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The dermal skull roof of *Acanthostega gunnari*, an early tetrapod from the Late Devonian

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ABSTRACT: The dermal skull roof of *Acanthostega gunnari* Jarvik is described in detail, giving new information on the anatomy, and new reconstructions of the skull in dorsal, lateral and occipital views, as well as sections through the skull at two points. The types of suture are compared with those of temnospondyls and discosauriscids, comparable animals in terms of habit and skull shape. The skull-bones of *Acanthostega* are much more closely integrated with each other than those of the two later groups. However, regions of relatively less firmly and more firmly sutured regions are comparable in position. This may be connected with having the lateral lines accommodated in tubes in *Acanthostega* rather than grooves, or some other property of the dermal bone in the later groups that reduced the need for stronger integration. The post-orbital region of the skull (skull table) is the most strongly integrated region, possibly connected with the need for attachment of occipital musculature. The skull table and dentition are the most labile of cranial features among Devonian tetrapods, whereas the snout, cheek, palate and infradentary regions remain conservative. These are for the most part the lateral-line-bearing regions of the skull. The specimens of *Acanthostega* found at one site on Stensiö Bjerg may form part of a year-group that had perhaps come together for spawning.

KEY WORDS: dermal bones, East Greenland, Fammennian, skull structure, sutures

Acanthostega gunnari was first described in 1952 by Erik Jarvik, based on two incomplete skull roofs from the Famennian of East Greenland. Since that time, much more material has been collected (Bendix-Almgreen *et al.* 1990) and most of the anatomy of the animal is known in great detail. The postcranial skeleton (Coates 1996), palate (Clack 1994), braincase (Clack 1998a) and lower jaw (Ahlberg & Clack 1998) have all been fully described; the skull roof is the one remaining aspect of the anatomy for which only outline drawings and descriptions have currently been published. An outline reconstruction of the dermal skull roof was first presented by Jarvik (1952) based on the holotype, and a revised version was included in the description of the palate (Clack 1994).

Acanthostega is notable not only as one of the earliest tetrapods known (Marshall *et al.* 1999), but also, in many respects, as the most primitive. Most analyses have placed it at a node below the contemporary *Ichthyostega* on a cladogram; furthermore, since the recent studies it has become clear that it bears no specially close relationship with that genus. The taxon 'Ichthyostegalia' has emerged as a paraphyletic one with no taxonomic validity (e.g. Carroll 1995; Lebedev & Coates 1995; Ahlberg & Clack 1998; Clack 1998b, c, 2001; Laurin 1998; Ruta *et al.* 2001).

Acanthostega, as the most primitive known tetrapod, has provided a new perspective on the origin of the group, the acquisition of terrestriality and the sequence of evolution of tetrapod characters. For example, its suite of primitive characters suggested that digits appeared in tetrapods before full terrestriality had been achieved, and that digits evolved before supportive joints at elbows, knees, wrists and ankles (Coates & Clack 1990, 1995; Clack & Coates 1995). Its complement of eight digits on fore and hind limbs, in combination with the discovery of seven digits on the hind limb of *Ichthyostega* and six in *Tulerpeton*, suggested early variation in the number of digits in tetrapods, which only later became stabilised at five (Coates 1991, 1993, 1996; Coates & Cohn 1998), perhaps in conjuction with terrestrialisation.

Acanthostega had well-ossified gill bars and a post-branchial lamina suggesting retention and use of internal gills (Coates & Clack 1991).

Other primitive characters of *Acanthostega* include an anocleithrum, small straight ribs with little differentiation along the column, poorly developed zygapophyses, longer and more numerous lepidotrichia in the tail than *Ichthyostega*, and a radius which is considerably longer than the ulna. It shows similarities to *Ichthyostega* in the ankle construction, having fewer and flatter tarsals than most other early tetrapods (where these are known) (Coates 1996).

With respect to the skull roof, the situation is less easy to assess. Both taxa have a number of unique characters especially of the posterior parts of the skull. Both lack a bone occupying the site of that usually called the intertemporal in other early tetrapods. Though this similarity has sometimes been used to suggest a close relationship between the two, most analyses have found this character-state to be a homoplasy (e.g. Ahlberg & Clack 1998; Clack 1998b, c, 2001). *Acanthostega* is unique in having an embayed tabular bearing the spike-like process which gives it its name, and in the arrow-head shape of the supratemporal. It is apparently primitive in having no facets on the underside of the skull roof to receive the braincase, in which it is similar to fishes such as *Eusthenopteron*. *Ichthyostega* by contrast has large flanges extending downwards from the supratemporal and postparietal (the latter unique among early tetrapods in being a single ossification) to which the braincase is attached. Whereas the braincase of *Acanthostega* is not dissimilar in many respects to that of later Palaeozoic tetrapods and is also comparable with that of fish such as *Eusthenopteron*, that of *Ichthyostega* has been seen as highly specialised to the extent that Jarvik (1996) was unable to interpret it easily in terms of other animals. This aspect of *Ichthyostega* is currently under study by the author and P. E. Ahlberg.

The stapes of *Acanthostega*, a robust bone with a single head, relatively large stapedial foramen and a flattened distal plate terminating in unfinished bone, has been of interest in studies of the evolution of early tetrapod hearing, and its form appears to be that common to most early tetrapods (Clack 1992, 1994, 1998a). Clack & Ahlberg (1998) identified a possible stapes of *Ichthyostega* which does not conform to this pattern. A future programme of work by the author, P. E. Ahlberg and H. Blom includes a complete revision of the anatomy and morphology of *Ichthyostega*.

The lower jaw of *Acanthostega* bears similarities to those of some of the other Devonian tetrapods that have been discovered in recent years, such as *Ventastega* and *Metaxygnathus*. Lower-jaw anatomy, however, is one of the few aspects of the animal in which *Ichthyostega* has emerged as more generally primitive than *Acanthostega* (Ahlberg & Clack 1998).

This study does not attempt a further cladistic analysis of early tetrapods, since that exercise forms part of a larger study being undertaken by M. Coates and M. Ruta (e.g. Ruta *et al.* 2002), and is ultimately contingent upon more detailed knowledge of *Ichthyostega*. However, here I present a detailed description of the roofing bones of *Acanthostega* with previously unpublished anatomical details, and include new, detailed skull-roof reconstructions. Further information on the collection of *Acanthostega* made in 1987 is also presented.

1. Material and methods

The original material of *Acanthostega* consisted of the holotype specimen, MGUH 6033 (formerly A33, Jarvik 1952), showing most of a skull roof lacking the left suspensorium, cheek and snout. This skull has now been discovered to include braincase material, although it has not been further exposed. A second skull roof, MGUH 6085 (formerly A85 Jarvik 1952), preserved as a natural mould, shows the skull table, left suspensorium, orbit and cheek. Three skulls were discovered on Stensiö Bjerg in 1970 (Clack 1988) and, subsequently, a large number of skull roofs varying in completeness were discovered in 1987. Twelve of these provide skull tables complete enough to be measured and compared with each other and the two original specimens. Another ten vary from nearly complete, three-dimensionally preserved skulls with attached braincases, to partial skull roofs preserved as eroded bone which nonetheless provide useful information. It is unfortunate that of the best-preserved skulls, there is little overlap between the exposed or preserved parts of the skull, so that they cannot provide comparable measurements. Several of the skulls have been distorted during preservation, varying from laterally compressed (e.g. MGUH f.n. 1300b, ‘Grace’ Clack 1998a) to dorsoventrally compressed (e.g. MGUH f.n. 1227a ‘Boris’ Clack 1998a). Fortunately, some of the skulls appear almost undistorted (e.g. MGUH f.n. 1227b, MGUH f.n. 1300a ‘Rosie’ Clack 1998a) and these have been most useful in constructing the profile of the intact skull.

Most of the material discovered in 1987 derives from a single site in the Britta Dal Formation on Stensiö Bjerg (Bendix-Almgreen *et al.* 1990; Clack 1994; Coates 1996). Two skulls were found at different sites, one in the Aina Dal Formation on Stensiö Bjerg, and one in the talus below the Britta Dal Formation, at 520 m on Wiman Bjerg (MGUH f.n. 1400). The holotype also derives from the talus of Wiman Bjerg but at 350 m, much lower down than MGUH f.n. 1400. It is nevertheless likely to have come from the Britta Dal Formation, as it was found above the top of the Aina Dal Formation, and the Wimans Berg Formation that lies between these two has not been known to yield vertebrates. The second of the original specimens came from the southern side of Celsius Bjerg at 735 m, a height likely to be the equivalent of the Britta Dal Formation. The stratigraphical relationship between the Gauss Halvø and Celsius Bjerg sediments has not been fully resolved, however (Olsen 1993; Olsen & Larsen 1993; Clack & Neininger 2000). New studies by H. Blom are in progress to investigate the systematic and stratigraphic relations of *Ichthyostega* specimens.

Until recently, the dating of the East Greenland tetrapod deposits rested almost entirely on the vertebrate fauna and they were placed broadly within the Famennian. This has been disputed (e.g. Westoll 1941, 1951). A study based on radiometric and palaeomagnetic data suggested a much younger date for the deposits (Hartz *et al.* 1997, 1998). However, the issue has recently been resolved by palynological methods and the tetrapod-bearing strata are shown to be Famennian 2b in age (Marshall *et al.* 1999). That report suggests that the East Greenland tetrapod deposits were the oldest of the Famennian tetrapod-bearing strata, and also gave a tighter control on the dating of the contemporary fish fauna. The suggestion that the *Acanthostega* site on Stensiö Bjerg (Bendix-Almgreen *et al.* 1990) represents an active river channel may require revision (T. Astin & J. Marshall, pers. comm. based on field work in 1996).

Most specimens have been prepared mechanically, where necessary, using a dental mallet and fine-pointed tungsten carbide rod under a binocular microscope. A few specimens have been acid-etched using dilute hydrochloric acid to reveal a natural mould of the bone (see Coates 1996 for more details). The following specimens were used in this study:

Museum Geologicum Universitatis Hafniensis (MGUH, Geological Museum, University of Copenhagen):
- MGUH 6033 holotype specimen (figured by Jarvik 1952);
- MGUH 6085 (figured by Jarvik 1952).
- MGUH field numbers (f.n):
  - 219 left half of a skull acid-etched to show natural mould of internal surface;
  - 222 right half of skull roof in internal view with sclerotic ring, lacking snout and maxilla;
  - 230 (figured by Bendix-Almgreen *et al.* 1988) left half of skull in part and counterpart lacking snout and maxilla;
  - 236 (figured by Clack 1998a) eroded skull lacking palate, snout and maxillae, but preserving skull roof and braincase, sectioned through braincase;
  - 1274 (figured by Bendix-Almgreen *et al.* 1988) almost complete skull in part and counterpart split near internal surface and showing aspects of suturing very well; lacks snout and maxillae;
  - 1227 a & b: (a) (‘Boris’ figured by Clack 1994, 1998a; Coates 1996) dorsoventrally compressed skull lacking skull table and midline bones; (b) almost complete skull lacking posterior skull table and suspensoria as well as snout and maxillae; excellent ornament, original profile undistorted;
  - 1300a & b: (a) (‘Rosie’ figured by Clack 1998a; Ahlberg & Clack 1998) almost complete skull broken across posterior to nasals, and with braincase exposed from behind giving good information on snout and skull table; (b) (‘Grace’ figured Clack 1998a; Ahlberg & Clack 1998) excellent skull, laterally compressed but complete, with good ornament;
  - 1305 (figured by Clack 1994, 1998a; Ahlberg & Clack 1998) skull lacking posterior region, right half sectioned, part parasagittally, part transversely;
  - 1400 (figured Bendix-Almgreen *et al.* 1988) small flattened skull, specimen preserves part of the shoulder girdle and tail;

1602 left half of skull in part and counterpart, lacking snout, skull table acid-etched to remove bone but leave vascular system preserved as tubules lined with iron-rich matrix;

1604 (figured by Clack 1998a; Ahlberg & Clack 1998) disrupted skull lacking anterior region, split through skull roofing bones; lower jaws and braincase sectioned;

218, 231, 243, 251 (figured by Bendix-Almgreen *et al.* 1988), 261, 268, 1377 all skull portions in different states of completeness but including measurable skull tables.

