly. The best exposed are those associated with specimen MGUH f.n.1300B, in which part of the posterior surface can be seen (Fig. 10 qu). The specimen is slightly disarticulated, but the dorsal exposure of the quadrate appears to have been very limited. The mesial overlap area for the quadrate ramus has been uncovered to a small degree. Its junction with the pterygoid was apparently fairly loose, and it was not sutured to the dermal bones of the cheek at the quadratojugal or preopercular. The articular surface is still in contact with the lower jaw and cannot be described. All specimens which retain the palate in association with the skull roof also retain the lower jaws, suggesting a firm attachment in life.

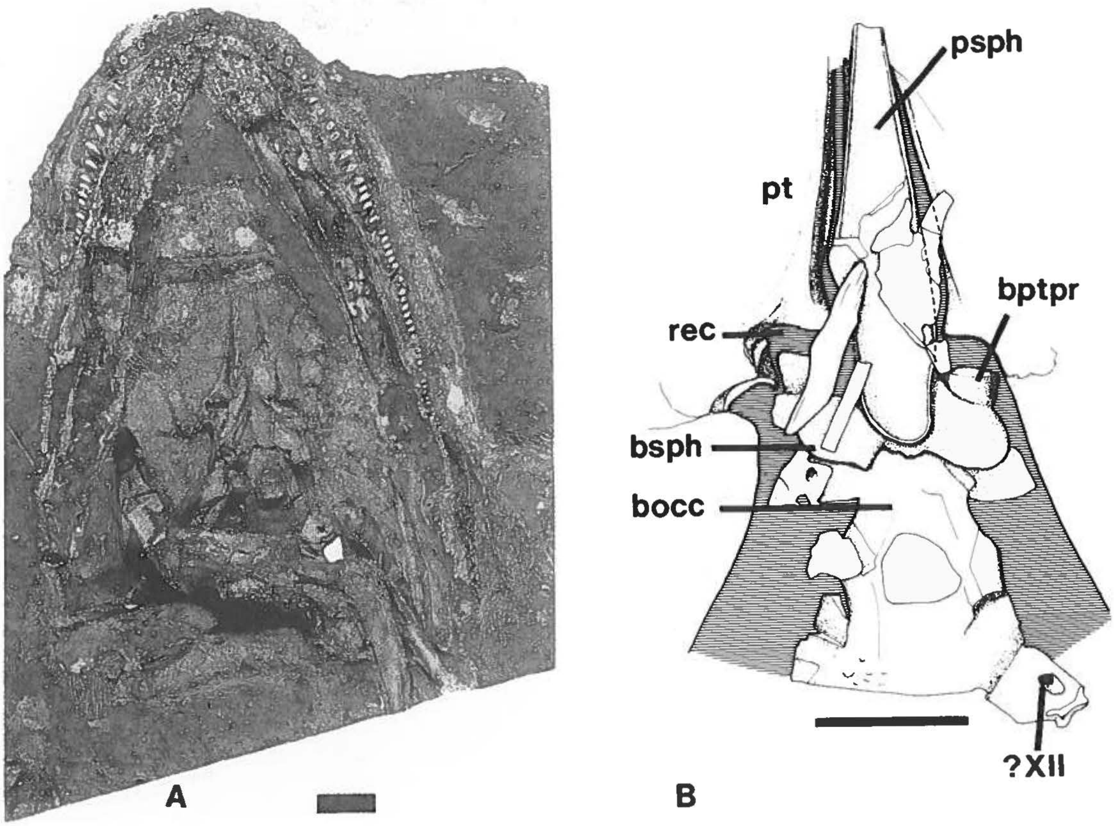


Fig. 9. *Acanthostega gunnari*. A: photograph of skull of MGUH f.n.1227 in ventral view. B: interpretive drawing of braincase and parts of palate of MGUH f.n.1227 in ventral view. Scale bar: 10 mm.

