

# Patterns and Processes in the Early Evolution of the Tetrapod Ear

Jennifer A. Clack

University Museum of Zoology, Cambridge, Downing St., Cambridge CB2 3EJ, United Kingdom

*Received 19 July 2002; accepted 19 July 2002*

**ABSTRACT:** This article reviews some of the latest information on the evolution of the tetrapod ear region as seen in the fossil record. It looks at the changes that can be documented across the fish–tetrapod transition, the patterns that they show and what can be inferred of the processes that brought some of them about. These processes include an increased role for neural crest, and heterochronic processes such as pedomorphosis. The earliest tetrapods show a common pattern of a short stout stapes with a large stapedia foramen, that primitively contacted the palatal bones and probably supported the braincase. Modifications to this pattern can be seen in tandem with changes to the occiput and are bound up with changes to jaw and breathing mecha-

nisms. By the Late Carboniferous, tetrapods had diversified into a range of groups showing a wide variety of otic morphologies, some of which were probably tympanic, while others were not, and some which are very different from those found in extant tetrapods. In amniotes, the evolution of a tympanic ear appears to correlate with consolidation and integration of the occiput to the skull roof. Competing phylogenies suggest different numbers of iterations for the origin of a tympanic ear, but a minimum of four separate occasions is implied.

© 2002 Wiley Periodicals, Inc. *J Neurobiol* 53: 251–264, 2002

**Keywords:** tetrapod; ear region; evolution; Paleozoic; stapes

## INTRODUCTION

The ear region has been of abiding interest for vertebrate palaeontologists more or less since the science began, because the ear is the sensory system that has the best fossil record. Apart from the lateral line, the other sensory systems seem to be represented almost entirely by negative evidence (although in some cases, the negative evidence can be meaningfully interpreted, as suggested below). Because the ear region and its associated skull modifications are often prominent features of tetrapod fossils, in early studies they

were used as a key to evolutionary relationships among the animals. In recent years, the characteristics associated with the ear region are no longer used by themselves as key features in phylogeny but contribute to a suite of features in cladistic studies. The evolution of the ear is still a topic of interest, however, because of the profound modifications that it shows through the evolution of tetrapods. Some of the most profound occurred around the origin of tetrapods, but further modifications accompanied the evolution of full terrestriality in tetrapods and the origins of amphibians and amniotes. This account attempts to put recent discoveries of fossil tetrapod-like fish, fish-like tetrapods, early amphibians, and early amniotes into this context, using recent phylogenetic analyses as a guide.

The picture that has emerged over the last 15 or 20 years differs radically from that which was current around the middle of the 20th century. Far from a terrestrially adapted ear with a tympanic membrane

Parts of this article were presented at the Sixth International Congress of Vertebrate Morphology, July 21–26, 2001, Jena, Germany. Supported by DRF.

Correspondence to: J.A. Clack (j.a.clack@zoo.cam.ac.uk).

Contract grant sponsor: Deafness Research Foundation (DRF).

© 2002 Wiley Periodicals, Inc.

DOI 10.1002/neu.10129

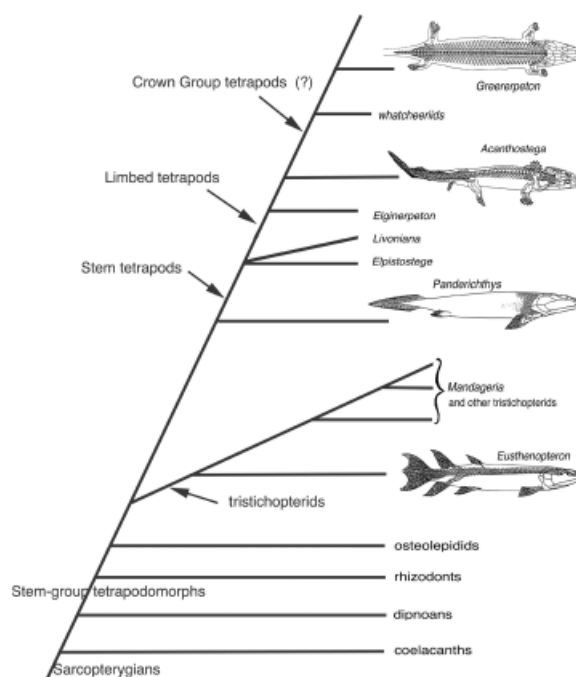
being the common property of tetrapods from the earliest stages in their history, it now seems clear that at least a tympanum with its associated accoutrements for aerial acoustic reception have evolved several times in slightly differing guises in each of several tetrapod groups. The earliest tetrapods that we know about were probably not terrestrial, and are seen as unlikely to have had aerially adapted ears. These changed perceptions were summarized by Clack (1993), and the evolution of several (at least four, just among the extant forms) iterations of tympanic ears were summarized by Clack (1997). The most recent challenges, put forward on the grounds of competing hypotheses of early tetrapod relationships (Laurin and Reisz, 1997, 1999), imply additional origins for the evolution of a tympanic ear, not fewer.

With recent progress in understanding the immediate fossil relatives of tetrapods, and in understanding some of the developmental processes in skull ontogeny, it is now possible to give some thought to what might have happened in the earliest stages of ear evolution during the fish–tetrapod transition. There still remains a morphologic chasm between the construction of the ear region as seen in tetrapod-like fishes (tetrapodomorphs) and even the most primitive tetrapods with limbs and digits, but some new discoveries are beginning to show that the gap may not be unbridgeable. A similarly large disparity lies between the otic morphology seen in the earliest tetrapods and that of the earliest amniotes. Although it is still difficult to envisage intervening stages between these, some functional correlates may be invoked to explain how the ear region subsequently changed as it did.

The “patterns” of the title may be interpreted as the morphology of the otic region and its distribution on a cladogram, with the “processes” being, more speculatively, the developmental, embryogenic, or selective processes that might have brought about these patterns. These include extrapolations of the role of the neural crest in braincase evolution, pedomorphosis in the appearance (in both senses) of tetrapods, or environmental or behavioral changes that may have been associated with the emergence (literally) of tetrapods. “Processes,” of course, also refers to anatomical processes, in particular the paroccipital process of the otic capsule, whose appearance can be shown to accompany, and may be key to, acquisition of a tympanic ear in some amniotes.