University Museum of Zoology, Cambridge (UMZC):

T1300 d & f (figured by Clack 1988, 1998a; Ahlberg & Clack 1998): (d) skull table with attached braincase, good tabular; (f), small skull retaining patches of roofing bones and the rest as natural mould, suspensoria preserved on MGUH f.n. 1258 (also figured Coates 1996) (as 'individual Z').

2. Systematic description

Osteichthyes Huxley 1880
Sarcopterygii Romer 1955
Tetrapodomorpha Ahlberg 1991
Acanthostegidae Jarvik 1952
Acanthostega gunnari Jarvik 1952

Amended diagnosis (revised from Jarvik 1952; Coates 1996) Devonian tetrapodomorph with skull characters as in Jarvik (1952) and postcranial and hyobranchial characters as in Coates (1996), but with the addition of the following. *Skull:* maximum known length about 150 mm; tabular with small cup-shaped ventral facet to receive pro-otic process of braincase; paired median rostrals, anterior tectal present above naris but superficial; junction between median rostrals, premaxillae and nasals loosely sutured; preopercular approximately hexagonal; premaxilla bearing 13 teeth increasing in size posteriorly; maxilla bears up to 52 teeth, largest at positions 7–11; naris small, beneath anterior tectal; lateral line mostly enclosed in bone and opening by pores, but grooves present along interorbital canal across jugal–postorbital suture; sclerotic ring of 19–20 plates, larger at the top of the ring. *Palate:* closed with shagreen-covered pterygoid; vomer bearing fang-pair at the midpoint of a row of smaller toothlets, a few denticles lateral to tooth row, otherwise smooth surface; palatine with fang pair at approximately the mid-point of a toothrow of smaller toothlets, with a few denticles laterally, otherwise smooth surface; ectopterygoid with row of small toothlets, no conspicuous fang pair, though teeth at midpoint of row very slightly enlarged, a few denticles lateral to tooth row, otherwise smooth surface, ectopterygoid forms significant part of adductor fossa; choana, paired anterior palatal fenestrae, adductor fossae, all oval in shape; maxilla and premaxilla meeting at unsutured junction. *Braincase and stapes:* parasphenoid cultriform process elongate teardrop-shaped and lacking shagreen, concave, but lacks hypophysial foramen; basisphenoid co-ossified with parasphenoid; basal processes bulbous and bifaceted, fitting into socket in epipterygoid; basisphenoid–basioccipital junction sutured but visible; exposed part of basioccipital longer than wide; stapes stout with flared distal portion, bilobate footplate. *Lower jaw:* dentary with about 60 more-or-less uniform teeth, and a pair of dentary fangs at the symphysis; parasymphysial plate bearing toothlets and denticles but no larger teeth; three coronoids each with a row of small teeth but no larger teeth or fang-pairs; prearticular bearing shagreen in a patch along the dorsal margin, not sutured to infradentary bones except for the splenial.

Remarks. The above diagnosis concentrates on providing specific, recognisable details of the anatomy of *Acanthostega*, rather than attempting to divide characters into plesiomorphic or derived categories. For example, rather than stating simply 'preopercular present', I have defined it as 'approximately hexagonal'. Based on outgroup comparison its presence would be plesiomorphic, but whether its shape is so remains unclear.

The original description (Jarvik 1952) of *Acanthostega* gave an accurate account of most of the bone patterns in the skull roof apart from the snout region, which was missing from the available specimens. The bones were described using the names that have become conventional for early tetrapods, rather than the alternative system later (1980) preferred by Jarvik. Therefore, details of the bone relationships need not be repeated here. However, the unusually large number of skull specimens now available for this Palaeozoic tetrapod provide details of the construction not normally available, including suture types and both internal and external views of the bone patterns. Such aspects of the skull form a focus for the following description.

The bones of the snout, including the premaxillae, anterior tectals and median rostrals as well as the maxillae and dentition, were described in Clack (1994) and need little further treatment here.

The large, broadly rectangular nasals give the intact skull a somewhat spatulate snout. The junction with the premaxillae and median rostrals is very weakly sutured, and these snout bones are often lost from the fossils. The midline suture between the nasals is likewise not strongly interdigitated. The suture with the lacrimal is short in external view and interdigitated, though not strongly. However, there are overlap surfaces visible in section (1305) (Clack 1994, fig. 5, G, I). In internal view, the nasal–lacrimal suture is about twice as long as in external view, because the anterior tectal appears to be a superficial bone that does not appear in internal view (MGUH f.n. 219) (Fig. 1). No section shows the internal three-dimensional structure of the nasal–frontal sutures, but in surface view they are deeply interdigitating. Ornament on the nasals mainly consists of non-directional pit and ridge pattern, but is elongated near the sutures with the lacrimal and prefrontal. The nasals carry a component of the supraorbital lateral line canal, and bear a series of eight or nine large pores (MGUH f.n. 1300b) (Fig. 2) towards the lateral side of the bone, which may coalesce near the frontal suture to form a groove.

The lacrimal has a different appearance externally from internally. Externally in some specimens it nearly reaches the orbit margin, but internally it is excluded from the orbit where the prefrontal and jugal meet in an overlap suture. This region, at the anteroventral sector of the orbit margin, therefore has a compound structure where three thin but broad sheets of bone overlie one another. A similar situation is found in *Crassigyrinus* (Clack 1998b). Some of Säve-Söderbergh's (1932) original five *Ichthyostega* species were in part distinguished by whether or not the lacrimal contributed to the orbit margin. Differences may, however, be accounted for by such a bone overlap being split through at different levels in different specimens. This region is also the one to show the greatest degree of elongation in the ornament ridge pattern and so might represent an area subject to rapid growth. In some specimens (e.g. MGUH f.n. 1274) the suture with the nasal is also marked by a spike-like process from the

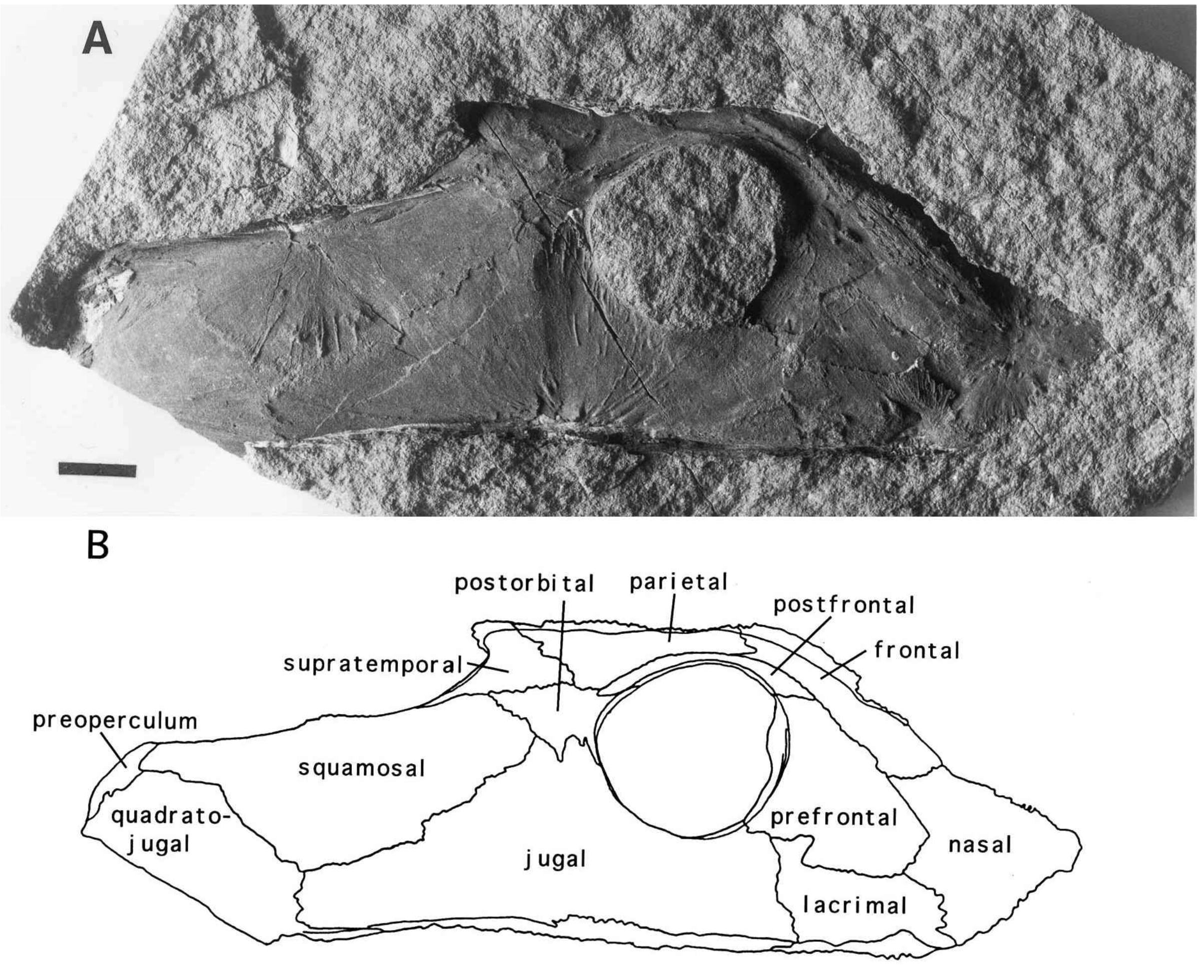

Figure 1 *Acanthostega gunnari*: (A) MGUH f.n. 219, specimen acid-etched to show internal surface of bone as a natural mould; the internal suture pattern can be clearly seen in most places; scale bar 10 mm. (B) Interpretive drawing of A.

lacrimal onto the nasal (Fig. 3A), though this is not seen in external view. The suture with the jugal is of a standard interdigitating pattern, while that with the prefrontal appears more or less straight in surface view. The suture between the lacrimal and maxilla is an uninterdigitated butt-joint (MGUH f.n. 1300b) (Clack 1994, fig. 5, F, H) which may spring open in preservation (Fig. 2). Similar to the nasal, the more or less non-directional ornament is elongated into ridges and furrows only near the prefrontal and jugal sutures. The lacrimal carries a component of the infraorbital lateral line canal, consisting of a row of about three large pores at its anterior end, in line with the single pore found at the anterior end of the maxilla (Clack 1994), followed by about seven much smaller pores that lie very close to the suture with the maxilla (Fig. 2).