## Braincase

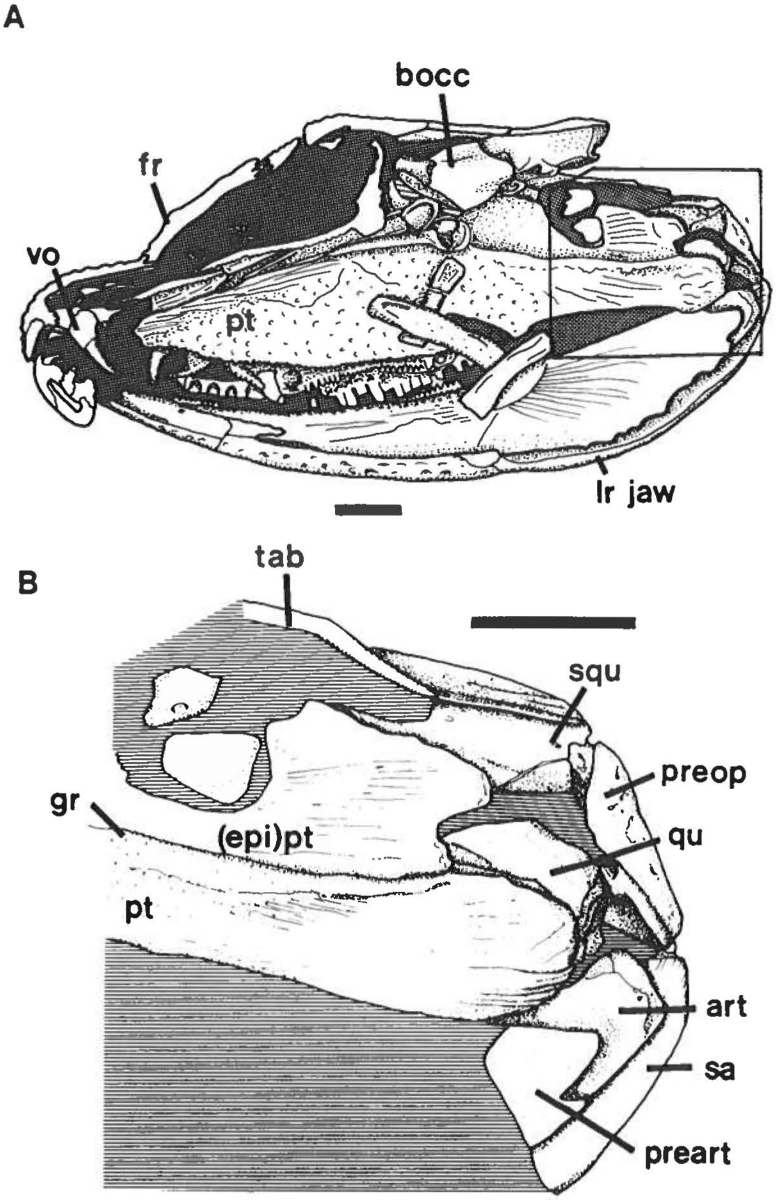
The braincase is clearly divided into two units ventrally, though there is no evidence of any gap or hinge mechanism between them. The sphenethmoid and otic capsule are, however, co-ossified dorsally. The anterior portion, consisting of sphenethmoid, basisphenoid and parasphenoid forms one unit, loosely united to the posterior basioccipital. The basioccipital has been lost from a number of specimens, and was poorly incorporated into the rest of the braincase. The otic capsule forming a third, posterodorsal unit, was only loosely attached to the basioccipital, but was continuous with the dorsal region of the sphenethmoid. Only the ventral parts of the braincase will be described here. Descriptions of parts of the otic capsule can be found in Clack (1992).

The parasphenoid forms a conspicuous feature of the ventral view of the braincase (Figs 9, 11, Clack 1988). An elongated tear-drop shaped region is demarcated by sharp ridges and forms the anterior portion, concave in cross-section and denticulated in some specimens. It reaches from the point at which the pterygoids meet, to a level just behind the basal articulation.

In section, the parasphenoid and basisphenoid appear firmly co-ossified, raising some doubt about how much each contributes to the ventral parts of the anterior braincase (Fig. 7). Lateral 'wings' from this region just lap over onto the basioccipital, closing but not completely sealing the ventral cranial fissure, but it is not clear whether the wings are formed by the basi- or parasphenoid (Fig. 9). In early tetrapods such as *Crassigyrinus*, *Eoherpeton* and the embolomeres, it is the parasphenoid which is produced into the wings underlying the basioccipital, and there is often a gap between the basisphenoid and basioccipital, floored only by dermal bone (Clack & Holmes 1988). In *Eusthenopteron* (Jarvik 1944), the posterior margin of the parasphenoid is more obvious, and it seems clear that it possessed laminae partly covering the basisphenoid, but not the basipterygoid processes, in addition to its dental plate area.

The anterior and dorsal faces of the basipterygoid processes cannot be seen fully in any specimen, but it is clear from 3-dimensional specimens and sections that they had a synovial joint surface as seen in other early tetrapods. The complex shape of the pocket in the epipterygoid which housed the processes suggests that their articular faces were also complex. The processes were separated

Fig. 10. *Acanthostega gunnari*. A: drawing of suspensorial region of MGUH f.n.1300B in medial view. B: sketch of MGUH f.n. 1300B in medial view, region shown in A in box. Skull has been sectioned in the midline; stipple shows matrix. Scale bar: 10 mm.



from the rest of the basisphenoid by shallow grooves, which presumably carried the internal carotid arteries.

The basioccipital is known from four specimens; MGUH f.n.1227, 1300A and B and UMZC T1300a-c (skull A, Clack 1988). It is relatively long compared with those of other tetrapods, and more reminiscent of *Ichthyostega* and fishes. It lined the notochordal tunnel ventrally, also as in *Ichthyostega* and fishes. The ventral surface forms distinct angles with the lateral walls, as in *Eusthenopteron* (Jarvik 1980). The side-walls have been crushed ventrally in MGUH f.n.1227, allowing some of their features to be seen. Most conspicuous of these is a posterodorsal wing penetrated by a large foramen on the morphological left side. Comparative studies of the embryology of recent tetrapods suggests that this was probably for a branch of the hypoglossal nerve. Anteriorly, on the morphological right side is another foramen which is less easy to interpret. It may be a separate element which bears this foramen – other unidentified elements perforated by foramina are present associated with the braincases of MGUH f.n.1227 and MGUH f.n.1300B.