## FROM “FISH” TO “TETRAPOD”

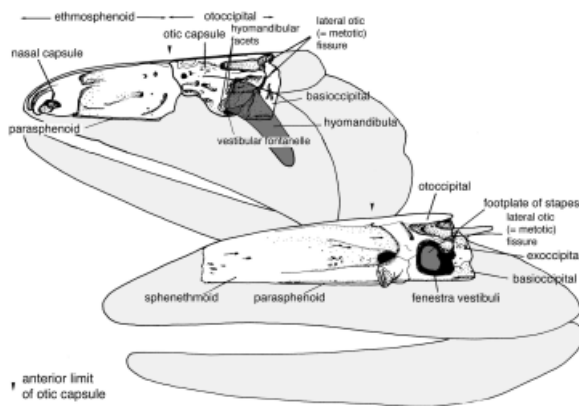
Tetrapods, informally defined here as vertebrates with limbs and digits (note that this may be different from



**Figure 1** Cladogram of the tetrapodomorph groups (based on Ahlberg and Johanson, 1998; Ahlberg et al., 2000; Clack, 2001; Johanson et al., in press; with permission of the Systematics Association).

some formal definitions of the taxon Tetrapoda), belong to a lineage of sarcopterygians more closely related to amphibians and amniotes than to other living sarcopterygians, the lungfish (Dipnoi) and the coelacanth (Actinistia). The name for this lineage is often given as Tetrapodomorpha Ahlberg, 1991. It includes a number of “fish” groups such as rhizodonts and osteolepidids, and, closer to tetrapods, the tristicopterids including the widely known *Eusthenopteron*. Closer still to tetrapods lie a number of odd genera (plesions) whose anatomy has only recently become better known. Other members of the tristicopterids have also been described recently that play a part in this story. Figure 1 is a cladogram showing the “fish” and “tetrapod” groups and their relationships, to aid in the comparison of their ear regions that follows.

Among the tetrapodomorph fish, braincase and otic regions are known for *Eusthenopteron foordi*, described in detail by Jarvik (1980), for *Panderichthys rhombolepis*, known in less detail but holding a pivotal position (Vorobyeva and Schultze, 1991; Ahlberg et al., 1996) and the newly discovered tristicopterid *Mandageria fairfaxi* (Johanson and Ahlberg, 1997; Johanson et al., in press). The earliest tetrapod braincase known in detail is that of *Acanthostega gunnari* (Clack, 1994a, 1994b, 1998), followed by *Greererp-*



**Figure 2** Comparison between the braincases of *Eusthenopteron* (above) and *Acanthostega* (below). Skull profiles shown light-shaded, stapes/hyomandibular dark-shaded. (From Clack, 2001; with permission of the Systematics Association.)

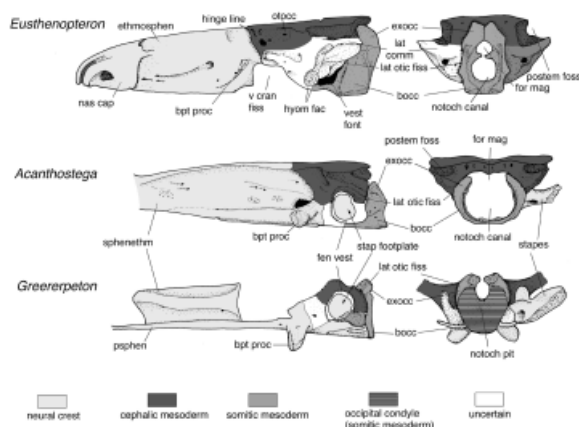
*ton burkemorani* (Smithson, 1982). All except *Greer-erpeton*, which comes from the mid-Carboniferous, are Late Devonian in age, with *Eusthenopteron* and *Panderichthys* coming from the earlier Frasnian stage, and *Mandageria* and *Acanthostega* from the later Famennian stage.

Figure 2 gives lateral views of the braincases of *Eusthenopteron* and *Acanthostega*, showing the contrast in construction. The main differences in the otic regions to note are (1) the shorter otic region in *Acanthostega*, (2) the large fenestra vestibuli in *Acanthostega*, compared with a small and more ventral vestibular fontanelle in *Eusthenopteron*, (3) the absence of the bridge of bone (the lateral commissure) in *Acanthostega* that in *Eusthenopteron* and other fish bears facets for the hyomandibula, and (4) the fact that the stapes (equivalent to the hyomandibula) inserts into the fenestra vestibuli in tetrapods instead of articulating against the otic wall at the lateral commissure as in fish. Other differences, not directly connected with the otic region, are that in *Eusthenopteron*, there is a large ventral gap between the anterior (ethmosphenoid) part of the braincase and posterior (otocapsule) part, but that in *Acanthostega*, these two are joined at the base as well as dorsally. In fact, in *Eusthenopteron*, there is a hinge-like structure to the dorsal part of the junction. Prominent processes—the basiptyergoid processes—serve to link the braincase and palate in *Acanthostega*, whereas in *Eusthenopteron*, these are small, and more dorsally placed. In its otic region, *Acanthostega* is fairly typical for an early tetrapod, and for this comparison, almost any early tetrapod would serve. In other words, the changes in structure occurred early in tetrapod history and then were conserved.

*Panderichthys* shows many features in which it resembles tetrapods more closely than does *Eusthenopteron*: the proportions of its skull, in which the snout is relatively long; the pattern of snout bones with paired frontals; the interdigitation of some skull sutures; the shorter shoulder region and opercular series; loss of the cranial hinge in the skull roof; loss of the midline fins except the tail. Nonetheless, although there are minor differences in otic proportions between *Panderichthys* and *Eusthenopteron*, their otic morphologies are virtually identical. In other words, *Panderichthys* is essentially fish-like and conservative. Because its skull roof is in some respects intermediate in form between *Eusthenopteron* and *Acanthostega*, it has been suggested that the transition in braincase structure was a rapid one, and took place between *Panderichthys* and *Acanthostega*. In that respect it is comparable in speed and time of occurrence with the change from fins to limbs, and in contrast to the changes to skull roof structure, which appear to have been gradual (Ahlberg et al., 1996). Why this change occurred is unknown, although it might have been accompanied by other changes to the inner ear, discussed below. Whether it was associated with sound reception specifically or even primarily remains in doubt.

*Mandageria* is a derived tristichopterid from the Devonian of Australia (Johanson et al., in press). The tristichopterids as a whole show many parallels in their evolution to tetrapods, and seem to have been inhabiting similar ecological niches (Ahlberg and Johanson, 1997). The otic region of *Mandageria* has some unique features that show that in this lineage closely related to tetrapods, the otic region was capable of evolutionary flexibility. *Mandageria* has a relatively much larger vestibular fontanelle than *Eusthenopteron* (or *Panderichthys*), and a smaller lateral commissure. The hyomandibular facets make a larger angle to the vertical in *Mandageria* and is much shorter than in *Eusthenopteron*, and there is evidence of specialization of the spiracular chamber. The spiracular chamber is what ultimately gives rise to the tetrapod middle ear cavity.