The prefrontal is an elongate triangular bone with its narrow apex inserting between the lacrimal and nasal and almost reaching the anterior tectal, the pointed tip being an overlap that does not appear in internal view (Figs 1, 2). This anterior tip bears conspicuous elongation of the ornament, as does the region close to the suture with the jugal. Along its dorsal edge, however, the ornament is simply but coarsely pitted. This area is somewhat thickened and marks the beginning of a ridge running up the snout, between the orbits and onto the skull table (see below). The suture with the frontal is not conspicuously interdigitated in surface view, but there are no good sections of this suture to inform about its internal structure. The prefrontal contributes most of the anterior portion of the orbit margin and, about midpoint, it bears an external lip or process that gives the orbit margin a heart-shaped appearance (Fig. 2). When the bone is split through, as is often the case, the internal view does not show this feature but the orbit appears simply rounded (Fig. 3A). The lip might have supported the base of an eyelid.

The frontals are narrow and basically rectangular, but gradually increase in width anteriorly. In some specimens (MGUH f.n. 1274, 1227b) (Fig. 3A, B), they show noticeable asymmetry. In MGUH f.n. 1227b, one of the frontals spans the midline, running between the parietals for a little way (see also specimen MGUH f.n. 236, Fig. 4A; Clack 1994, fig. 7B). This is partly explained by the form of the suture between the orbits, in which one bone forms an underlap surface to the other. External and internal views can thus show different patterns. Further anteriorly, the midline frontal suture appears almost uninterdigitated. In MGUH f.n. 1227b (Fig. 3B) the bones have separated to reveal a tongue-and-groove arrangement. Whereas elsewhere the ornament is non-directional, at the midline grooves run parallel to the suture, in contrast to the usual pattern of elongation at right angles to a suture. The grooves form part of the sutural tongue-and-groove surface. The suture with the postfrontal is very complex, interdigitating in three dimensions (MGUH f.n. 236, Fig. 4A, B; Clack 1994, fig. 7B), and it is set on a thickened ridge seen both dorsally and ventrally, that bounds the dorsal part of the orbit margin (Fig. 4A, B). The ridge is a continuation of that which arises on the prefrontal. The supraorbital lateral line continues from the nasal up the

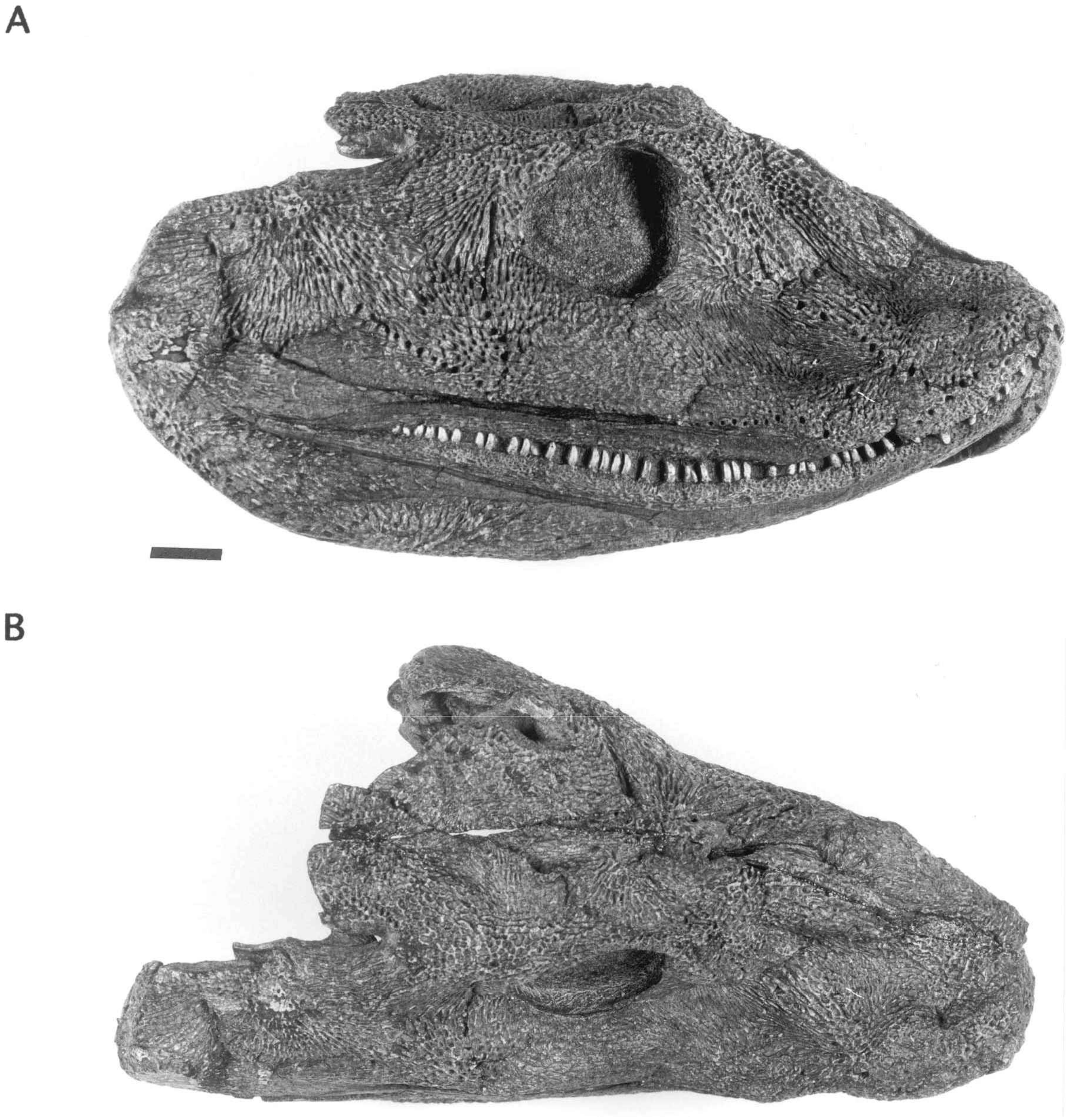

Figure 2 *Acanthostega gunnari* MGUH f.n. 1300b, three-dimensional skull: (A) right lateral view; (B) dorsal view; scale bar 10 mm.

length of the frontal to a point level with the anterior margin of the orbit (Fig. 2). It runs close to but not on the lateral edge. Five conspicuous pores lie at the orbital end of the line, while closer to the nasal, they coalesce into a short section of groove that may continue onto the nasal.

The jugal is one of the two major bones of the cheek region, and provides the lower quarter of the orbit margin. This tetrapod characteristic is present in all Devonian tetrapods whose jugals are known, so that even isolated jugals can be identified as tetrapod or fish. In *Acanthostega*, generally the jugal is nearly as deep below the orbit as the orbit is wide, and sutures with the lacrimal anterior to the orbit. In profile it has a characteristic bowed shape, so that the junction with the maxilla (a continuation of the butt joint seen between the maxilla and lacrimal) is not visible in dorsal view. The jugal often retains this shape even in crushed skulls. The bone underlaps all those bones surrounding it except for the maxilla, and so lies entirely internal to them. It has conspicuously interdigitated sutures with the postorbital and squamosal, in the sense of high amplitude, short wave-length zig-zags. Though these are not reflected in internal view, at least one section (MGUH f.n. 1305) shows the postorbital–jugal suture to have a complex internal structure, with the jugal broadly underlapping the postorbital. The postorbital cuts a shallow V shape into the posterodorsal margin of the jugal externally, in common with *Ventastega* (Ahlberg *et al.* 1994) and *Tulerpeton* (Lebedev & Clack 1993). The jugal does not reach the jaw margin, but is excluded by a long tapering process from the quadratojugal (Fig. 2). The bone is thickened at its ventral margin just level with the back of the orbit, at the point of origin of the adductor fossa, and this also appears to be the growth centre of the bone. Internally, this surface is marked by ridges radiating from the centre of growth (Fig. 1). Ornament consists of basic non-directional pit and ridge except where it is slightly elongated near the suture with the postorbital and squamosal (Fig. 2). The infraorbital lateral line canal continues from the lacrimal onto the jugal by a series of about six to eight small pores (MGUH f.n. 1300b) very close to or on the ventral edge of

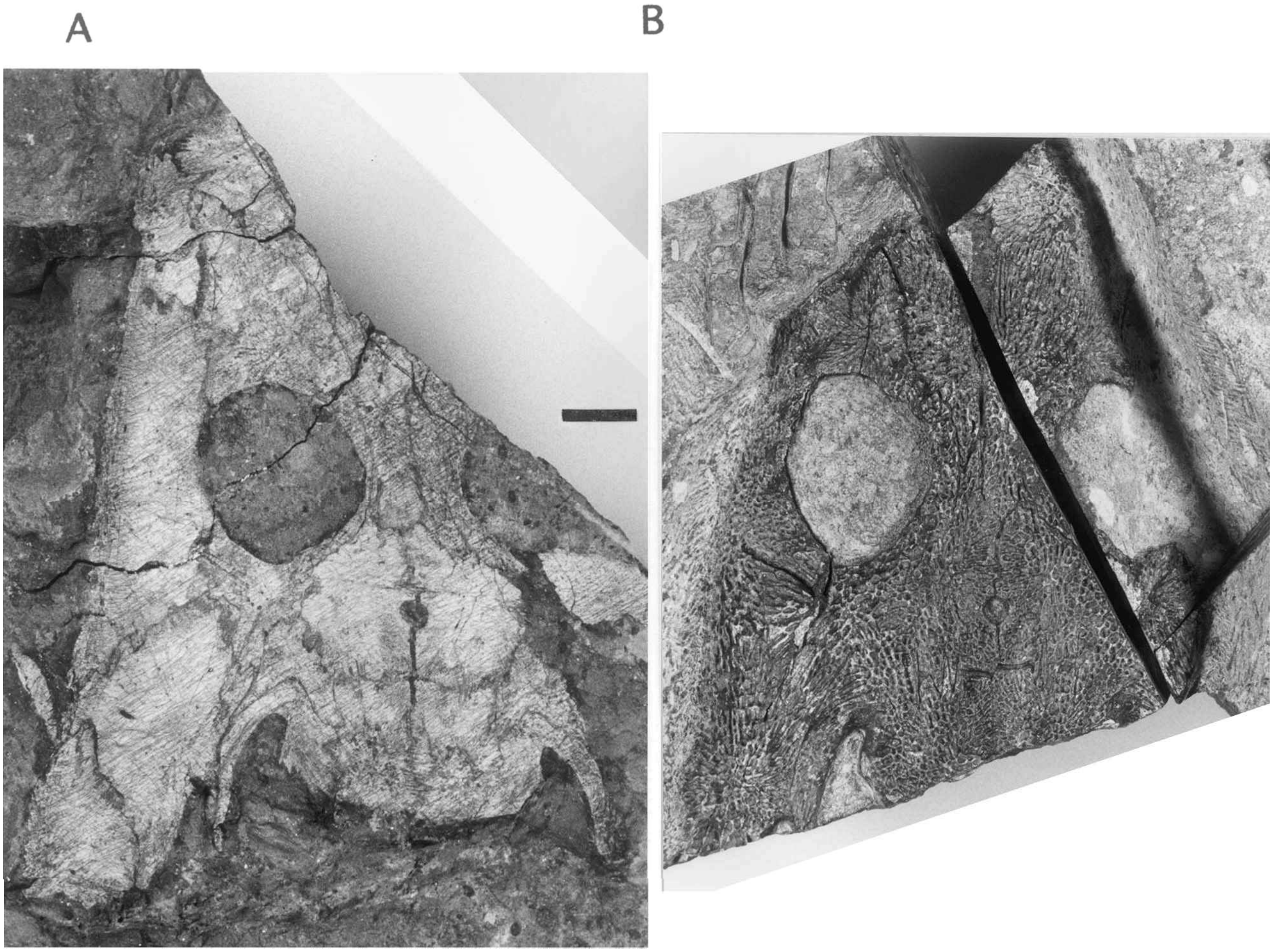

Figure 3 *Acanthostega gunnari*: (A) MGUH f.n. 1274 skull exposed mostly in ventral internal view; (B) MGUH f.n. 1227b *Acanthostega gunnari* skull exposed in dorsal, external view; for interpretive drawings, see Figure 9B, C; scale bar, 10 mm.

the bone, and then splits into two branches over the growth centre. One branch rises at a steep angle onto the postorbital, with about six to eight large pores. Towards the postorbital, the pores usually coalesce into a groove (Figs 2, 3B). The lower branch rises at an angle of about 40° in a series of about ten closely spaced pores (MGUH f.n. 1300b) continuous with those on the squamosal.