# Discussion

*Acanthostega* has proved to be the most primitive and fish-like tetrapod so far discovered. In addition to the

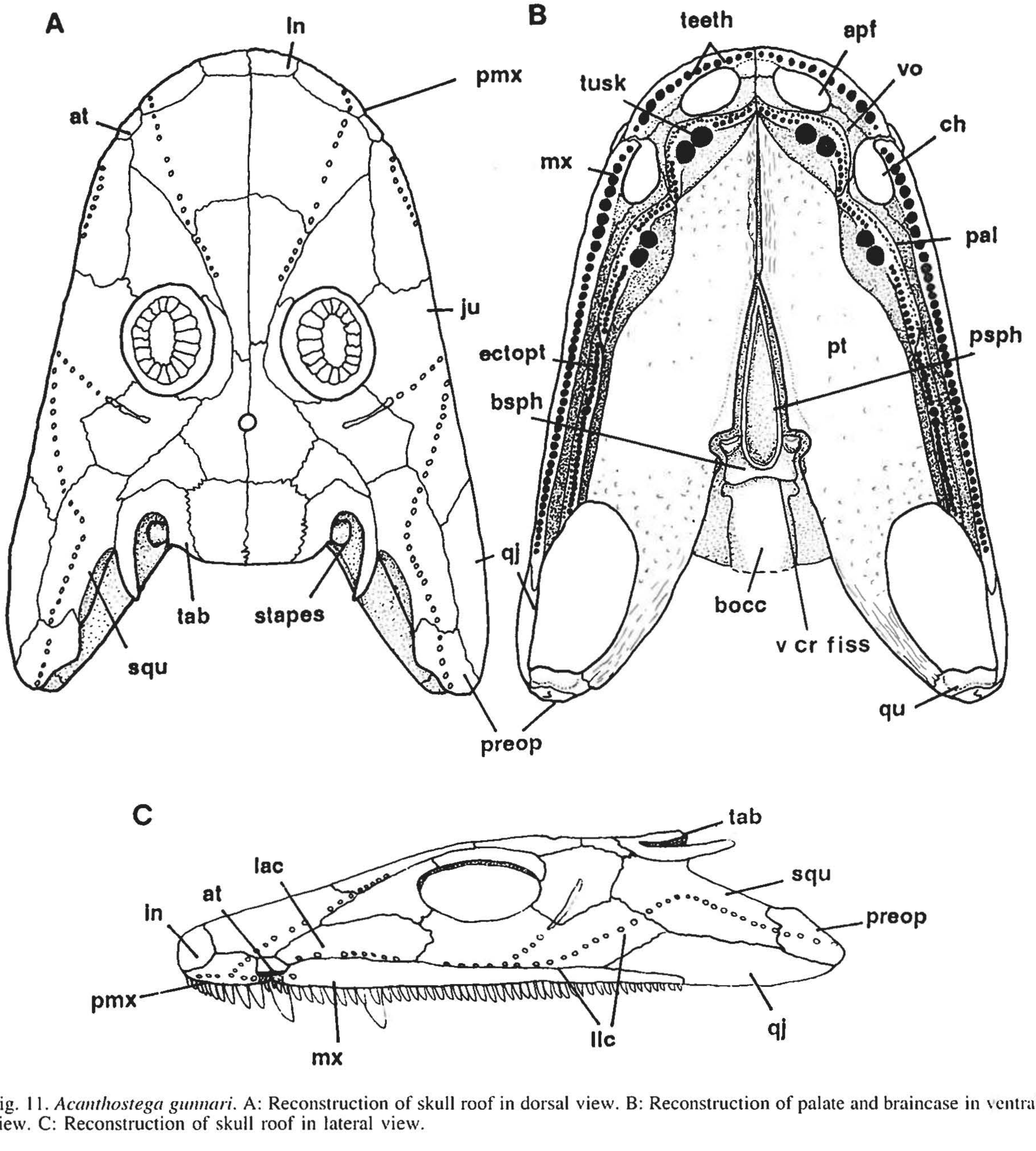


Fig. 11. *Acanthostega gunnari*. A: Reconstruction of skull roof in dorsal view. B: Reconstruction of palate and braincase in ventral view. C: Reconstruction of skull roof in lateral view.

primitive characters already described in the limbs, pectoral girdle and hyobranchial apparatus, we can add features of the snout, palate and braincase. Of particular interest are the dentition of the palate, the form of the parasphenoid, the structure of the external and internal narial openings referred to in this paper as naris and choana, respectively (see, however, Bjerring 1989, 1991), and the condition of the ventral cranial fissure of the braincase.

## Palatal dentition and parasphenoid

The palatal dentition and parasphenoid are unlike those of any previously described tetrapod. However, a similar arrangement of teeth has been found on an isolated premaxilla/vomer specimen attributed to *Tulerpeton*, a Devonian tetrapod from Russia (Lebedev & Clack 1993), and on the palate of *Crassigyrinus* (BMNH 30532; Clack in press). Panchen (1985) interpreted the vomers as mis-