The radical changes to the otic region seen across the fish-tetrapod transition are not matched by changes to the occipital region, despite the anatomically close relationship of these two braincase components. The occiput of *Acanthostega* is very similar to that of *Eusthenopteron* in having no occipital condyle, and in the degree of attachment (or lack of it) between the occipital region itself (basioccipital and exoccipital) and the otic capsules. The embryonic gap (metotic fissure), which separates these structures in all vertebrate embryos, remains unsealed in both these



**Figure 3** Comparison between the braincases of *Eusthenopteron*, *Acanthostega*, and *Greererpeton* in left lateral and posterior views. Embryonic origins of regions shown shaded. (From Clack, 2001; with permission of the Systematics Association.) boc, basioccipital; bpt proc, basipterygoid process; ethmosphen, ethmosphenoid; exocc, exoccipital; fen vest, fenestra vestibuli; for mag, foramen magnum; hyom fac, hyomandibular facets; lat comm, lateral commissure; lat otic fiss, lateral otic fissure; nas cap, nasal capsule; notoch canal, notochordal canal; otocc, otoccipital; stap, stapedial; v cran fiss, ventral cranial fissure; vest font, vestibular fontanelle.

fossil genera, as in all early tetrapodomorphs, fish, or tetrapod. Clack (2001) suggested that the contrast between the otic and occipital morphologies might mean that the two regions were subjected to different rates of evolutionary change, related to the fact that they were formed from different embryonic tissues.

Based on studies of the chick embryo, it seems that the skull is formed from tissues of three different embryonic origins: neural crest, somitic mesoderm, and cephalic mesoderm (Couly et al., 1993). The boundaries limiting the domains of these tissues correspond closely to fissures in the early embryonic skull, of which the metotic fissure is an example. Thus, in skulls such as those of *Eusthenopteron* and *Acanthostega*, in which some of these fissures remain unsealed, the domains of each of these tissues can be determined. With a few areas of uncertainty, these areas appear as in Figure 3 (Clack, 2001). The occiput and otic capsule are formed chiefly from somitic and cephalic mesoderm, respectively, meeting along the metotic (or in the adult form the lateral otic) fissure. The vestibular fontanelle lies at the end of this fissure in the tetrapodomorph fish.

Most striking is that the major areas of change are those formed from neural crest material. In tetrapods, the ethmosphenoid and the dermal parasphenoid (both neural crest) grow back to join the otoccipital ven-

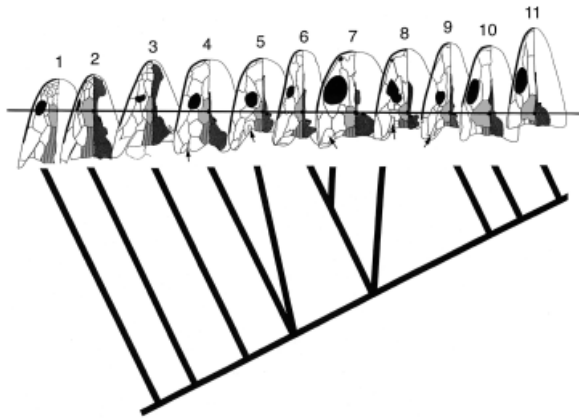
trally, producing the enlarged basipterygoid processes as they do so. The hyomandibula (hyoid arch material and thus also neural crest) is transformed into the stapes, and its head is transformed from paired articulations to a single round footplate. The vestibular fontanelle contributes to the fenestra vestibuli (FV), although this hole also represents further loss of the braincase wall around the junction between the otic and occipital components, possibly involving loss of the lateral commissure. In *Greererpeton*, the FV lies where these two components meet the ethmosphenoid (i.e., the basisphenoid) and the dermal parasphenoid. The whole event could represent renewed activity of the neural crest, a tissue particularly involved in the formation of the vertebrate head.

The loss of ossification seen in the otic wall that results in the formation of the FV is paralleled by loss of ossification elsewhere in the braincase. This and other features described below may be evidence of pedomorphic changes at the fish-tetrapod transition, a process that has been suggested as operating at some level in the origin of tetrapods (Long, 1990; Coates and Clack, 1995; Clack, 2002a).

Two regions of the braincase show loss of ossification, the ear region, and the nasal capsule. During the fish-tetrapod transition, there is a general loss of definition in fossils of the inner ear region. The semicircular canals and the pars inferior chamber are usually quite well represented in fish fossils, because they are often lined with periosteal bone. In early tetrapods, occasionally the grooves (unlined by periosteal bone) for anterior and posterior semicircular canals can be recognized in the otic capsule, but other parts of the inner ear are not usually represented. Furthermore, no tetrapod has an ossified nasal capsule, often a conspicuous and informative feature of tetrapodomorph fish fossils. In fact, this lack applies to all tetrapods, extinct and extant, so the loss here appears to be irreversible. The reason for this loss of ossification is not clear, although it coincides with several changes to the snout during the transition, including general lengthening and consolidation of the dermal bones. However, it also coincides with increase in orbit size, a feature also associated with pedomorphosis.

Important and linked changes to the occipital and otic regions are set in train during the fish-tetrapod transition, despite the generally conservative construction of the occiput across the fish-tetrapod divide. Figure 4 shows a range of fishes and tetrapods set on a consensus cladogram to illustrate some of them. Romer (1937) first noted a decrease in size of the rear part of the skull from fish to tetrapod, noting also that it continued into the evolution of amniotes. It





**Figure 4** Cladogram of fish and tetrapod skulls aligned on the parietal foramen and drawn to the same snout-quadrate length. (From Clack, 2002a, reproduced with permission from Indiana University Press.) 1, *Osteolepis*; 2, *Eusthenopteron*; 3, *Panderichthys*; 4, *Ichthyostega*; 5, *Acanthostega*; 6, *Greerpeton*; 7, *Dendrerpeton*; 8, *Baphetes*; 9, *Pholiderpeton*; 10, *Westlothiana*; 11, *Paleothyris*.

seems to correspond with changes to the skull table (the region of the skull roof that sits over the braincase) (Clack, 2002b) as well as the occiput itself.