The squamosal is a large, approximately D-shaped bone with the straight edge forming part of the posterior margin of the skull (Fig. 1). About halfway along the straight edge is a hook-like process that clasps the tabular. The tabular then springs away from the skull roof to produce its characteristic prong. This produces an embayment between the tabular and squamosal, below which the squamosal margin bears a longitudinal, inturned, unornamented flange (Fig. 2B). As shown in Clack (1994, fig. 10), this forms a free edge to the rear of the skull, and is not attached to the palatal ossifications. The flange terminates where the preopercular sutures with the squamosal. The squamosal shows a variety of sutural types. There is a lap surface with both jugal and postorbital, and in surface view they show high-amplitude, short wavelength zigzags. The suture with the quadratojugal by contrast appears almost straight and fairly simple in section. The junction where the squamosal meets the supratemporal and tabular is unique in the skull, being a smooth slightly curved lap surface in section, with no interdigitations (MGUH f.n. 236) (Fig. 4C–E). Ornament on the bone is of the star-burst pattern, radiating in elongated pits, furrows and ridges from the centre of growth just anteroventral to the tabular process. The lateral line canal continues from the jugal up onto the squamosal with about six widely spaced pores. It then turns down at the growth centre to run parallel to the posterior margin, exposing about seven further pores (MGUH f.n. 1300b) (Fig. 2).

The quadratojugal completes the posteroventral margin of the skull roof. It is an elongate triangle in shape, whose apex is a narrowly tapering process passing between the jugal and maxilla, separating the jugal from the jaw margin. Much of this process must be a superficial overlap surface as it is not reflected in internal view (MGUH f.n. 219) (Fig. 1). The posterior margin of the quadratojugal is slightly embayed over the quadrate, though the latter can hardly be seen in lateral or dorsal view. As it turns posteroventrally the quadratojugal margin droops somewhat below the general line of the ventral margin of the skull (Fig. 2). It forms a short length of suture with the preopercular.

The preopercular is a small, more or less oval or hexagonal bone forming the posterior corner of the suspensorial margin (Clack 1994, fig. 10B). It has a free edge posterodorsally that continues that from the squamosal, though without the latter's inturned flange. It has a deeply interdigitated suture with the squamosal, seen in an isolated example on MGUH f.n. 1227. It bears three or four lateral line pores continuing the line on the posterior edge of the squamosal. It is not a superficial scale-like bone as in *Whatcheeria* (Lombard & Bolt 1995), nor elongate as in osteolepiform fishes (see Panchen & Smithson 1987).

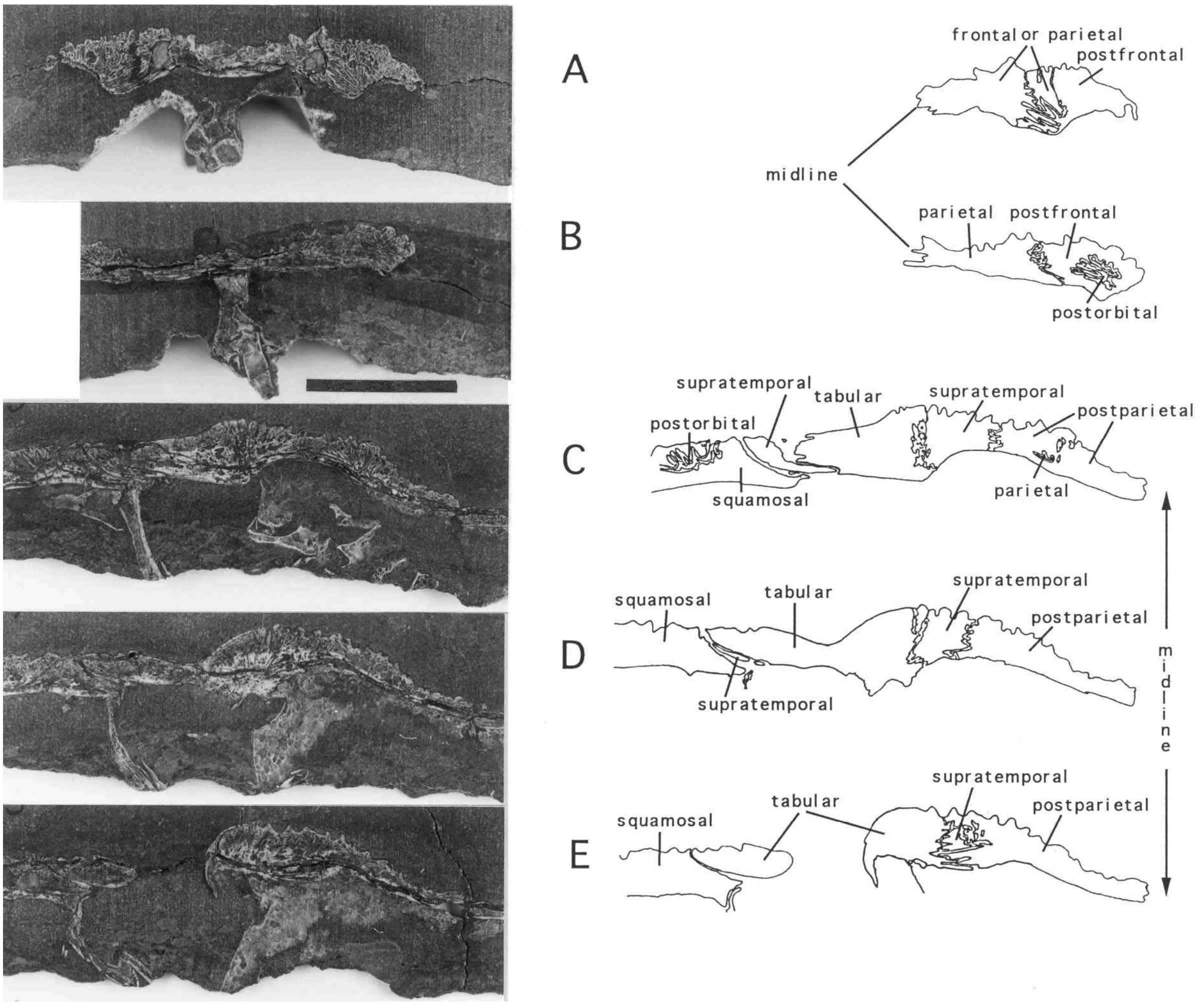

Figure 4 *Acanthostega gunnari* MGUH f.n. 236 sections through a skull; approximate positions of sections shown in Figure 7; scale bar 10 mm.

The postfrontal is a very narrow bone that spans most of the dorsal margin of the orbit. It is much thickened, and in section has complex, deeply interdigitated, three-dimensional sutures not only with the frontal but with the prefrontal, parietal and postorbital. Lateral to the ridge bearing the suture, the bone thins out to form a lip over the orbit, seen in section (MGUH f.n. 236) (Fig. 4A, B).

The parietals between them form the roughly pentagonal central portion of the skull table. The parietal foramen, which is circular, conspicuous, but without any raised rim, lies towards the posterior third of the structure, well behind the level of the orbits (Fig. 3A, B). The central region of the parietal pair is depressed, while laterally, the ridges from the postfrontals continue onto the parietals and postorbitals to produce a broader, raised area around the posterodorsal corner of the orbit. The ornament forms ridges and pitted furrows running parallel to the sutures along the raised area of the parietals, but in the central depressed region, they run at right angles to the suture. Internally, this is reflected by a transverse ridge running across the parietals anterior to the foramen (Fig. 3B). At this point also, the midline parietal suture is a complex one with high amplitude zig-zags, whereas elsewhere it is minimally interdigitated (MGUH f.n. 1227b, 1300a) (Fig. 3A, B). This is clearly a region of strengthening. The other sutural section to show a similar structure is that with the postparietal. Running away from the midline, this suture is very simple, and has parted slightly in MGUH f.n. 1227b to reveal a simple overlap surface (Fig. 3C, D). Further laterally, however, is a stretch of deep zig-zags that is obvious not only in surface but in internal view. The suture with the supratemporal is also a complex interdigitating one. The undersurface, apart from gentle undulations where the bone thickens or thins, is smooth, and without any scarring for attachments of muscles or braincase.

The postorbital is a relatively large bone in external view compared to that of most other early tetrapods, but MGUH f.n. 219 shows that very little was exposed internally (Fig. 1, cf. Fig. 2). The bone forms the rear portion of the orbit margin, and as with the jugal this is characteristically a tetrapod feature, allowing isolated examples to be assigned to tetrapods (Ahlberg *et al.* 1994). The suture with the postfrontal and supratemporal forms a more or less continuous line, that would be a weakness in the skull if it were not a complexly interdigitated one anteriorly (Fig. 3A). There is a marked change in profile from the dorsalmost thickened area continuous with that on the parietals, to a sloping cheek section more ventrally. The thickened area bears non-directional pit-and-ridge ornament, whereas on the cheek portion ornament is of the starburst type, radiating from the centre of growth midway along the edge of the ridge. The postorbital carries the continuation of the lateral line canal from the jugal, but it almost always consists of a groove rather than individual pores. In one case (MGUH f.n. 1227a) the groove is still spanned at one point by a narrow bridge of bone. In MGUH f.n. 1602, the canal has been revealed from the inside by etching and ends just at the centre of growth.

The supratemporal is unique among tetrapods in its arrowhead shape (MGUH f.n. 1274) (Fig. 3A). It lies at the meeting point of all the skull table bones and is strongly and complexly sutured to all of them at some point. The exception to this is its posterolateralmost corner, that sends a sharply pointed process between the tabular and squamosal (Fig. 4C–E). As in its suture with the squamosal, the surface appearance of the tabular portion is straight and simple, though a section (MGUH f.n. 1300a; Clack 1994, fig. 4B) suggests this is more complex than it appears externally. The ornament is entirely non-directional pit and ridge.

The postparietals are both more-or-less rectangular, between them forming an almost-square structure (Fig. 3A, B). The central depression from the parietals is continued onto the postparietals, and the lateral portions of the bone are correspondingly raised. The bones provide much of the rear skull table margin, where the bone thins out and is produced in some specimens into a 'widow's peak'. However, this is unlike that of embolomeres, for example, in that it lies in the plane of the rest of the skull table (Figs 3, 4). On the underside there is a small region of low ridging, presumably associated with attachment of the braincase (see Clack 1998a, fig. 3 inset). Most of the midline suture is scarcely consolidated, except for a short section of complex interdigitations towards the posterior margin (Fig. 3A–D). Sutures with supratemporal and tabular are very complex indeed and represent a region of strengthening. Ornament is more-or-less non-directional pit and ridge except near the suture with the parietals.