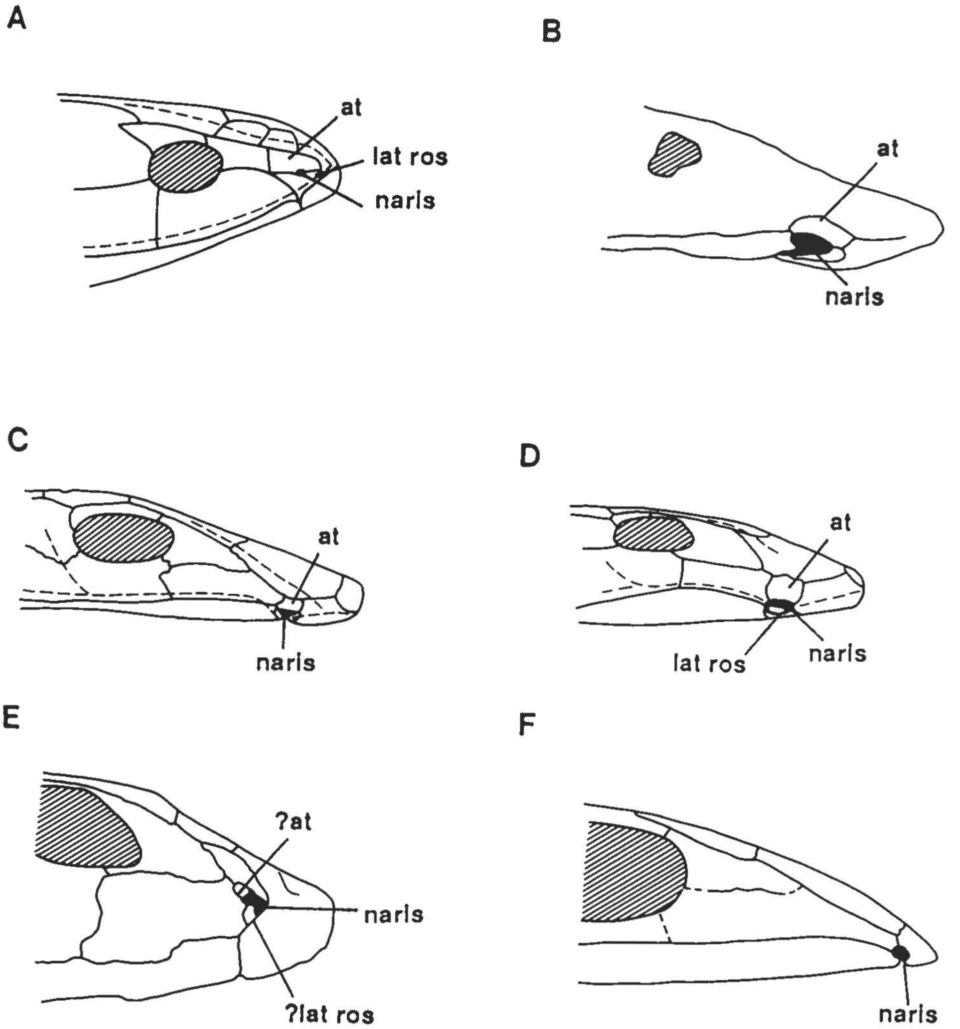


Fig. 12. Lateral views of snouts of sarcopterygian fishes and early tetrapods to show external naris, teeth omitted for clarity. A: *Eusthenopteron* (from Jarvik 1980). B: *Panderichthys* (from Vorobyeva & Schultze 1991). C: *Acanthostega*. D: *Ichthyostega* (from Jarvik 1980). E: *Crassigyrinus* (from Panchen 1985). F: *Proterogyrinus* (from Holmes 1984). Dashed line: course of lateral line canal.

sing on this specimen, but further inspection reveals that they are present, but were described as palatines. The author and P. E. Ahlberg are preparing a review of lower tetrapod jaws and dentition, in which the implications of this will be discussed.

No other tetrapod has a parasphenoid like that of *Acanthostega*, but it resembles closely some, though not all, specimens of *Eusthenopteron* (Natural History Museum, Stockholm Specimen no. P6849A) and *Megalichthys* (S. M. Andrews personal communication 1989), except that unlike the fishes, there is no open hypophysial fenestra. The parasphenoid of *Ichthyostega* has a similar outline, but appears to be neither concave nor denticulated, and some specimens show an open hypophysial fenestra. In the latter respect, therefore, *Ichthyostega* appears to be more primitive than *Acanthostega*, since a closed fenestra is otherwise a consistent feature of tetrapods.

The form of the naris and choana and the persistance of the ventral cranial fissure are of considerable theoretical interest because of the attention these areas have received in debates about the origin and relationships of tetrapods. They will therefore be treated in some detail.

## Naris

The form of the naris and choana have both been critical to the recent debate about whether tetrapods are more closely related to dipnoans or osteolepiforms (especially Rosen *et al.* 1981, Panchen & Smithson 1987). The form