Several explanations have been put forward for the reduction (see discussion in Clack, 2002a, discussion in 2002b), but one that can be tested is that it relates to a reduction in the size of the semicircular canals. This suggestion was first put forward by Bernacsek and Carroll (1981), but since that time, more early tetrapods and more tetrapod-like fish have been discovered. In “fish,” the dermal postparietal bones scale exactly as the size of the otic capsules beneath and thus to the size of the canals, although in “tetrapods” the linkage is not quite as clearcut. The role of semicircular canals may have been modified when first heads and then bodies came to be emersed and subject to significant gravitational forces (e.g., a response to falling was required for the first time). Work is in progress by the author and colleagues to monitor just when this change began and whether it coincides with, precedes, or follows the origin of tetrapods with digits. Certainly, there are differences in the neurobiology of the inner ear between extant fish and tetrapods including the orientation of hair cells in the lagena (Popper and Platt, 1996), the course of the chorda tympani nerve branch of cranial nerve VII, and the route of the perilymphatic canal (Lombard and Bolt, 1979). Both of the latter two features differ fundamentally between modern amphibians and amniotes, but their states in early tetrapods might have been like neither of the modern groups, but more like those of fishes. The evolution of the divergent states

seen in modern forms may thus postdate the appearance of tetrapods as a group.

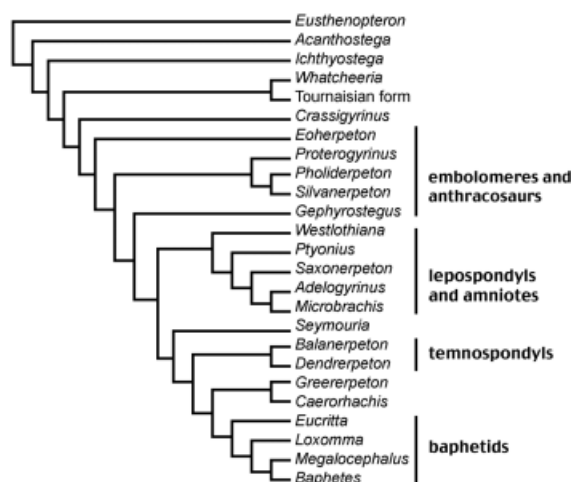
Changes to modes of air breathing would also affect the otic and occipital regions. Although it is likely that the earliest tetrapods were habitually aquatic rather than terrestrial, there is evidence that they were increasingly using air breathing. Loss of the opercular and gular series of bones, reduction of the hyomandibula and modification of the gill apparatus, and disconnection of the head and shoulder skeletons are seen in the earliest tetrapods (all are paralleled in lungfish), and may have been devices to allow the head to be raised, to increase the gape, and allow greater expansion of the buccal cavity (Coates and Clack, 1995). The subsequent modifications to the occiput directly affect the otic capsules, particularly the opisthotic, as well as the back of the dermal skull roof (the skull table).

Lacking the dermal connections between head and shoulder, alternative muscular, or ligamentous connections had to substitute to tie the head to the postcranial skeleton. Expaxial musculature, serving to raise the head, inserted onto the back of the skull, both on the dermal skull table, and on the posterior braincase wall formed by the opisthotic. Even in the earliest tetrapods, the skull table is the region whose bones show the strongest sutural integration with each other, presumably as a result of having to resist stresses from the epaxial muscles (Clack, 2002b). In *Acanthostega*, the otic capsule was not firmly sutured to the overlying skull table, nor did the animal have an occipital condyle (a condition similar to that in *Eusthenopteron*). Head movements were probably fairly limited. In later forms, with the development of an occipital condyle allowing increased excursions of the head, elaborate means for stabilizing the connection between skull roof and braincase developed. They directly affect the structure of the opisthotic and thus the ear region.

## THE EARLIEST TETRAPODS

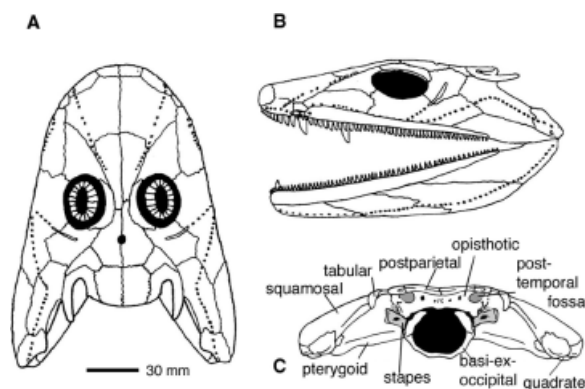
The phylogeny of early tetrapods (in contrast to that of the tetrapodomorph fishes) is highly contentious, with little in the way of a consensus for the Carboniferous groups (see below). Figure 5 shows a recent cladogram derived from the author’s work, and it will be used as a base for the following arguments outlining changes to the stapes and otic regions of early tetrapods.

Stapes and at least partial otic capsules are now known from a range of the earliest tetrapods: *Acanthostega* (Late Devonian of Greenland) (Clack, 1989,

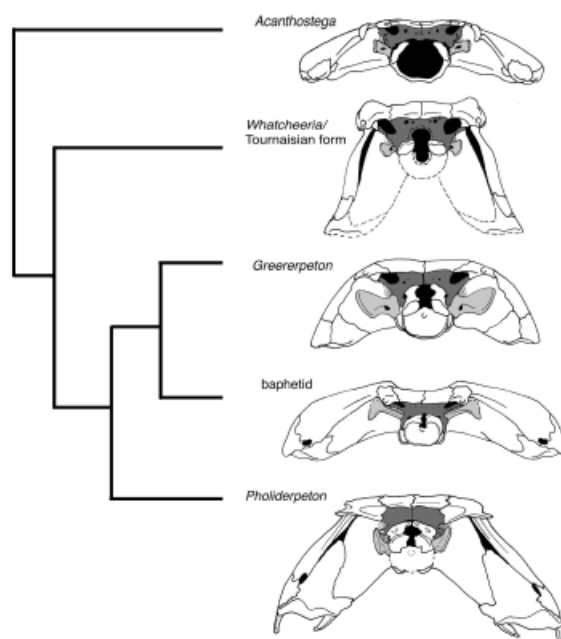


**Figure 5** Cladogram of early tetrapod relationships based on the author's work. Note the position of *Seymouria* in this cladogram, which is unusual. In most phylogenies, *Seymouria* appears close to amniotes and/or embolomeres. Nonembolomeric anthracosaurs (in the traditional sense) are *Eoherpeton* and *Gephyrostegus*.

1994a) (see Fig. 6); *Pederpes finneyae* from the earliest Carboniferous (Tournaisian) of Scotland (Clack, 2002c); *Greererpeton* (mid-Carboniferous of the USA) (Smithson, 1982; Godfrey, 1989); a new baphetid from the Late Carboniferous of England (Clack, in press); and *Pholiderpeton* and *Palaeoherpeton*, two embolomeres from the Late Carboniferous of England (Clack, 1983). Work is currently in progress on the iconic Devonian tetrapod *Ichthyostega* sp. but its otic region is specialized and difficult to interpret (see Clack and Ahlberg, 1997, Clack et al., 2002). When it is better understood, its morphology may fundamentally change the ideas put forward in this article.