The tabular is morphologically the most complex bone of the skull roof in *Acanthostega*, carrying the eponymous 'spine' or prong from which the name is derived. Medial to that is an embayment or 'notch' that Clack (1989) suggested was spiracular in function. Medial to that is the portion that forms the dorsal covering to the post-temporal fossa. At the apex of the embayment is a region of smooth, unornamented bone, continuing a little way round onto the medial side (Fig. 3B). Otherwise the main body of the tabular bears non-directional pit-and-ridge ornament.

The prong bears low-relief ornament, of somewhat elongate ridges, that continues almost to the tip in some specimens, though is less marked in others. The prong is oval in section, with its lateral part forming a lapping junction with the squamosal. The length of the prong varies from individual to individual and, for example, is particularly small in MGUH f.n. 1300b (Fig. 2B). However, there is no detectable pattern to the size distribution, and it does not seem related to skull size.

The underside of the tabular is also complex. The margin forming the medial edge of the embayment forms a lip curving over the roof of the post-temporal fossa. Medial to this is a curving ridge starting parallel to the posterior margin and running along the edge of the bone to a facet near the junction with

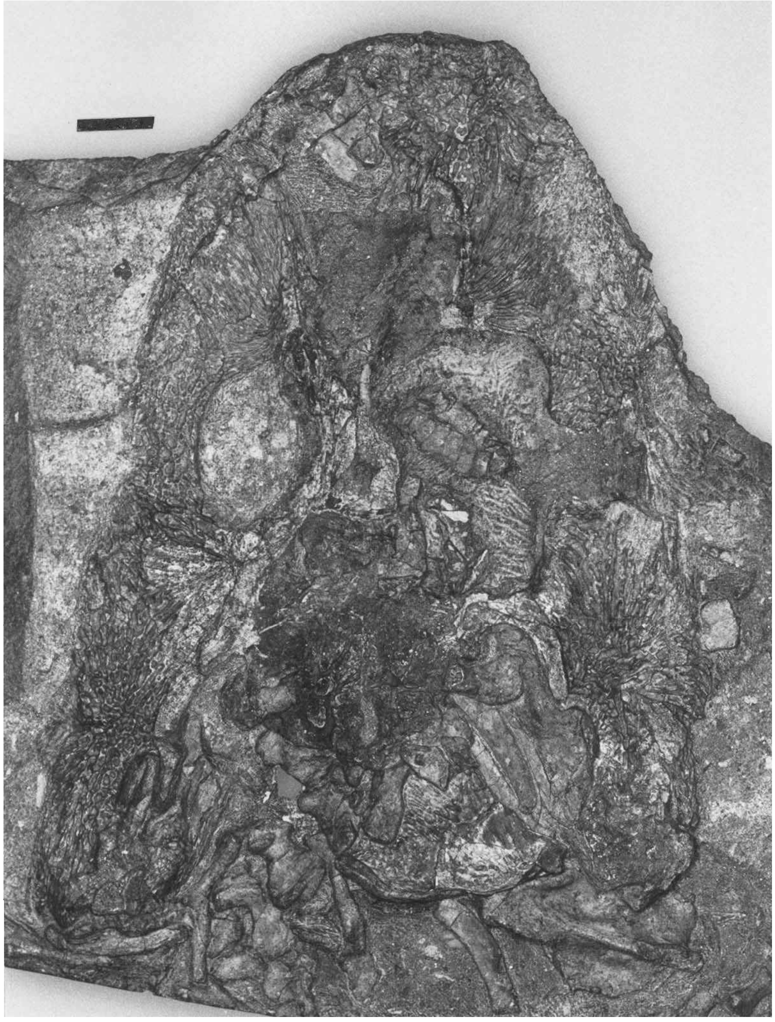

Figure 5 *Acanthostega gunnari* MGUH f.n. 1227a skull exposed in dorsal view, with skull table bones removed to show braincase; sclerotic ring present in right orbit; scale bar 10 mm.

the supratemporal. The facet, buttressed by a process of the supratemporal, clasped a process from the braincase (Clack 1998a, fig. 3 inset, 4, B, D,). Enclosed by the curving ridge is an area of fluting for further attachment of the braincase. The tabular ridge, and its groove running externally to it, also runs onto the posteroventral margin of the postparietal, though much reduced in profile. From sections (MGUH f.n. 236, 1604) and from the preservation of 1300b, it is clear that the palatal ossifications attached close up along the tabular–squamosal and supratemporal–squamosal sutures (Fig. 4C–E).

The sclerotic ring consists of about 19 or 20 plates, preserved more or less *in situ* in MGUH f.n. 1227. They are larger and almost rectangular dorsally, but smaller and having shallow W-shaped adjacent edges in the lower part of the circle (Fig. 5).

3. Skull reconstruction

External reconstructions in lateral, dorsal and occipital views are given in Figure 6A–C. Readers are referred to the photographs for details of the ornament. Figure 7, X and Y show sections through the skull at two points, their positions indicated at right, as are the positions of sections illustrated in Figure 4.

The skull has a spatulate snout, slightly depressed between the orbits to give low 'eye-brows', similar to those seen in *Ichthyostega* (Jarvik 1996), *Panderichthys* (Vorobyeva & Schultze 1991) and *Elpistostege* (Schultze & Arsenault 1985; Schultze 1996). The ridges either side of the central depressed area are formed by thickened bone, suggesting that bite-forces may have been transmitted to these areas above the orbit. Schultze (1996) suggested that the 'eye-brows' in *Elpistostege* might have supported upwardly bulging eyes, but in that case the support might be expected on the ventral rather than dorsal rim. Internally, the skull shows little in the way of struts or fluting that might otherwise be interpreted as strengthening devices, being essentially smooth except for a few minor ridges such as those on the jugal radiating from the growth centre.

The orbits are placed about the mid-point of the skull, and the eyes presumably could look both laterally and dorsally. The spatulate snout might have allowed a limited amount of forward vision also. With its lateral line canals enclosed in tubes through the bone, *Acanthostega* shows one of the most fish-like conditions among early tetrapods, rivalled only by *Ichthyostega* (Jarvik 1996) and *Ventastega* (Ahlberg *et al.* 1994). However, the distinction between 'fish-like' enclosure, and 'tetrapod-like' exposure is by no means as straightforward as it sounds. S. L. Neininger is currently studying the expression of lateral line canals in early tetrapods and related fishes, to be published elsewhere.

Recent studies on the musculature involved in lung ventilation suggest that buccal pumping is the primitive method of lung ventilation in tetrapods (Brainerd *et al.* 1993). The broad, flattened skull and the small, straight ribs of *Acanthostega* (Coates 1996) are consistent with this hypothesis, and alongside the presence of internal gills emphasise its transitional nature. The dentition suggests a fairly unspecialised animal, feeding on relatively small, or possibly moribund, prey, other aspects of the skeleton suggesting a normally sluggish, aquatic-lurking predator capable of rapid bursts of speed, rather like the giant Japanese salamander *Andrias.*

4. Discussion

4.1. Size distribution and taphonomy

Fourteen skulls were complete enough to make comparable measurements of the skull table possible. Measurement of skull length as a whole was not possible in more than one or two skulls because of incompleteness or distortion. Measurements were made as follows: distance from midline to apex of tabular notch (1); apex of tabular notch to rear of orbit (2); distance from apex of notch to parietal foramen (3); maximum length of the postparietal (4); maximum width of the postparietal (5); distance from centre of parietal foramen to posterior edge of skull (6). The results are presented in Table 1 and Figure 8.

The main finding of this suite of measurements was that, apart from minor differences in proportion probably explained by distortion, the specimens from the Stensiö Bjerg Britta Dal Formation locality fell in close proximity to each other, whereas the largest and smallest specimens were from elsewhere. The holotype, from Wiman Bjerg, and MGUH f.n.6085, from Celsius Bjerg, were the two largest, and MGUH 6085 is also somewhat anomalous in proportion. MGUH f.n. 1400 (Figs 9, 10), the smallest specimen, is also from Wiman Bjerg. Figure 9 shows these two skulls alongside two from Stensiö Bjerg, drawn to the same scale and aligned on the parietal foramen. The specimen from the Aina Dal Formation locality on Stensiö Bjerg (MGUH f.n. 1330) also appears to be smaller than average, but unfortunately it is too incomplete to measure. There are too few specimens with snouts in the sample to establish reliably whether snout growth is allometric or isometric.

The closeness in size of the Britta Dal specimens suggests that they were part of a year-group, perhaps brought together

Table 1 Table of measurements of *Acanthostega* specimens

Specimen	Midline-notch	Notch-orbit	Notch-par.for.	Length postpar	Width postpar	Postpar-par.for
1400	13	15·5	18	13	7·5	22
243	15	16	?	18	9	?
268	15·5	?	?	21	6·5	?
1300b	15·5	20	21	18·5	9·5	21
231	16	?	20	16	9	23
1377	16	?	20	18	12	27
1300a	16·5	20·5	24·5	21·5	12	24·5
1274	17	19	22	18	11	25
261	17·5	?	24	20	11	29
218	18	20	22	20·5	15·5	27
1227b	18	21	25	?	11·5	?
251	18	21	23	21·5	12	31
6033	19	20	24	21	13	32
6085	20·5	18	26	18	11	28