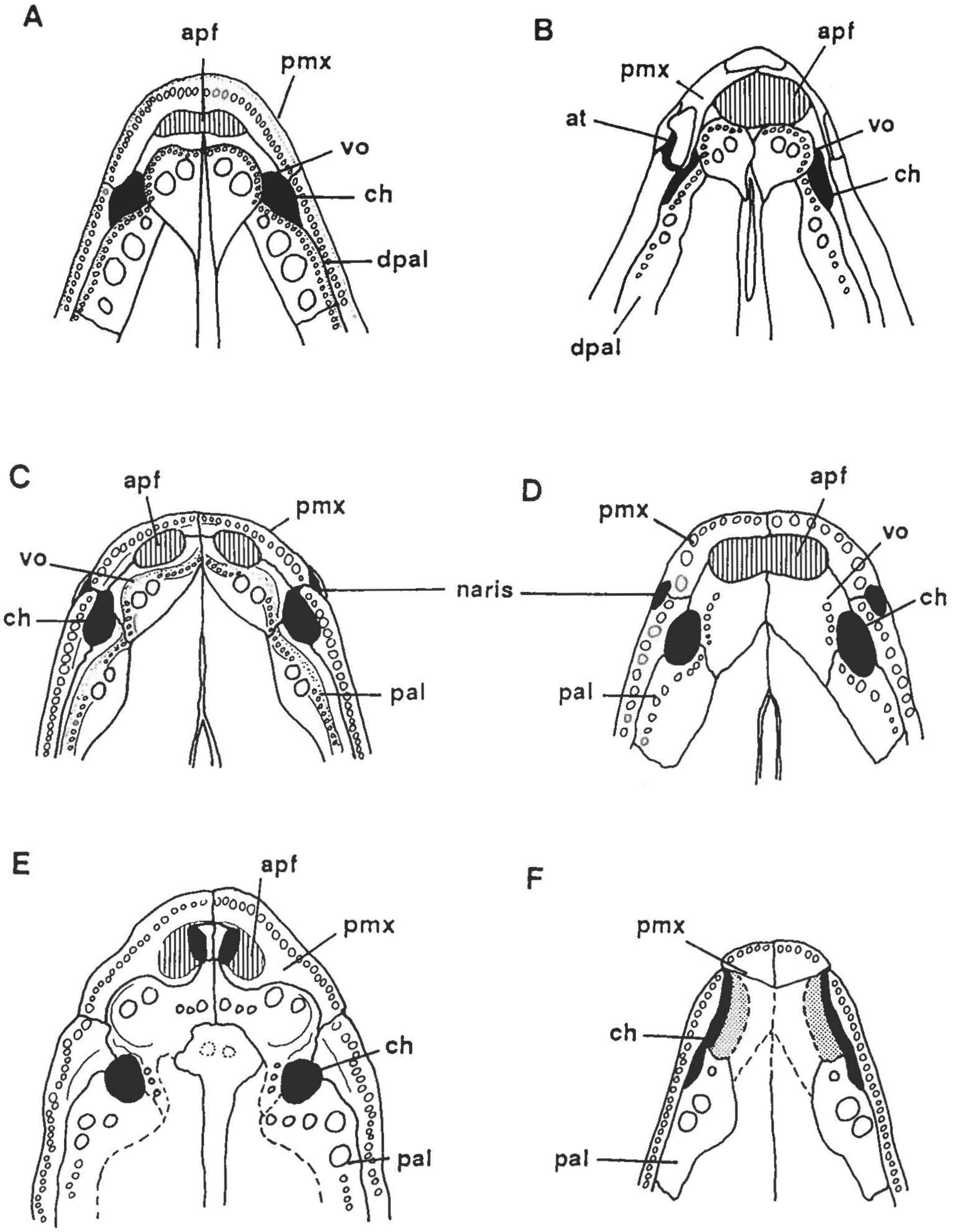


Fig. 13. Palates of sarcopterygian fishes and early tetrapods to show choanae. A: *Eusthenopteron* (from Jarvik 1980). B: *Panderichthys* (adapted from Vorobyeva & Schultze 1991). C: *Acanthostega*. D: *Ichthyostega* (from Jarvik 1980). E: *Crassigyrinus* (from Clack in press). F: *Proterogyrinus* (modified from Holmes 1984). Solid black: choana; hatch: anterior palatal fenestra; mechanical stipple: unknown extent of choana in *Proterogyrinus*.

of the naris in *Ichthyostega* in particular has been used in both of the above reviews to support the respective favoured hypothesis. To summarise briefly: Rosen *et al.* (1981), who favoured the dipnoans as the closest sister-group to tetrapods, regarded *Ichthyostega* as primitive in possessing a naris low on the snout (Fig. 12D), and proposed that its position was homologous to that in dipnoans. They interpreted the naris as separated from the choana "only by an internal prong of the maxilla" (Rosen *et al.*1981 p. 196), maintaining that the premaxillary – maxillary contact had been "breached" when, as they believed, the choana migrated onto the palate. Their belief that this had occurred forced them to reject Jarvik's (1980) interpretation of the course of the infra-orbital lateral line canal beneath the naris. They consequently predicted that the lateral rostral (Fig. 12D) which Jarvik described "does not exist" (Rosen *et al.* 1981 p. 196).

By contrast, Panchen & Smithson (1987), who favoured the osteolepiforms as closest sister-group to tetrapods, agreed with Jarvik (1980) that *Ichthyostega* represented a derived or specialised state in the low position of the naris, and were prepared to accept both the course of the lateral line canal and the existence of the lateral rostral as described by Jarvik. They also emphasised, as Jarvik had done, that the premaxillary – maxillary junction was not breached in *Ichthyostega*. As Jarvik described, and as shown by the cast of specimen MGUH A55, there is a sutural contact between the premaxilla and maxilla, in addition to a further suture between the premaxilla and vomer, which excludes the premaxilla from the choana (Fig. 13D). Although the naris is ventrally placed on the snout, it is still separate from the choana.

Panchen & Smithson (1987) viewed *Ichthyostega* and dipnoans as convergent in the low position of the naris. They took *Eusthenopteron* as their representative osteolepiform, and viewed the relatively high position of its naris as being that which is primitive for tetrapods (Fig. 12A). They found a similar condition in *Crassigyrinus* (Fig. 12E), and suggested that this exemplifies the naris of a truly primitive tetrapod, and that the condition represents a synapomorphy between the groups.

In 1985, Panchen had used the naris of *Crassigyrinus* to point out the inadequacy of cladistic methodology to resolve disputes about polarity of characters in certain circumstances. He showed elegantly that the choice of outgroup in such a debate determined the sister-group relationship which was favoured. Using dipnoans as an outgroup suggested that *Ichthyostega* was the most primitive tetrapod, whereas using *Eusthenopteron* as an outgroup suggested that *Crassigyrinus* was the more primitive. Conversely, using *Ichthyostega* as the representative tetrapod suggested dipnoans as the sister-group, while using *Crassigyrinus* as the representative tetrapod suggested that osteolepiforms were closer. Thus the argument could be completely circular. Parsimony analysis could not arbitrate on the issue as an equal number of characters could be found on each side. Though he was unable to resolve this argument in 1985, Panchen & Smithson (1987) took the view that *Crassigyrinus* is indeed primitive with respect to the naris.

Further complications in this argument arise when it is realised that the naris of *Crassigyrinus* is known from only two specimens, both of which are difficult to interpret. There are three possible positions for the naris if the holotype specimen is considered, though Panchen (1985) eventually rejected two of these interpretations. However, although the snout of *Crassigyrinus* appears unusual among tetrapods in possessing both an anterior tectal and a lateral rostral as in osteolepiforms (Fig. 12 E), the position of the naris remains in doubt.