**Figure 6** Skull (about 200 mm long) of *Acanthostega* in (A) dorsal, (B) right lateral, and (C) posterior views. (From Clack, 2002b, reproduced by permission of the Royal Society of Edinburgh.)



**Figure 7** Cladogram of occiputs of primitive tetrapods based on the author's work. Opisthotic bones dark-shaded, stapes light-shaded. (From Clack, 1987, in press.)

As things stand, there seems to be a broad pattern of similarity in the ear region of these early tetrapods (Fig. 7). The stapes is short, with a single rounded or 8-shaped footplate and a large stapedia foramen. There is a short robust shaft and a more distal broad flattened wing-shaped plate that has an "unfinished" (i.e., not lined with periosteal bone) distal margin. It appears in most of these taxa (e.g., *Acanthostega*, *Greererpeton*) to have contacted or even lain flat against the bones of the palatoquadrate, with no obvious space for a middle ear cavity (Smithson, 1982; Clack, 1989). The FV took up a good deal of the side-wall of the braincase, and the stapedia footplate filled or nearly filled it (Figs. 2 and 3). Whether the footplate replaced the braincase wall by the proximal end of the hyomandibular growing into it, or by the braincase wall becoming incorporated into the stapes is unknown, but could be tested by developmental techniques. An important point is that the FV lay at the junction of three braincase components formed of three different embryonic tissues (see above). In all of these, the occipital arch was a minor component of the back of the skull, and the lateral otic fissure was unsealed.

This profound realignment of tissues bordering the otic capsule meant the rerouting of several important soft tissue features, and again, this seems to have happened rapidly. In modern chondrichthyans, the chorda tympani branch of nerve VII runs through a

canal in the hyomandibula, and it is always assumed that it did so through the canal found in the hyomandibulae of fishes such as *Eusthenopteron*. In extant tetrapods, the chorda tympani loops around the stapes and middle ear cavity, taking different courses in amphibians and amniotes as noted above. In extant tetrapods, where there is a stapedia foramen, it is the stapedia artery, a branch of the orbital artery, that runs through it, and again, this is usually the pattern assumed for fossil tetrapods (Smithson and Thomson, 1982) (although this argument may be circular; Clack, 1993). The jugular vein, which ran between the lateral commissure and the otic wall in fishes, in tetrapods runs in the cranioquadrate passage, free of the braincase ossifications, dorsal to the stapes and alongside the chorda tympani (Goodrich, 1930). It is not clear how any of these structures came to be rerouted.

A notch in the rear skull margin at the place where the skull table meets the cheek bones (see Fig. 4, arrows) is seen in all early tetrapods apart from *Greererperton*. Formerly, this would have been termed an "otic notch," and have been viewed to house a tympanum, but in view of the shape and size of the stapes and lack of middle ear cavity, the term hardly seems appropriate. "Temporal notch" is a suitably neutral term (Godfrey et al., 1987), although it is possible that the notch was actually occupied by a spiracular opening. The spiracular chamber opened to the throat by the equivalent of the Eustachian tube, whose course is suggested by a groove running up the wall of the braincase just posterior to the basipterygoid processes (Clack, 1998). In early tetrapods, the spiracle may have allowed exhaled air to be expelled, as it does in the primitive extant air-breathing ray-finned fish *Polypterus*. *Greererperton* departs from this pattern in lacking a temporal notch. Its close relative *Colosteus* is known to have had gill-rakers preserved in the throat region (Hook, 1983), suggesting a water-filled pharynx. Colosteids such as *Greererperton* may have lost the spiracle if they were no longer air breathers.

The function of the stapes in these early tetrapods is not clear. Some auditory capability is suggested by the fact that the large footplate lay lateral to the location of the sacculus in the inner ear, a part of the inner ear probably associated with audition in fish (Popper et al., 1988), although it is difficult to define separate areas sensitive to acoustic and gravistatic stimuli in the inner ears of most fishes (Platt, 1983; Popper and Platt, 1993). Although modern tetrapods have lagenae that develop as outgrowths from the sacculus, the earliest tetrapods probably had a common sacculolagenar chamber as is found in primitive ray-finned fishes (Popper, 1978; Popper and Northcutt, 1983; Mathiesen and Popper, 1987), lungfishes

(Retzius, 1881; Popper and Platt, 1996), and where known, tetrapodomorph fishes such as *Eusthenopteron* (Jarvik, 1980) and the megalichthyid *Ectosteorhachis* (Romer, 1937). Any auditory facility was probably limited and confined to low frequency water-borne or ground-borne sound.

With its connection to the palatoquadrate ossifications, the stapes acted as a crossmember linking the braincase to the palate and via that to the cheek. As suggested above, in the earliest tetrapods, the braincase was not closely integrated with the skull roof. In *Acanthostega*, for example, there is no sign on the underside of the skull table of facets to receive occipital processes, although the form of the otic capsules suggests that unossified lateral walls (i.e., paroccipital processes) may have bounded the space occupied by the epaxial insertions (the posttemporal fossae) (Figs. 6 and 7). The same now seems to be true of the whatcheeriids, a group of very primitive Carboniferous tetrapods represented by *Whatcheeria deltae*, and *Pederpes finneyae* (Clack, 2002c). The whatcheeriids occupy a basal position in tetrapod phylogeny, the next most primitive after the Devonian forms (Figs. 5 and 7). It is known that *Acanthostega* did not have an occipital condyle; in other words, the notochord was the main point of attachment between the head and vertebral column, but the state of the same region in the whatcheeriids is not clear (Fig. 7). However, whereas in *Acanthostega* the unossified paroccipital processes met the skull table at a poorly defined and unspecialized junction, in whatcheeriids, the tabular bore small facets to receive the processes (Lombard and Bolt, 1995; Clack, in press), even though the latter too remained unossified.

In *Greererperton*, the occipital region was further developed. There was a large almost circular occipital condyle formed by the basioccipital, and tabular facets were larger than in the whatcheeriids, and although the contact to the paroccipital processes was poorly ossified, it did exist (Smithson, 1982) (Figs. 2, 7, and 8).

In the embolomeres, a rather different arrangement evolved to tie the braincase and skull table together. The tabular facets were much enlarged and reached further towards the midline, clasping the otic capsule and eliminating the paroccipital processes (Fig. 7). The epaxial musculature probably inserted onto the now expanded posterior face of the tabulars.

