Fish-like gills and breathing in the earliest known tetrapod

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THE origin of tetrapods is generally associated with the emergence of terrestrial vertebrate life. Anatomical features unique to tetrapods are usually considered to be adaptations to the terrestrial environment. Here we report the discovery of a fish-like branchial skeleton in *Acanthostega gunnari*, from the Upper Devonian of East Greenland, one of the earliest tetrapods known. It shows a proximally expanded ceratohyal and large, ventrally grooved ceratobranchials. Such grooves are found in the ceratobranchials of modern fishes, and house the afferent branchial aortic arches. The shoulder girdle bears a postbranchial lamina along its anterior margin. In fishes this supports the posterior wall of the opercular chamber. *Acanthostega* seems to have retained fish-like internal gills and an open opercular chamber for use in aquatic respiration, implying that the earliest tetrapods were not fully terrestrial. The discovery provides information on the sequence of acquisition of tetrapod characters, and supports previous suggestions that such characters as legs with digits[1] evolved first for use in water.

The material of *Acanthostega gunnari* was found in 1987 by a Cambridge-Copenhagen expedition[2]. Most of the information on the branchial skeleton has come from an almost complete articulated specimen MGUH (Geology Museum, University of Copenhagen), field number 1227, which has already yielded the earliest-known tetrapod stapes[3] and an eight-digited forelimb[1]. Other material yielding hyobranchial elements includes UMZC (University Museum of Zoology, Cambridge) T 1300 and MGUH 1258 and 1300. Associated with MGUH 1227 are six or seven ceratobranchial elements, the right ceratohyal and less certainly two hypohyals (Fig. 1). Most lie almost in the expected life position, although the right ceratohyal has been rotated by 180° and lies on the left side. An incomplete left ceratohyal is known from specimen MGUH field number 1300 (Fig. 2*b*), and Fig. 2*a* shows a reconstructed left ceratohyal in lateral view.

The best preserved ceratobranchial is bifurcated anteriorly for articulation with the basibranchial and, where exposed, the elements bear deep grooves along their ventral surfaces (Fig. 1*c*). Such grooves resemble those in the ceratobranchials of most bony fishes. The ceratohyal is expanded proximally (posteriorly) into a blade with a rounded end bearing a strong ridge on its lateral surface, whereas distally it is narrower and grooved. The ceratohyal, and other known elements of the hyoid arch, most closely resemble those of a Devonian lungfish such as *Chirodipterus*[4] rather than the proximally narrow, bipartite ceratohyal and large hyomandibula of the Devonian osteolepiform *Eusthenopteron*[5].

This branchial skeleton is more fish-like than that of any other known tetrapod. Some temnospondyl specimens, the group of largely Palaeozoic amphibians which is thought to have given rise to frogs and probably urodeles[6], preserve some of the branchial skeleton. In *Dvinosaurus* the ceratobranchials are stout blunt-ended elements, bearing faint groves on the ventral surface, interpreted as showing that this animal was perennibranchiate, with external gills[7,8]. The ceratobranchials of *Acanthostega* are much more deeply grooved and more thoroughly ossified; other early tetrapod ceratobranchials are short, suggesting incomplete ossification of the gill skeleton (see also those of the actinopterygian *Psephurus gladius*[9]). In modern fishes, such grooves are associated with the possession of paired gill filaments, and carry the afferent branchial aortic arches. The most gill-dependent of the living lungfishes, *Neoceratodus*[10], has cartilaginous ceratobranchials which resemble those of *Acanthostega* (M.I.C., unpublished observation). Morphologically similar and fully ossified gill skeletons are found in *Polypterus*[11], the fossil gill-breathing lungfish *Chirodipterus*[4,10], and *Eusthenopteron*[5].