The present information on *Acanthostega* may help to resolve some of these problems. In *Acanthostega*, as in *Ichthyostega* and also the osteolepiform *Panderichthys rhombolepis*, the naris is low on the snout (Fig. 12C). This position is probably correlated with possession of a dorso-ventrally flattened skull, but as I have argued elsewhere (Clack 1988), this shape is probably primitive for tetrapods. In *Acanthostega* a lateral line pit on the posterior end of the premaxilla matches a similar pit on the anterior end of the maxilla, suggesting continuation of the lateral line canal below the naris. There is no evidence in *Acanthostega* of a lateral rostral, but the condition reinforces Jarvik's view of the course of the lateral line, and argues against the position held by Rosen *et al.* (1981). If my interpretation of the lateral line canal is accepted, the course was not breached by the migration of the choana. On the other hand in *Acanthostega*, as in the early embolomere *Proterogyrinus* (Holmes 1984), the premaxillary – maxillary contact was unsutured and could be considered "breached", which might lend support to Rosen *et al.*'s (1981) view (Figs 12F, 13F).

*Panderichthys rhombolepis* has recently been considered as the sister-group for tetrapods (e.g. Gardiner 1980, Schultze & Arsenault 1985, Schultze 1986, Ahlberg 1991b). It is usually regarded as an osteolepiform in the family Panderichthyiidae (Vorobyeva 1973, Schultze & Arsenault 1985). Little information has been available about this form until recently, and the paucity of published information was probably the reason it was not considered in detail by either Rosen *et al.* (1981) or Panchen & Smithson (1987), in the debate about the relationships of tetrapods. Since their reviews, however, more information has come to light (Vorobyeva & Schultze 1991, Ahlberg 1991b), and I have been able to examine the material personally. Vorobyeva & Schultze cite a number of characters which *Panderichthys rhombolepis* shares uniquely with tetrapods, and I accept their hypothesis of a close relationship between the two. It provides an alternative outgroup by which to polarise characters of early tetrapods such as the position of the naris.

The external naris of *Panderichthys* is single as in other osteolepiforms, and like them, bounded by an anterior tectal and a lateral rostral. In *P. stolbovi*, Vorobyeva (1971) clearly figured the lateral line pits of the infraorbital canal (Figs 12B, 13B). However, correlated with a flattened skull shape, a character it shares with tetrapods, the external naris is low on the snout. The foramen for the naris is situated mainly within the premaxilla, unlike the condition in most early tetrapods, but like for example *Acanthostega* and *Proterogyrinus*, the premaxilla and maxilla meet but do not appear to suture (Vorobyeva & Schultze 1991).

From this reference point then, the low position of the naris of *Acanthostega*, *Ichthyostega* and *Proterogyrinus* would also represent the primitive condition. This condition is also found in the Devonian tetrapod material from Russia, mentioned above, so that a picture begins to build up in which this condition was both the most widespread and the earliest among tetrapods. These may not be rigorous arguments for judging polarity, but they are intuitively convincing.

A more convincing argument may be made following the realisation that it is not the position *per se* of the naris on the snout that is critical, but the form of the contact between the maxilla and premaxilla. In each of the fish *Eusthenopteron* and *Panderichthys* and the tetrapods *Ichthyostega*, *Acanthostega* and *Proterogyrinus* (Figs 12A-D & F) these bones meet laterally only by means of narrow processes which do not suture. The position of the naris in the fish is determined by the form of the lateral rostral, and in the three above tetrapods this bone is reduced or lacking, leaving the naris larger than in the fish and lower on the snout. In *Crassigyrinus*, the maxilla and premaxilla are massively sutured, which is not comparable to that in *Eusthenopteron*, and is most plausibly a derived condition.

## Choana

*Ichthyostega* does appear to be derived in the complete exclusion of the premaxilla from the choana (Fig. 13D). In osteolepiforms including *Panderichthys rhombolepis* (Vorobyeva & Schultze 1991), the premaxilla forms a substantial part of the lateral and anterior margins of the choana (Fig. 13 A-B), a condition which may therefore be regarded as primitive for tetrapods. In *Ichthyostega*, however, the maxilla and vomer meet in an interdigitating suture which can be seen in the cast of specimen MGUH A55.

The condition in other early tetrapods is less clear-cut. In *Acanthostega (*Fig. 13C*)*, the premaxilla clearly bears a sutural contact for the vomer, and the vomer can be interpreted as showing a sutural contact for the maxilla. However, the maxilla bears no clear evidence of a sutural contact with premaxilla, and only doubtfully with the vomer.

A survey of other early tetrapods revealed that in many, the relevant anatomy was unknown, and that where it was known, the premaxilla did not contribute much, or even at all, to the margin of the choana. For example, in the early anthracosaurs *Proterogyrinus* (Holmes 1984) and *Eoherpeton* (Smithson 1985), the vomers are unknown, and in *Eoherpeton* the ventral surface of the maxilla is likewise unknown, so that the margin of the choana in each is restored (Fig. 13F). Carroll (1970) restored *Gephyrostegus* with the premaxilla contributing to the choana, but from the specimen drawings, the material provides little justification for doing this. In loxommatids (Beaumont 1977), the choana of *Megalocephalus* is restored with the premaxilla making a point entry into the choana, while the specimen drawing of British Geological Survey specimen number G.S. 28319 shows it just excluded by maxillary – vomer contact. In *Baphetes planiceps*, the specimen drawing of the holotype, BMNH R4056, by Beaumont shows the premaxilla excluded, while in *Baphetes kirkbyi* a specimen drawing of HM G.15.70 shows a point entry.