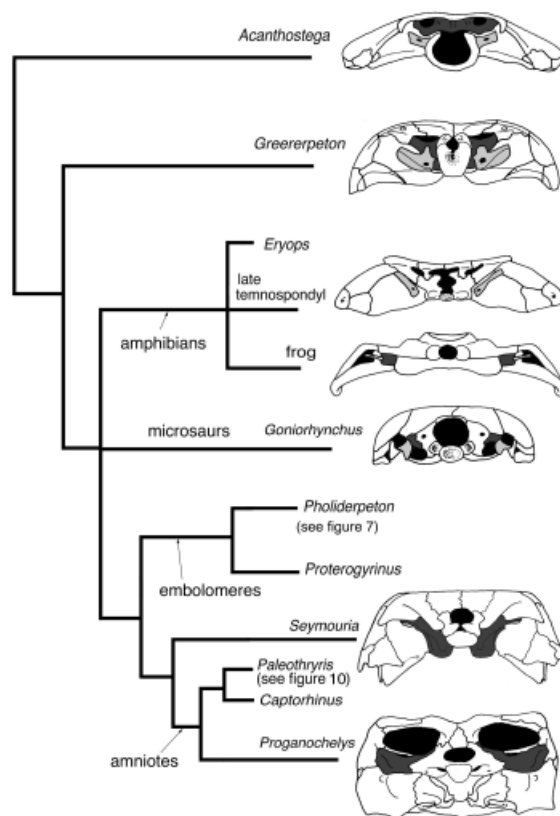
All these ways of strengthening the connection between the skull roof and the braincase presumably affected not only the size and construction of the otic capsule, but also the function of the stapes. As the skull became better consolidated, the role of the stapes as a strut was diminished.

One group of primitive tetrapods whose stapes

were poorly known until very recently are the baphetids (formerly called “loxommatids”). Their systematic position has been controversial, but the author’s recent work has suggested that they may be sister group to the temnospondyls. Both groups share fully ossified paroccipital processes, tying the tabulars to the paroccipital processes beneath the posttemporal fossae. The skull of a newly discovered baphetid preserves both stapes in a relatively uncrushed skull, for the first time (Clack, in press). The skull is robustly constructed, with no obvious possibilities for flexure at any sutures or junctions, but nevertheless, it has the primitive pattern of stapes, with a relatively large footplate and a flaring distal component not unlike that of *Greererpeton*. The shaft is robust but relatively longer than those of *Greererpeton* or the embolomeres, and the whole thing is relatively larger than in the latter group (Fig. 8). In addition, in contrast to *Greererpeton*, it is not obvious that it contacted the palatoquadrate directly—there is a small depth of matrix (the rock in which it is embedded) separating them, suggesting space there in life. As a strut, this stapes seems unnecessary, but as a sound-conducting element it still seems unlikely. Its function here therefore is unclear.

## THE DIVERSIFICATION OF TETRAPODS

By the time of the mid-Carboniferous, about 325–330 million years ago, tetrapods had diversified into numerous groups, many of which have left no descendants. The lineages leading to modern groups, Lissamphibia and Amniota, were already established by that time, whichever competing phylogenetic hypothesis is chosen. How much further back into tetrapod history their origins go is debated (Lebedev and Coates, 1995; Laurin, 1998). The Carboniferous groups show a range of body form, size, and skull structure far greater than seen before among tetrapodomorphs, or arguably any single vertebrate group before that time. They show the beginnings of adaptations for terrestrial living, for example, in elongation of limb bones, re-orientation of the wrists and ankles by modifications to the metapodials and digits, development of a sacrum for support on land, elaboration of the atlas-axis arches to support the head and allow movement, the differentiation of a cervical region, and changes to the shoulder girdle. Equally significant changes were taking place to skull structure affecting the form of the jaws and dentition, the back of the skull and occiput, and inevitably the otic region. It is clear that many of these occurred in parallel in different groups. The otic region of Palaeozoic tetrapods includes many mor-



**Figure 8** Cladogram of occiputs of tetrapods. Late temnospondyl from Schoch and Milner (2000; with permission of Verlag Friedrich Pfeil), “*Goniiorhynchus*” (*Rhynchonkos*) from Carroll and Gaskill (1978; reprinted with permission of the American Philosophical Society), *Seymouria* from Laurin (1996; copyright University of California Museum of Paleontology), *Proganochelys* from Gaffney (1990; illustration by Lorraine Meeker courtesy of the American Museum of Natural History), others from the author’s own work. Opisthotic bones dark-shaded, stapes light-shaded. Stapes in *Proganochelys* lies tucked up anterior to the opisthotic paroccipital process.

phologies not represented among modern tetrapods, and some of them are not easily interpretable in functional terms. This section describes the morphologic diversity found in the ear region and stapes of a range of them.

Temnospondyls, the group traditionally considered to have given rise to the Lissamphibia, were among the first to put some of these developments in train. Temnospondyls, at least primitive ones like *Balanerpeton* and *Dendrerpeton*, had deeply incised temporal notches. In *Balanerpeton* (Milner and Sequeira, 1994), the base of the stapes is known, and appears to have departed from the primitive tetrapod pattern in having a much more slender rod-like shaft, although its distal end is unossified. However, it conforms to

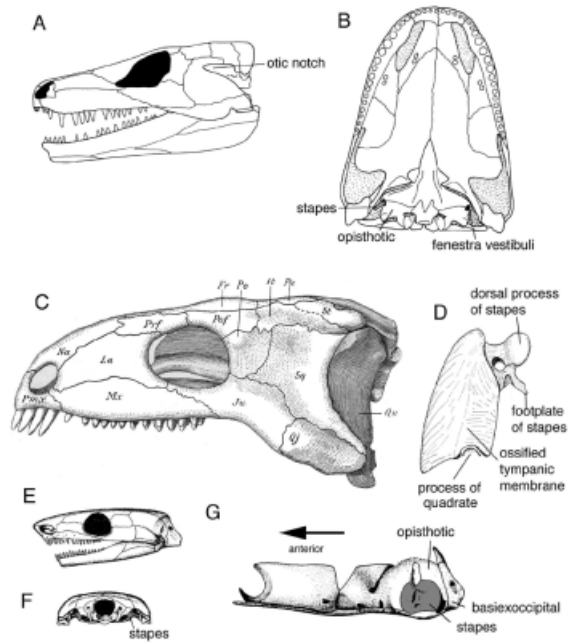


the pattern of later temnospondyls, being dorsolaterally directed. In many temnospondyls the distal end of the stapes lies close to the center of the temporal notch. They are usually described as having an ear region not unlike that of frogs (Bolt and Lombard, 1985; Milner, 1988), so their temporal notch was indeed probably “otic,” housing a tympanum as in the traditional view.