Abbreviations: par.for., parietal foramen; postpar, postparietal

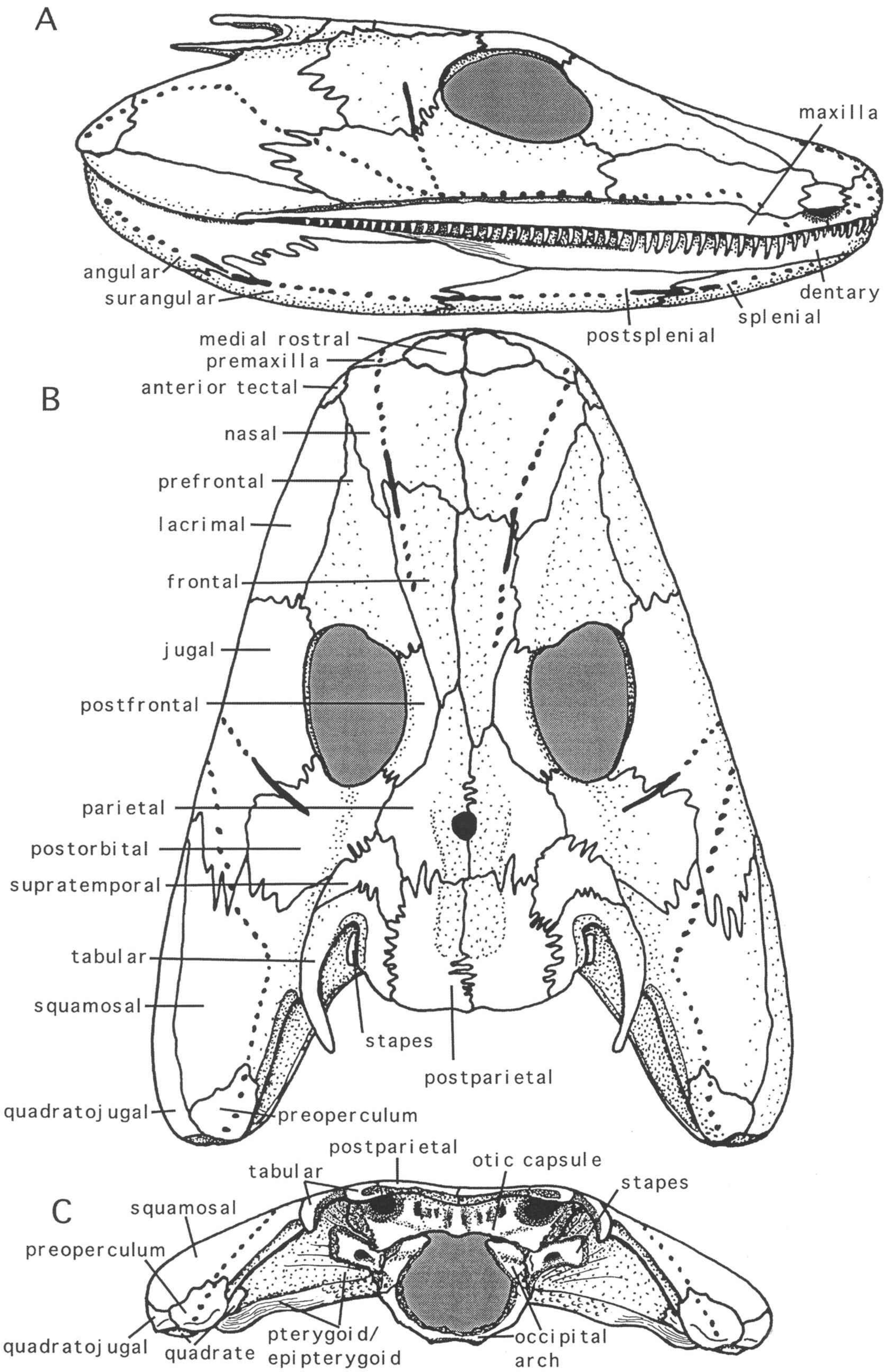

Figure 6. *Acanthostega gunnari*, skull reconstructions: (A) lateral view; (B) dorsal view; (C) occipital view.

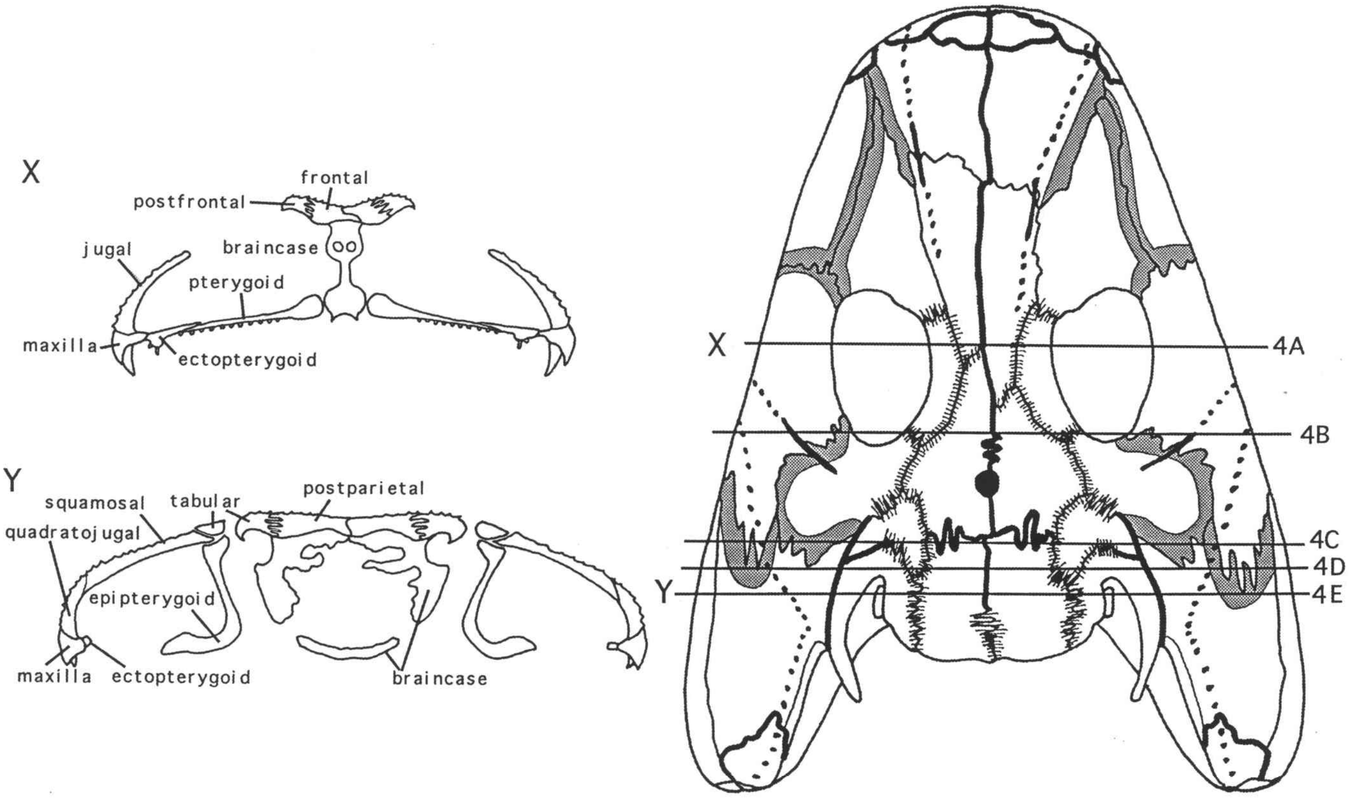

Figure 7 Left, reconstructed sections of the skull of *Acanthostega gunnari* at X and Y positions indicated at right. Right, diagram of skull roof showing conditions of sutures; grey shading shows regions of underlap (areas are approximate); heavy lines show sutures with minimal overlap or plain bevels; cross-hatched lines show complexly interdigitated sutures with 'plug contacts'; 4A–E show positions of sections illustrated in Figure 4.

for some purpose such as spawning. The most complete skeletons were all found on the same bedding plane (Bendix-Almgreen *et al.* 1990) and represent a single depositional event. However, a single small lower jaw specimen (Ahlberg & Clack 1998) found at this locality shows that at least a few younger individuals were preserved in the deposit. The deposit shows at least one other, and perhaps two other depositional events (Bendix-Almgreen *et al.* 1990), and it is not known at which event the small jaw was deposited.

Recent interpretations of the locality have suggested that rather than an active channel (Bendix-Almgreen *et al.* 1990; Coates 1996), the lens in which the specimens were found was formed as a flash-flood deposit (J. E. A. Marshall & T. R. Astin, pers. comm.), though their distribution still suggests they were swept against a point bar. Mud-cracks through some of the most complete specimens suggest they were exposed to the air for some period of time before burial, but the completeness of many specimens suggests that the bodies

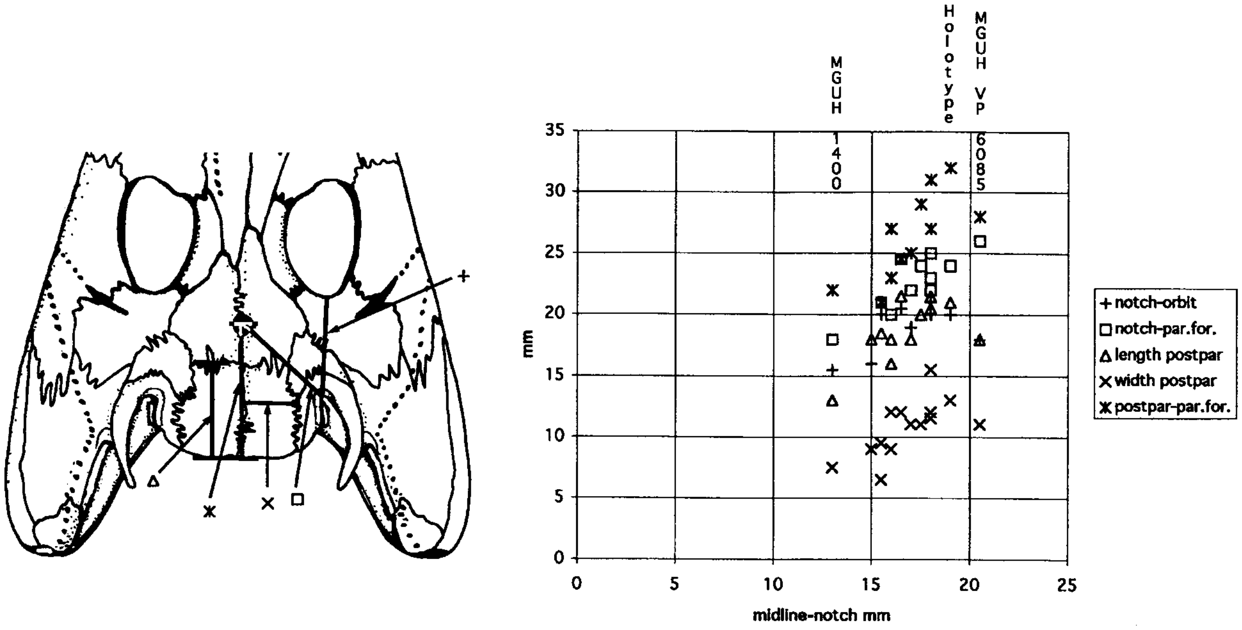

Figure 8 Graph showing measurements of skulls of *Acanthostega gunnari* given in Table 1.

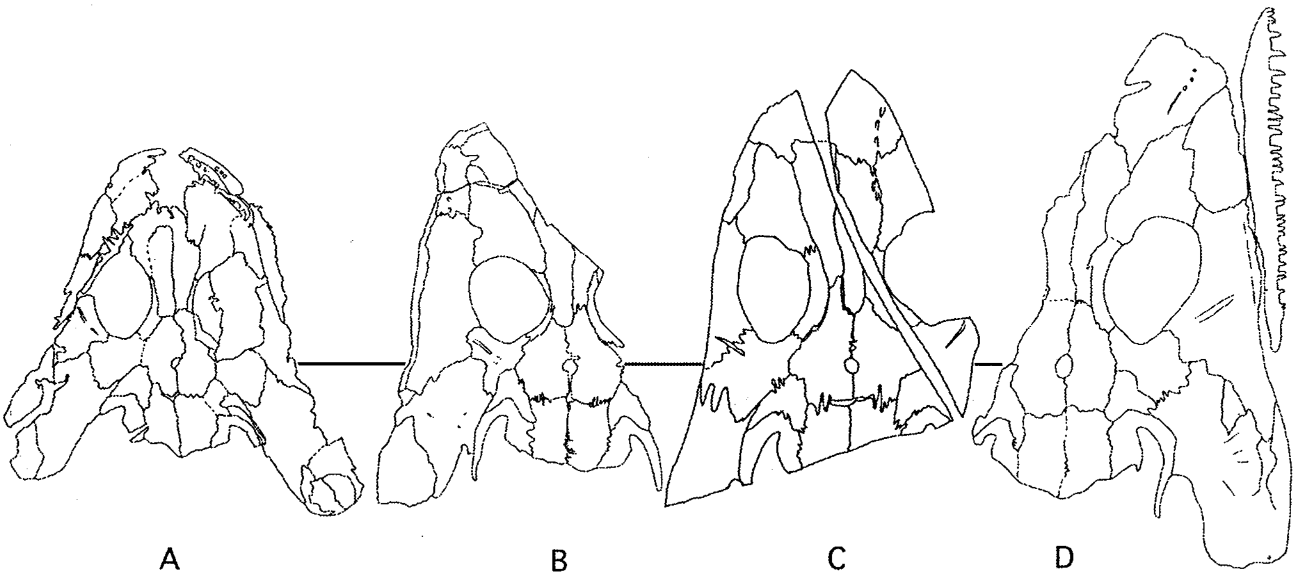

Figure 9 Drawings of four skulls contributing to Table 1: (A) MGUH f.n. 1400 (Wiman Bjerg), the smallest of the skulls; (B) MGUH f.n. 1272 (Stensiö Bjerg); (C) MGUH f.n. 1227b (Stensiö Bjerg); (D) MGUH 6033 (Wiman Bjerg) holotype, the largest (in some dimensions) of the skulls.