Further fish-like characters are found in the shoulder girdle (specimens MGUH 1258, 1227) (Fig. 3). The cleithrum is a large dermal element in *Acanthostega*, comparable only to that of *Ichthyostega* among tetrapods. The scapular blade is co-ossified with the cleithrum and its extent is uncertain, but there is no supraglenoid foramen. The anterior edge of the cleithrum carries a distinct anteroventral process which clasped the dorsal process of the clavicle. This character is unique to *Acanthostega* among tetrapods, but shared with Palaeozoic sarcopterygians such as the lungfish *Scaumenacia*[5] and the osteolepiform *Eusthenopteron*[5]. The cleithrum bears a smooth postbranchial lamina similar to that found in gill-breathing bony fishes, where it forms the posterior wall of the open opercular chamber. *Acanthostega* retains an anocleithrum, part of the supracleithral series of bones, generally lost in tetrapods. *Tulerpeton*, from the Upper Devonian of Russia[12], is the only other tetrapod known to retain an anocleithrum. In *Acanthostega* it is a large ovoid bone articulating with the dorsal end of the cleithrum mesially, and known from both isolated and articulated specimens. It resembles that of the extant lungfish *Neoceratodus*[5].

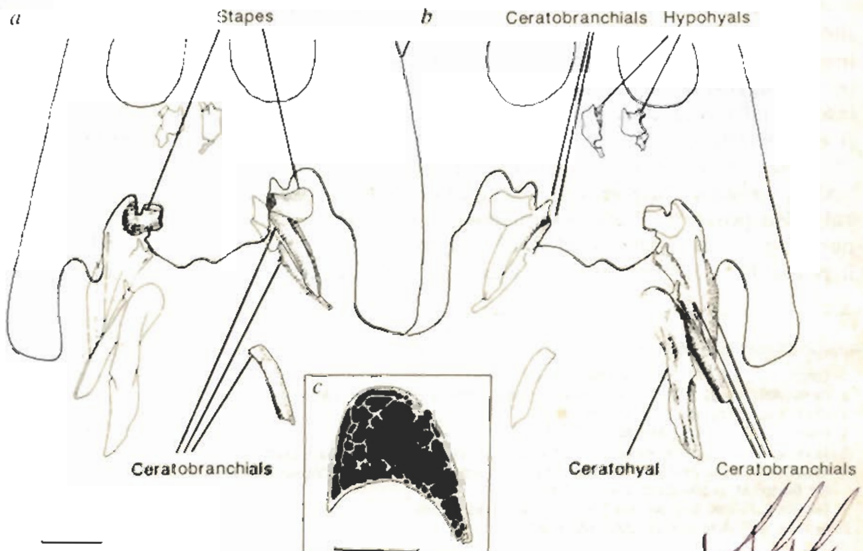

FIG. 1 *Acanthostega gunnari*. *a*, Dorsal view of branchial skeleton (MGUH 1227). Thick outer line indicates perimeter of postorbital region of skull. Outlines indicate relative position of branchial skeleton revealed on ventral surface. *b*, Ventral view of branchial skeleton (MGUH 1227). Diagram follows same convention as in *a*. Scale bar, 10 mm. *c*, Cross-section through ceratobranchial (UMCZ T 1300). White areas are preserved bone; black area is matrix infill of endochondral spaces. Scale bar, 2 mm.

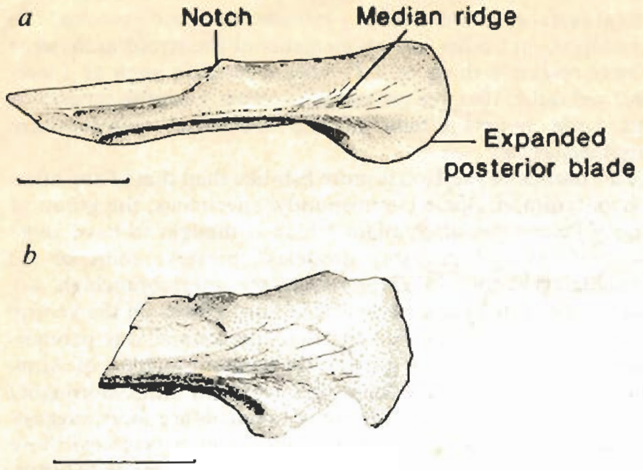

FIG. 2 *Acanthostega gunnari*. *a*, Lateral view of reconstructed left ceratohyal, anterior to left of plate. *b*, Incomplete posterior portion of left ceratohyal, UMZC T 1300. Scale bar, 10 mm.