In *Greererpeton* (Smithson 1982), there was a point entry by the premaxilla into the choana, while in the enigmatic *Caerorhachis* (Holmes & Carroll 1977), the ventral parts of the premaxilla are unknown and the margins of the choana are restored. Both these animals are considered to be related to temnospondyls, though further study may prove otherwise. *Dendrerpeton*, a true temnospondyl, is shown by both Carroll (1967) and by Milner (1980) as having a point entry of the premaxilla into the choana. Recent investigations (Clack in press) of the palate of *Crassigyrinus*, BMNH 30532, show that the premaxilla was excluded from the choana by a long and interdigitating suture with the vomer (Fig. 13E), as in *Ichthyostega*.

The polarity of this character among tetrapods as well as its condition among many of them thus remains uncertain. If a maxillary – vomer contact were after all the primitive condition, it would have relevance for the debate over whether the choana were derived by migration from the wall of the snout. The premaxillary-maxillary contact may be unsutured or even lacking among early tetrapods, but it could have been "breached" without breaking the bridge between the naris and choana, if the maxilla remained in contact with the vomer.

The naris of *Acanthostega* was very small in life (Fig. 12 C), smaller than in any other tetrapod except its contemporary *Ichthyostega*. It is also believed (Coates & Clack 1991) that *Acanthostega* breathed using internal gills in addition to lungs, as do modern lungfishes. This raises the question of whether the nose was involved with breathing in this animal. There is a superficial correlation to be found among modern vertebrates: in those which retain the use of gills (internal or external) air intake is via the mouth, and loss of gills is associated with narial breathing (E. L. Brainerd, personal communication 1992). This may be a coincidental association, or related to paedomorphism, perhaps reflecting the primitive condition in these animals. Presumably, the osteolepiforms took in air via the mouth, and this can be assumed to be the primitive condition for early tetrapods. Without evidence to the contrary, such as an enlarged naris, the null hypothesis for early tetrapods should be that they likewise took in air through the mouth.

The homologies of the tetrapod choana with comparable structures in other osteichthyans has received much discussion since the furore stirred by Rosen *et al*. (1981), for example, Panchen & Smithson (1987). Chang (1991) most recently reviewed what is known of the structure of the endochondral and dermal elements of fossil sarcopterygian taxa. She suggested a number of criteria by which a choana in, for example, osteolepiforms could be confirmed: 1) an opening in the dermal palate that is bordered by the bones of the premaxillary-maxillary arch, 2) a passage that extends from this opening to the nasal cavity, and 3) no blockage of the opening or the passage by other structures.

Panchen & Smithson (1987) pointed out that the nasal capsule of tetrapods is never ossified, but stated that (p. 377) "any choanate with an ossified or chondrified capsule would be expected to have a fenestra endochoanalis deep (dorsal) to the fenestra exochoanalis". The latter statement has at its root a functional hypothesis, even though Panchen and Smithson endeavour to remove such thinking from their analysis. The argument goes thus: all modern tetrapods have a canal from the nasal capsule to the palate through which air passes, because they use their noses to breathe through. Therefore all tetrapods, even the earliest, are assumed to have breathed through their noses, and that even though the nasal capsules of the earliest tetrapods are unknown, they must have had the same arrangement (see also Schultze 1991).

*Acanthostega* shows striking similarities in the proportions, structure and shape of the naris to osteolepiform fishes, in particular to *Panderichthys* (Figs 13 A-C). These similarities extend to the palate, especially the configuration and dentition of the vomers. *Panderichthys* undeniably has a fenestra in the palate in an exactly comparable position to that of *Acanthostega*. An isolated snout of *Acanthostega* could be mistaken for that of a panderichthyiid fish. Forey *et al.* (1991) nevertheless challenge the presence of a choana in *Panderichthys* and Chang (1991 p.11) argues that a "choana has not been identified unequivocally in any 'rhipidistian'", based on the form of the nasal capsule. It is to be noted that part of Chang's objection to the identification of a choana in *Panderichthys* was the lack of ossification of the posterior wall of the capsule (Vorobyeva & Schultze 1991) so that a fenestra endonarina posterior cannot be identified. However, this may represent a further similarity to tetrapods shown by this genus.

By contrast with *Panderichthys*, noone would deny *Acanthostega* a choana despite the lack of an ossified nasal capsule, simply because it is a tetrapod, though as I suggested above, *Acanthostega* may not have breathed through its nose. To emphasise the absurdity of the suggestion that *Panderichthys* or other osteolepiforms may not have had a choana because of the structure of the nasal capsule, it is instructive to turn the argument on its head. It is logically possible that the similarities of *Acanthostega* to osteolepiforms may have extended to the nasal capsule in which the fenestra endochoanalis may have been occluded by dermal bones, as Chang (1991) suggests for most osteolepiforms. My argument is that it is not possible to compare the structure of the snout in osteolepiforms or any other osteichthyan with early tetrapods in terms of the form of the nasal capsule, nor to define the choana on the form of the capsule as Chang does. Only the dermal elements can be compared, and on that basis *Panderichthys* and *Eusthenopteron* show the closest similarities to tetrapods.

Under this hypothesis, the function of the fenestra exochoanalis in both osteolepiforms and tetrapods remains unknown, or even whether it were open or not in life. It is difficult to believe that it was not open, given the single external opening in these groups, as Schultze (1991) points out. If it were open in both groups, the possibilities are 1) for water sampling, as the nasal capsules are used in most fishes, in which case the choana would have allowed for passage of water, or 2) for breathing air. In either case, the direction of travel of the medium is debatable. If it were involved with air breathing, exhalation through the nares may have preceded inhalation, but there seems no immediate prospect of testing any of these hypotheses.