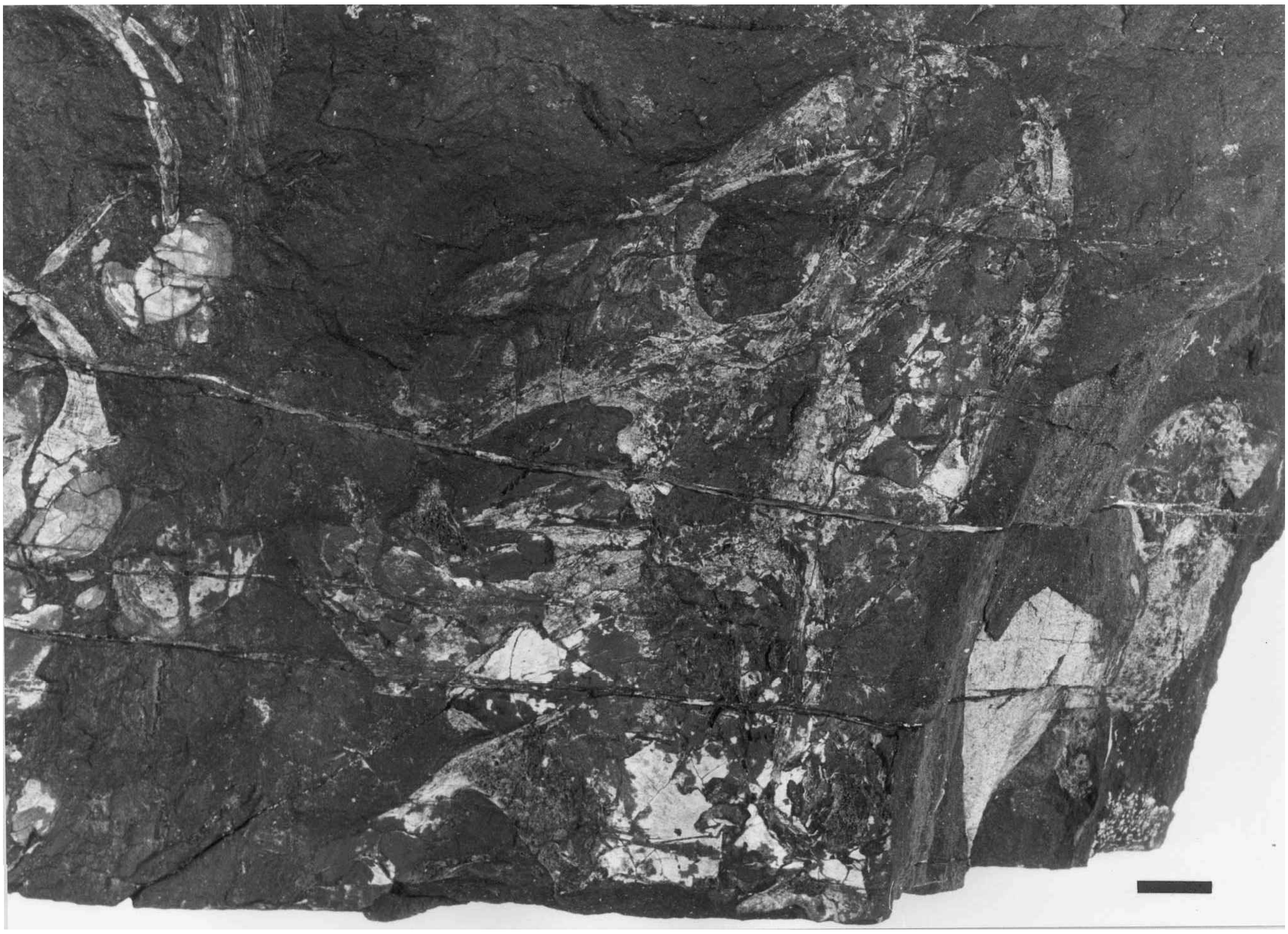

Figure 10 *Acanthostega gunnari* MGUH f.n. 1400: photograph of the smallest skull, found on Wiman Bjerg; for interpretive drawing, see Figure 9A; scale bar 10 mm.

may not have been transported far. There is no evidence that the exposed bones were transported further by water once the flood had deposited the carcases and they show no sign of tumbling or other wear, indeed the preservation of the external surface of *in-situ* material is extremely good. In some cases the internal structure has also been very well preserved, showing histological and microarchitectural detail, though in other places diagenesis has damaged the internal structure by post-mortem dissolution (S. L. Neininger, pers. comm.). The differential distortion of the skulls, some flattened dorso-ventrally, some laterally, suggests that though the bodies had been piled against the point bar, with many of the skulls orientated in approximately the same direction (see Coates 1996), others had been piled at random, and often after partial disintegration. Some skulls, notably MGUH f.n. 1300b, have also been twisted as well as compressed. In the area of deposition, the strata lie almost horizontally, though below the collecting site a low-angle fault runs through the underlying Wiman Bjerg Formation, and it is not clear whether tectonic activity along this fault, regional metamorphism, or partial post-mortem decalcification of the bone has brought about the distortion.

4.2. Sutures

Kathe (1995, 1999) studied the types of sutures found in a series of discosauriscid and temnospondyl skulls, and his are the only studies to examine the sutures of early tetrapods. Though Permian in age, these animals might provide good analogues for *Acanthostega* in that they were largely aquatic, have comparably flattened skulls, and in some cases a similar snout outline. Comparison between positions and types of suture in their skull roofs should be instructive. Kathe (1995) categorised sutures into eight different forms varying in complexity and function, and distinguished between the external exposure of the suture, which he termed the ‘seam’, and the cross-sectional appearance. In 1999, he simplified the categories into three main types: (1) simple sutures with moderate obliquity, (2) sutures with extreme obliquity, and (3) complex sutures. (Note that Kathe used the term ‘suture’ for bone-to-bone contacts of all types, regardless of whether he postulated movement between them. Kathe’s is the sense in which the term is used here, and among early tetrapod workers generally.)

Category 1 included sutures with regularly or irregularly rugose surfaces, termed ‘lamellae’ or ‘basal lamellae’, and sutures lacking the lamellar surfaces, termed ‘flat bevels’ (also called ‘scarf joints’: Busbey 1995; Hildebrand & Goslow 2001). Category 2 included sutures with steep walls or butt joints. Category 3 included sutures that showed grooved contacts (‘tongue-and-groove’) or ‘plug’ contacts in which fingers of bone inserted into holes in the adjacent bone (also called ‘serrate joints’: Hildebrand & Goslow 2001). The different sutural types have different mechanical properties: some may be totally immovable while others allow a certain amount of flexibility. Bolt (1974) suggested that areas of underlap should help to resist torsion and studies on mammals show that they can absorb shock (Jaslow 1990). Where the underlap is ridged or lamellar, movement can only occur along the direction of the ridges, and where there are no ridges, movement can occur along the bevel, but torsion is still resisted. Thus they are likely to be found where the skull undergoes asymmetrical biting forces or twisting. Butt joints may also allow some mobility across the joint, but can resist forces acting at right angles to the joint. Grooves and plug contacts reduce mobility to the greatest extent.

Kathe found a largely consistent pattern in the overlaps and complexity of sutures among the animals he studied. Firstly, category 3 sutures were not found. Secondly, bones with lamellae or basal lamellae all had their underlapping surfaces in consistent places. In the snout, the underlap surface was placed under the bone anterior to it, though the parietals and postparietals also had underlaps beneath bones lateral to them. In the temnospondyl series, sutures with no overlaps at all were found in the snouts and the postfrontal–postorbital sutures of the long-snouted forms, though in the short-snouted forms, these were almost entirely confined to the maxilla and its suture with the lacrimal and jugal and the postfrontal–postorbital sutures. Kathe noted a trend towards increasing overlap areas from long to short-snouted forms, and that this changed during ontogeny as well as according to the final adult form. The postorbital region of the skull was always more firmly sutured with overlap joints than the preorbital region.

Acanthostega shows a marked and surprising contrast with the temnospondyls and discosauriscids studied by Kathe. The first thing to note is that one suture may show different forms along its length, so that they do not fit easily into Kathe’s categories. The second is that Kathe’s categories appear to be too simple to accommodate all the sutural types found in *Acanthostega*. Some sutures are difficult to evaluate because the material does not always provide good sections, so, for example, it is not possible to see whether the underlap surfaces are ridged or not (though most of the underlap surfaces probably are). However, in some cases it is clear that several types may be combined. So, for example, the midline suture between the frontals appears in part to show a tongue-and-groove as well as an overlap surface. There are many places where extremely complex sutures are found, so that the bones interdigitate in three dimensions in a hypertrophied version of the ‘plug contact’. There are also places where three bones over- and under-lap each other, forming a ‘sandwich’.

Figure 7 shows the distribution of sutural types as accurately as the material currently allows. One observation that is consistent with Kathe’s (1999) findings is that the bones in the postorbital region of the skull are more firmly sutured, with plug-contacts in *Acanthostega*, than those in the preorbital region. The midline suture preorbitally is one of the weakest areas, as it is in *Archegosaurus* and *Chelidenpeton*, and, as in *Chelidenpeton*, *Acanthostega* also shows a poorly sutured region at parts of the midline parietal suture. In the field, it was noted that many *Acanthostega* skulls were split down the midline, and median rostrals, premaxillae and maxillae were often missing, an observation corroborated by the sutural types found between these bones and their neighbours. In contrast to temnospondyls and discosauriscids, there appears to be no consistent pattern to the position of the underlap surfaces. As described above, the jugal has underlap surfaces to all the surrounding bones except the maxilla, and where the jugal, prefrontal and lacrimal meet, the three bones form a complex three-layered overlap. If the implications drawn from specimen MGUH f.n. 219 are correct, the postorbital is broadly underlapped by the squamosal and the jugal, similar relations to those found in the discosauriscids, but an exaggerated version of them.

Some sutures have a complex seam in external view, but this does not necessarily mean a complex suture in section. For example, in specimen 1227b, part of the parietal–postparietal suture showing high-amplitude waves has begun to open up, suggesting that it is not firmly interdigitated (Fig. 3C–D). By contrast, the postfrontal–parietal suture is simple in external view, belying the fact that in section it is extremely complex.

Butt-joints between the maxilla and the bones above it (noted by Jarvik (1952)) suggest resistance to vertically acting forces from the teeth, and a matching butt-joint is found between the dentary and the underlying bones (Ahlberg & Clack 1998). These junctions are hypothesised to permit some 'give' laterally, perhaps from struggling prey. The forces from biting would be transmitted vertically to the lacrimal and jugal, which could explain the bowed shape of these bones, that only more dorsally begin to curve inwards. Broad overlap areas are found at the sides of the snout and behind the orbit where jugal, squamosal and postorbital meet, resistant to torsion, but absorbing forces (Bolt 1974). Broad 'scarf joints' are also found in analogous places in the snout of alligators and other secondarily flattened crocodilians, even though these animals have much more massively constructed and complex skulls with secondary palates (Busbey 1995). In *Acanthostega*, the remaining forces would probably be transmitted to the most consolidated parts of the skull such as the ridges between the orbits, and round the skull table. The squamosal–tabular suture with its simple bevel might have acted as a shock-absorber, analogous in function to the 'kinetic' cheek–skull-table joint of embolomeres (see Panchen 1970).