Temnospondyls have skulls with ossified paroccipital processes, and in which the palate and skull roof were firmly sutured together. The exoccipital bones, part of the embryonic occipital arch, come to play a significant role in formation of the occiput, effectively replacing the opisthotics as the main point of attachment between braincase and skull roof (Fig. 8, “late temnospondyl”). They form a large part of the occipital surface of the braincase and provide the condyles. Furthermore, there seems to have been little possibility for movement at the junction between the palate and braincase—the basal articulation.

With no requirement for a stapes acting as a brace between the palate and braincase, this group might have been the first to have developed a tympanic ear. It has been suggested that temnospondyls, with their flattened skulls, breathed air by buccal pumping, retaining at least part of the primitive form and function of the hyoid apparatus (Janis and Keller, 2001). Shoulder girdles incorporated expanded dermal plates under the thorax and extending forwards under the back of the skull. The neck was short and movement was limited. This might have been a limitation imposed by retention of the primitive mode of ventilation and hyoid function, whose muscles originate on the shoulder girdle. The buccal pumping action in frogs is what powers the sound production system, and the same might have been true of temnospondyls, such that sound production went hand in hand with the evolution of sound reception (Clack, 1992).

Other Carboniferous tetrapods with retained temporal notches do not all show evidence of tympanic ears. These include the embolomeres and baphetids mentioned above, whose stapes are of the primitive pattern. Somewhat later, however, the seymouriamorphs, “reptile-like” postcranially but possibly more closely related to embolomeres, do appear to have developed an auditory ear with several specializations of the otic capsule and surrounding bones. There is a deeply incised temporal notch, and the stapes is slender and more or less cylindrical though poorly ossified where it is known [Fig. 9(A) and (B)]. There is some uncertainty about the phylogenetic position of seymouriamorphs. Although in some (most) phylogenies, seymouriamorphs appear closely related to amniotes and/or close to embolomeres, in my own

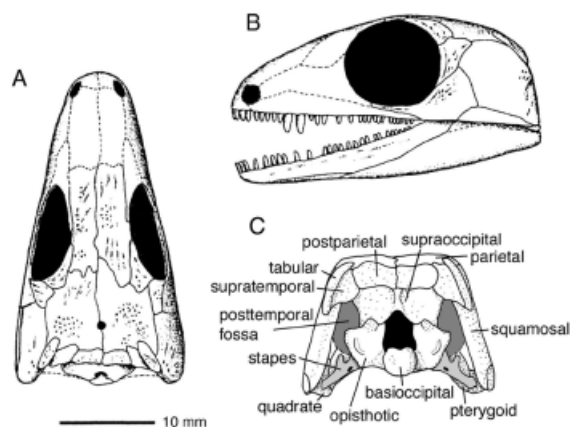


**Figure 9** Skulls of Carboniferous and Early Permian tetrapods to show diversity of ear morphologies. (A,B) Skull (about 132 mm long) in left lateral and ventral of the seymouriamorph *Seymouria baylorensis* (from Laurin, 1996; copyright University of California Museum of Paleontology); (C) the skull in left lateral view of the diadectomorph *Diadectes* sp. about 220 mm long (from Olson, 1947; with permission from Fieldiana); (D) the ossified tympanic membrane and stapes of *Diadectes* in posterior view (from Olson, 1966; with permission from Fieldiana). The ossified plate fills the quadrate embayment. (E,F,G) skull (about 18 mm long) in dorsal and posterior views and braincase respectively of the microsauro “*Goniorhynchus*” (*Rhynchonkos*) stovalli (from Carroll and Gaskill, 1978, reprinted with permission of the American Philosophical Society).

most recent work, they have appeared closer to temnospondyls. As either stem amniotes or embolomere relatives, their ears appear to be independent developments, unlike any others.

Another possibly tympanic ear is found in another amniote-like group often taken to be the sister-group to amniotes, the diadectomorphs. Here, there is a deeply excavated margin to the back of the cheek, and the stapes is slender but with many processes coming from it to link to what in some specimens appears as an ossified tympanic membrane [Fig. 9(C) and (D)]. There is no similarity between this arrangement and the ears of the earliest amniotes, and again it appears to be a unique development.

Among other Carboniferous tetrapods, a temporal notch is absent altogether. These include a collection of small tetrapods called lepospondyls. In microsaurs, a group of small lepospondyls some of which show



**Figure 10** Skull (about 26 mm long) of *Paleothyris acadiana* in (A) dorsal, (B) right lateral, and (C) posterior views. (From Carroll, 1969; reproduced with the permission of The Paleontological Society).

numerous terrestrial adaptations, the back of the skull is smooth, and although the braincase is relatively large (probably a consequence of minaturization), the occiput is not firmly sutured to the skull roof. The stapes of microsaur, where known, is shaped like an antique collar-stud having a large (very large compared to the braincase wall) footplate, and a tiny button-like shaft (Carroll and Gaskill, 1978) (Figs. 8, 9(E)–(G)). Its function is quite obscure, although its large footplate may suggest low frequency reception. Stapes for other lepospondyls groups, the nectrideans and aïstopods, are not known (Carroll et al., 1998).

A temporal notch is absent from the skulls of all early amniotes (Fig. 10), and in this they resemble the lepospondyls. However, the stapes is very different from that of lepospondyls or indeed any other early tetrapods. In the earliest amniotes, the stapes is robust and strut-like, usually with a long shaft reaching or almost reaching the jaw articulation at the quadrate. It may be orientated lateroventrally or horizontally, but never dorsolaterally as it is in temnospondyls. The footplate is still relatively large as in other early tetrapods, but usually has a separate dorsal process attaching to the otic capsule.

Very few of the earliest amniote skulls are preserved in three dimensions, so the condition of the otic capsule is difficult to assess. However, in those where it is known the paroccipital processes are short, poorly ossified, and do not reach the dermal skull roof (e.g., in early synapsids such as *Sphenacodon* (Romer and Price, 1940) and stem diapsids such as *Paleothyris* (Carroll, 1969, 1986) (Fig. 10) and captorhinids (Heaton, 1979). By contrast to temnospondyls and baphetids, for example, the paroccipital processes of early amniotes are horizontally directed, having a

presumably cartilaginous contact with the cheek rather than the skull table. There has been debate about whether the paroccipital processes and the post-temporal fossae that they enclose are equivalent structures in these groups.

## EARLY AMNIOTES AND THE ROLE OF THE STAPES

The earliest amniotes have a consistently different skull shape and construction from that of the majority of the earliest tetrapods. Only lepospondyls are in any ways similar, and a close phylogenetic relationship between these groups has been suggested (see below). However, the detailed anatomy and the form of the stapes are quite different between them, and other factors may be at work to produce convergent similarities of overall skull form. What follows is speculative, but is consistent with the known anatomy of both fossil and extant amniotes, and produces a coherent scenario. The factors involved in the changing role of the stapes may be related to modes of breathing and feeding that indirectly affected its form and function. Further details may be found in Clack (2002a).