## Lateral rostral

Panchen (1967) argued that the lateral rostral of osteolepiforms was the homologue of the tetrapod septomaxilla, so that the anterior tectal clearly could not also be so. The evidence on which this is based comes mainly from living forms, that from Palaeozoic forms being difficult to interpret. Since Panchen's analysis, several genera have been redescribed and show a different pattern from that understood in 1967. The septomaxilla of loxommatids (Beaumont 1977) shows some resemblance to the anterior tectal of *Acanthostega* in having a substantial dermal component, and in almost occluding the narial opening. However, the narial opening, according to Beaumont, lies either dorsal (*Megalocephalus*) or anterior (*Baphetes*) to the septomaxilla in loxommatids, while it lies ventrally in *Acanthostega*. This variation among loxommatids must cast some doubt on the real position of the septomaxilla.

*Palaeoherpeton*, (as *Palaeogyrinus*) was described by Panchen (1964) as showing a septomaxilla, but later was shown (Panchen 1970) not to possess one, and while *Eoherpeton* was described by Panchen (1975) as having one, Smithson's (1985) description of this form makes no mention of it. I have examined the specimen personally and find no strong evidence for the presence of a septomaxilla, though the narial region is somewhat crushed. *Crassigyrinus* (Panchen 1985) apparently possesses both an anterior tectal and a lateral rostral. Bones conventionally described as septomaxillae are known from many temnospondyls, where they usually incorporate a superficial component, and from early reptiles, where they do not. The homologies of these bones to one another must remain in doubt, but the condition in *Acanthostega* does not appear to clarify the situation.

## Ventral cranial fissure

The persistence of a ventral cranial fissure in the braincase of early tetrapods has been debated in the context of their relationships to other groups. Rosen *et al.* (1981 p. 165) expressed reservations about the presence of the fissure in *Ichthyostega*, and noted the common character of a long parasphenoid in dipnoans and all other tetrapods, while Gaffney (1979), Schultze (1986) and Panchen & Smithson (1987) all accepted Jarvik's (1980) account. It is clear from both published photographs, including one reproduced in Rosen *et al.* (1981), and personal examination of the specimens, that Jarvik's description is correct. However, the condition of this region is not a simple character, to be scored present or absent in a cladistic analysis. It involves at least two interrelated characters; degree of separation or integration of ethmoid and otic-occipital braincase moeties and length of parasphenoid, both of which are gradational in nature. In the first of these, an osteolepiform such as *Eusthenopteron* shows an extreme condition, with a wide gap between the ethmosphenoid and the otic-occipital ventrally. In *Ichthyostega*, a narrow fissure lies between the two braincase elements, and the parasphenoid does not reach the junction. In *Acanthostega* however, small lateral wings are produced from the basi-parasphenoid region which lap over onto the basioccipital. Whether both basi- and parasphenoid elements contribute to these wings is not clear. There is no visible gap between the two halves of the braincase, but the junction is poorly consolidated, especially in the midline, where there is almost no overlap. This results in the basioccipital having fallen out in most of the braincase specimens examined. The condition in *Acanthostega* forms an almost perfect intermediate between *Ichthyostega* and *Crassigyrinus* (Panchen 1985). In the latter, the parasphenoid is longer, lapping over most of the length of the basioccipital, but in the midline the contact is reduced. As in *Acanthostega*, the basioccipital of *Crassigyrinus*, BMNH R1000, had fallen out, and its lateral sutural attachments for the parasphenoid are clearly visible. In other early tetrapods, such as the embolomere *Archeria* (Clack & Holmes 1988) the ossified parts of the basisphenoid and basioccipital do not meet, the ventral cranial fissure being sealed only by the parasphenoid. One thing is apparent from this analysis, which is that a long parasphenoid bridging the ventral cranial fissure is a synapomorphy of a sub-group of tetrapods, and not a synapomorphy of tetrapods and dipnoans, as Panchen & Smithson (1987) emphasise.

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## Abbreviations used in figures

| | |
|---|---|
| apf | anterior palatal fossa |
| art | articular |
| at | anterior tectal |
| bocc | basioccipital |
| bsph | basisphenoid |
| bptpr | basipterygoid process |
| ch | choana |
| col cran | columella cranii |
| dent | dentary |
| dpal | dermopalatine |
| ectopt | ectopterygoid |
| (epi)pt | (epi)pterygoid |
| fr | frontal |
| gr | groove at possible junction of pterygoid and epipterygoid |
| in | internasal |
| ioc | infraorbital lateral line |
| ju | jugal |
| lac | lacrimal |
| llc | lateral line canal |
| lat ros | lateral rostral |
| lr jaw | lower jaw |
| mx | maxilla |
| na | nasal |
| pal | palatine |
| pmx | premaxilla |
| preart | prearticular |
| preop | preopercular |
| psph | parasphenoid |
| pt | pterygoid |
| qj | quadratojugal |
| qu | quadrate |
| rec | recess for basipterygoid process |
| sa | surangular |
| soc | suborbital lateral line |
| sphet | sphenethmoid |
| sut | sutural surface joining vomer and premaxilla |
| squ | squamosal |
| tab | tabular |
| v cr fiss | ventral cranial fissure |
| vo | vomer |
| V | notch for mandibular branch of fifth cranial nerve |
| XII | foramen for hypoglossal nerve |

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