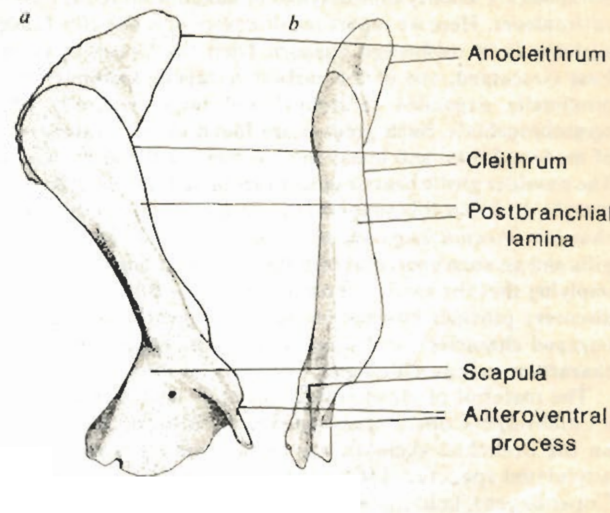

FIG. 3 *Acanthostega gunnari*. Right pectoral girdle (incomplete ventrally) (MGUH 1258), showing articulation between cleithral blade and anocleithrum, broad postbranchial lamina, and anteroventral process. *a*, Lateral view; *b*, anterior view. Scale bar, 10 mm.

Many modern tetrapods retain the branchial skeleton, though it is not used to support respiratory internal gills. The unossified branchial skeleton of the urodeles resembles most closely the fish condition. In urodeles it supports the tongue musculature and the floor of the buccal cavity, moving it during buccal ventilation[13]. Larval and perennibranchiate amphibians retain an open operculum and gill clefts supported by the branchial skeleton. The branchial arches are not grooved but oval in section, and the shoulder girdle makes no contribution to the posterior wall of the opercular chamber. There are only external gills and no paired filaments (M.I.C. and J.A.C., unpublished observation). Specimen MGUH 1227 was not apparently full-grown, having a skull and humerus about one-third smaller than the largest known individuals; however, the gill skeleton, phalanges and tarsus were well ossified and the dermal ornament well developed. There is no evidence that this individual was premetamorphic or paedomorphic.

Acanthostega combines characters of the gill skeleton and shoulder girdle that are associated in fishes with functional internal gills. The morphology is most parsimoniously explained by the suggestion that *Acanthostega* also possessed functional internal gills, a primitive retention unknown in other tetrapods. It is generally believed that possession of lungs is a primitive character in osteichthyan fishes, and they are found in the actinopterygian *Polypterus* and lungfishes. *Acanthostega* probably also possessed lungs, ventilated by movements of buccal pumping involving the hyoid arch[3] as in these fishes. Like them, it probably used both modes of gas exchange in appropriate circumstances.

Retention of fish-like internal gills by a Devonian tetrapod blurs the traditional distinction between tetrapods and fishes[14]. It shows that the opercular, submandibular and gular series of bones were lost from the skull while the internal gills were still functional. It implies that metamorphosis was a less profound process in this early tetrapod than in modern amphibians; probably restricted to loss of external gills, if any. The form of this gill skeleton and shoulder girdle suggests that *Acanthostega* was not an obligate air-breather, that it was primarily aquatic and did not derive from an even earlier but more terrestrial tetrapod. Alternatively, the ossified, deeply grooved ceratobranchials may be interpreted as having borne only external gills, or representing a retained larval morphology no longer associated with gills but incorporated into a muscular buccal ventilation system. Similarly, the postbranchial lamina may be a primitive feature of gill-less early tetrapods, unmodified from the fish condition. But none of these alternative interpretations can be found among extant vertebrates. *Acanthostega* resembles gill-breathing lungfishes: both show increased contact between the palate and braincase associated with loss of the operculogular series, reduction of the upper half of the hyoid arch (hyomandibula/stapes), proximal expansion and growth of the lower half (ceratohyal), retention of a substantial grooved gill skeleton and a pectoral girdle with a broad postbranchial lamina[4,10]. This adds further support to the suggestion that unique tetrapod characters such as limbs with digits evolved first for use in water[1,15] rather than for walking on land. □

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