The most complex and interdigitated sutures are found where the bone is thickest, such as dorsal to the orbits between the postorbitals and parietals, and between the postparietals and tabular, and supratemporal and postorbital. This is consistent with the idea that these are places that undergo most stress. In contrast, the areas of broadest overlap occur where the bone is thinnest, on each side these being the mid-snout and mid-cheek regions, perhaps allowing a degree of flexibility there.

In section, it is sometimes difficult to trace the precise course of a suture because of the presence of 'overwritten' sutural contacts, known as 'nahtfaserknochen' (Gross 1934), left behind as the animal grows. There is no real evidence that sutures closed entirely during life as is often the case in tetrapodomorph fishes.

The overall pattern of sutural types in *Acanthostega* contrasts strongly with both fishes such as *Eusthenopteron* on the one hand, and the temnospondyls and discosauriscids on the other. In *Eusthenopteron* (Jarvik 1980) and 'osteolepiform' fishes generally, seams are all relatively straight, and overlap areas narrow. *Panderichthys* and *Elpistostege* (Schultze & Arsensault 1985; Vorobyeva & Schultze 1991; Schultze 1996) are exceptions, in that they have seams that suggest strongly interdigitating sutures, although the three-dimensional structure of these has not been studied. This may suggest that *Panderichthys* and *Elpistostege* were more tetrapod-like in their habits and the stresses that their skulls underwent. This could be read to mean that they were subject more to the effects of gravity than *Eusthenopteron*, in raising the head out of water for feeding or breathing, or that the feeding method was different and involved more torsional forces on the snout. Schultze (1996) suggested that *Elpistostege* swam with its eyes out of the water, but that it still breathed with gills with its snout immersed.

By contrast with the temnospondyls and discosauriscids, the skull roof of *Acanthostega* seems overengineered. Despite what may have been analogous life-styles, the sutures in *Acanthostega* are far more complex, as if they had to cope with greater stresses. However, given the tooth morphology and formula, that seems unlikely. Rayfield (pers. comm.) suggested that *Acanthostega* was quite amniote-like in its suture pattern, but it remains to be seen how widespread this construction is among early tetrapods. Other factors may also be at work. During the evolution of tetrapod skulls, as is seen within other groups of vertebrates, initially heavily armoured skulls are gradually replaced by lighter, often kinetic skulls in which the dermal bones are reduced to struts. One suggestion for the origin of dermal bone has been that it served as a foundation for electro- and mechano-receptive systems in early vertebrates (Gans 1989). In *Acanthostega*, the lateral line canal still ran through tubes in the bone for the most part, as it did in tetrapodomorph fishes. In temnospondyls and discosauriscids, the lateral lines run in broadly open grooves, and in discosauriscids additionally, pits for possible electroreceptors have been described (Klembara 1996). These two groups retain a complete dermal skull roof covering, as do other early tetrapod groups that retain lateral lines, but having them more superficially placed may have allowed the bone to be relatively thinner. Among modern tetrapods, amniotes lack lateral lines altogether, while among lissamphibians, lateral line canals are lost and only superficial neuromasts are retained, in aquatic adults. Skull roofs may only have been able to become reduced, as they become among lissamphibians and amniotes, once the lateral line canal system was reduced or lost. Alternative ideas may be that some microarchitectural property of the dermal bone in the later forms allowed them to reduce the strengthening of the skull roof at the sutures, or that greater flexibility was desirable for some reason in these animals. This might be difficult to verify, however, as it would involve looking at suture patterns and average bone thickness in a much wider range of early tetrapods than has yet been done. It will be interesting to see whether *Ichthyostega* shows a similar phenomenon to *Acanthostega* in this respect.

This subject demands a fuller study using modern methods such as Finite Element Analysis (FEA) (e.g. Rayfield *et al.* 2001) to determine the stresses undergone by an early tetrapod skull such as that of *Acanthostega*. The shift from feeding in water to feeding on land implies quantitative and qualitative changes in the stress patterns experienced by the skull, and the technique could explore whether an early tetrapod showed adaptations for the latter. Ahlberg & Clack (1998) showed a series of changes to the lower jaw that might also be explicable as responses to changed mechanical stresses during the shift from water to land, and the FEA technique could test such an hypothesis. It could also test proposals for possible kinetism at certain bone junctions such as the skull table–skull roof (e.g. Panchen 1972 for '*Eogyrinus*'), the maxilla–cheek junction (above and Jarvik 1952), the pterygoid–palatine/ectopterygoid junction in early tetrapods (e.g. Clack 1992), along the back of the suspensorium (e.g. Beaumont 1977 for baphetids) or at the basipterygoid joint (see Clack 1998a).

4.3. Observations on the skull roof of Devonian tetrapods

Of all the known Devonian tetrapods, *Acanthostega gunnari* bears the closest resemblance to *Ventastega curonica* (Ahlberg *et al.* 1994) from Latvia. There are detailed differences in the dentition that confirm the animals as different species, especially in the dentition of the lower jaw, where *Ventastega* retains paired coronoid fangs at the centre of the tooth-row on coronoids one and two. Other differences include: the retention of a surangular pit-line in *Ventastega* and a somewhat higher position to the articular region; a frontal that widens more anteriorly (if the isolated bone is correctly interpreted as a frontal (Ahlberg & Lukševičs 1998)); differences in the position of the fang pairs on the vomer and palatine, and in the absence of an accessory row of denticles on these bones; and an interclavicle with a very slightly longer anterior portion in *Ventastega* (*ibid.*) The most diagnostic skull bones in *Acanthostega*, namely the supratemporal and tabular, are unfortunately missing from the *Ventastega* material, but similarity of the skulls in other respects could make one anticipate similar features in *Ventastega*. The shape of the premaxillae certainly suggests the presence of paired, but loosely sutured median rostrals in this animal as in *Acanthostega*.

The similarity in skull form is not, however, borne out by the limb bone attributed to *Ventastega*. Interpreted as either an ulna or a tibia, this incomplete element appears broader and flatter than either of the equivalents in *Acanthostega.* The bone (re-)interpreted as an ilium by Ahlberg *et al.* (1994) appears to me to be a cleithrum, as they were initially inclined to think. Only further finds from Latvia will confirm just how close *Ventastega* and *Acanthostega* actually are. Ahlberg & Clack's (1998) analysis of lower-jaw characters placed *Ventastega* as consistently more primitive than *Acanthostega.* However, this stemmed largely from the dentition and pit-line characters mentioned above, and additional information could easily overturn their results.

If *Acanthostega* and *Ventastega* eventually prove to be very similar, with similar postcranial anatomy, they may represent a widely distributed radiation of closely related Devonian tetrapods of similar life-style and habits. However, should they turn out to be very different in critical regions of the skull and postcranium, they may indicate that some Devonian tetrapods, while remaining highly conservative in certain cranial features, nevertheless acquired different body-forms and adapted to different niches. The latter may prove correct, since the lower-jaw morphology of known Devonian tetrapods is distinguished, like *Acanthostega* and *Ventastega*, largely on dentition. A recently described jaw-fragment from Latvia (Ahlberg *et al.* 2000) shows just how extreme dental morphology could be among stem-tetrapodomorphs.

Conservative parts of the cranial anatomy of Devonian tetrapods generally are the bone configuration of the lower jaw (Ahlberg & Clack 1998), and of the palate, cheek and snout, while the major distinguishing features appear in the dentition and skull table regions. Not only are *Ventastega* and *Acanthostega* similar in jaw construction, cheek, snout and palate, but this is also the region where *Ichthyostega* resembles *Acanthostega.* The major differences between the latter two lie in the skull table and dentition, as well as the postcranial skeleton, where they differ radically. The braincase will be one area of future interest, as this region also differs fundamentally in *Ichthyostega* and *Acanthostega.* Information on the braincase of *Ventastega* would be of especial value.

Looking more broadly at the evolution of the skull table region, it appears that across the fish–tetrapod transition, this region of the dermal skull roof is subjected to particularly great change. It is this region that has caused so many problems and arguments in the past in terms of working out bone homologies, while other parts like the cheek, suspensorium and palate have not proved nearly so difficult to equate. This may partly result from the close apposition under the skull table of the otic region of the braincase, another region subject to great and probably quite rapid change (Ahlberg *et al.* 1996) in the early evolution of tetrapods. The region continues to undergo change and it has been known since Romer's and Westoll's work (Romer 1937; Westoll 1943) that the postorbital portion of the skull gets proportionately shorter across the fish–tetrapod transition (see also Bernacsek & Carroll 1981), and on into the origin of amniotes. However, some component of change must also be connected with the evolution of the occiput and construction of the tetrapod neck. This region, as shown above, is the most strongly constructed in terms of suturing. It may reflect not simply forces generated from feeding but from the need to attach axial musculature for holding up the head.

By contrast with the skull table, the conservative units of the skull are, for the most part, those associated with the passage of a lateral line canal, and it may be significant that among early tetrapods, one of the first parts of the skull (apart from the skull table) to undergo radical modifications is the palate, lacking lateral line canals, in which temnospondyls develop large vacuities at an early stage of their evolution.

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6. Note added in proof 19 April 2002

As a result of the recent discovery of an internasal fontanelle in new material of *Ventastega curonica* (P. E. Ahlberg, pers. comm.; pers. obs.), it has become apparent that a reinterpretation of the snout sutures of *Acanthostega* is necessary. No specimen shows a complete uncrushed snout in which the nasal–nasal or nasal–median rostral sutures are well displayed. It was previously assumed that *Acanthostega* had simple but conventional sutures at these junctions. However, re-examination of MGUH f.n. 1227a and b, 1300a, 1305, 1400 and the holotype specimen reveals that the nasal bones do not suture together in the midline, and there is also a gap between the nasals and anterior tectals. The width of the gap is unclear because of crushing of most specimens. In one of the best-preserved specimens MGUH f.n. 1227b (Figs 3B, 9C), an almost complete and scarcely distorted skull, neither the nasals nor the frontals meet in the midline but are separated by a gap of about 4 mm. This may represent the natural degree of separation of these bones. The smallest skull, MGUH f.n. 1400 (Figs 9D, 10) shows a hole in this region previously assumed to be damage, and in the holotype, the medial margin of the right nasal is not only offset from the midline, but has a slight embayment at its anterior end (Fig. 9D; Jarvik 1952, plate 21). In MGUH 1227a, the left nasal is missing altogether (Fig. 5). Specimen MGUH 1305 shows the region in longitudinal section, where a gap between the right and left nasals can be seen. Specimen MGUH f.n. 1300a shows a gap between the nasals and median rostrals, though the nasals touch (but do not suture) in the midline, at least anteriorly.

The existence of this vacuity helps to explain the distortion of this region in the few specimens where the snout is preserved, and indeed the loss of snout bones in most skull specimens, noted in the field during collection. The gap would have exposed part of the, presumably cartilaginous, anterior ethmoid region of the braincase, but its function, if any, is unknown.

A revised reconstruction of the skull of *Acanthostega* will be presented in a forthcoming issue of the *Transactions.*

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