It has been suggested above that temnospondyls breathed air by means of buccal pumping, and this was probably the primitive mode of air intake for all the earliest tetrapods. Broad flattened heads are characteristic of this mode of ventilation (Janis and Keller, 2001), that employs the mechanism and musculature as seen in fishes in an almost unmodified form. Lower jaws are long and slender, the quadrates set wide apart, and the palate more or less horizontal (Fig. 6, 7, and 8). Modern anurans (Fig. 8) and urodeles exemplify modern exponents of the mode. In the earliest tetrapods as well as most temnospondyls, because the hyoideal musculature would have originated on the shoulder girdle to a large degree, the shoulder girdles remained conservative in form, and lay close behind the head. The heart, as in fishes, probably also lay close to the back of the head. These constraints limited the length of the neck, as well as the shape of the skull itself. It is not clear what role the stapes would have played in the operation of the hyoid skeleton, but in lungfishes to which the earliest tetrapods can be compared, the hyomandibula is reduced or lost altogether.

Feeding mechanisms affected the stapes by emphasizing its role as a brace from the braincase to the palate. The earliest tetrapods were probably unspecialized gulpers living as ambush predators in marginal swamps and lagoons. Their long slender lower

jaws and flattened heads would have exerted their greatest force when the jaws are wide open (Olson, 1961). When the jaws are shut the musculature is relatively weak. Prey is captured and impaled on a long tooth-row of numerous sharp teeth. This method is sometimes called the “kinetic inertial system” of jaw closure, but it is characteristic of primitive tetrapods and is associated with buccal pumping (Janis and Keller, 2001).

Skulls that are as deep or nearly as deep as wide with short tooth rows that take up little more than half the jaw length are characteristic of a second mode of jaw closure known as the “static pressure” system. In this system, the jaws operate at greatest force when they are closed or nearly so. Prey can be tightly gripped or even crushed. This is the jaw mechanism associated with the earliest amniotes (Fig. 10), whose skulls are box-like in section. Furthermore, the system seems to have allowed more precise jaw closure—amniotes were also the first to evolve differentiated teeth, opening up a range of other terrestrial niches including herbivory, insectivory, or mollusc-crushing.

The additional forces imposed on the skull by this system required supplementary bracing of the jaw joint, especially in a skull in which the braincase and cheek were not firmly sutured together (Carroll, 1986). The strut-like stapes would have prevented the jaw joint from being pulled inwards during biting. Amniotes appear to have taken the stapes’ primitive function and adapted it further.

Amniotes with their box-like skulls are also associated with a different method of breathing—costal ventilation. Use of bodywall muscles for aspiration seems to have proceeded from the evolution of the transverse abdominus for exhalation, found in tetrapods but not elsewhere, to the acquisition of intercostals for inhalation, a feature unique to amniotes (Brainerd et al., 1993). Development of an alternative means of lung ventilation broke the constraint imposed by use of the hyoid musculature in its primitive form (coincidentally freeing it up to act in manipulation of the tongue, and facilitating the evolution of a longer neck). This facilitated modifications to the skull that allowed evolution of a deeper, narrower profile and in consequence, the static pressure jaw system. Thus modifications to the means of breathing had consequences for the means of feeding, for the role of the stapes, and thus to the form of the otic region.

Although the paroccipital processes remained poorly ossified and only loosely attached to the skull, the stapes remained the chief means of stabilising the back of the skull (Fig. 10). Its conversion and reduction in size to a specialized hearing ossicle parallels

the development of alternative means of fastening the braincase to the skull roof (Clack, 1997). Diapsids developed stout dorsally positioned paroccipital processes that link the otic capsule to the corner of the skull where the cheek and skull table join (e.g., *Pro-lacerta*; Gow, 1975; Evans, 1986), whereas in turtles the paroccipitals ran horizontally to the cheek below very much enlarged posttemporal fossae (e.g., the earliest known turtle *Proganochelys*; Gaffney, 1990). Mammals incorporated the otic capsule to the skull table dorsally and sutured the braincase to the palate via the pterygoid as well as the basal articulation (Allin and Hopson, 1992). Convergent means of stabilising the back of the skull were accompanied by convergent development of the stapes as a specialized hearing ossicle in a tympanic ear in these groups.

## PHYLOGENY AND THE EVOLUTION OF A TYMPANIC EAR

Perceptions of middle ear evolution have changed radically since the middle of the last century. At that time the early tetrapod middle ear was considered to have been that of the “labyrinthodonts,” that is to say temnospondyls plus anthracosaurs (i.e., embolomeres plus a few other genera). In the wake of new fossil discoveries, new information from neontology and new concepts of tetrapod phylogeny, many ideas about early tetrapods and their middle ears have been turned upside down. In the first place, temnospondyls and anthracosaurs had manifestly different otic structures: whereas the anthracosaurs’ ears were unlikely to have been tympanic, the resemblance between the ears of temnospondyls and frogs suggests that those of temnospondyls were. The idea of multiple convergent origins for a tympanic ear results as much from revised phylogenetic hypotheses as much as from new information about structure (Clack, 1993).

At the present, there are two competing phylogenetic frameworks on which to peg hypotheses of middle ear evolution, both of which imply multiple origins for tympanic ears. In the more traditional view, temnospondyls are the group that gave rise to frogs, or to all of Lissamphibia, explaining the resemblance noted above (Coates and Ruta, 2002; Ruta et al., in press). By contrast, amniotes are considered to be more closely related to anthracosaurs, seymouriamorphs, and diadectomorphs, the anthracosaurs being the plesiomorphic group, without tympanic ears. Given that no early amniote had a tympanic ear, seymouriamorphs and the various groups of later amniotes may represent at least four separate origins

(diapsids, turtles, mammals, seymouriamorphs), possibly five counting the diadectomorphs.

In the competing scheme, amniotes and lissamphibians are more closely related to each other than either is to temnospondyls, anthracosaurs, or seymouriamorphs, all of which are seen as more or less primitive stem tetrapods (Laurin and Reisz, 1997, 1999; Laurin, 1998). The closest fossil relatives of amniotes and lissamphibians ("crown group tetrapods") are the lepospondyls, none of which appears to have had a tympanic ear. This phylogeny suggests at least one additional derivation for the system, because frogs would represent a separate iteration from temnospondyls.

Much effort is currently in progress to try to resolve early tetrapod phylogeny, although all are hampered by the dearth of information for tetrapods of the earliest part of the Carboniferous, the time when tetrapods diversified into many different terrestrial niches (Coates and Ruta, 2002; Ruta et al., in press). For those that are known, the otic region could contribute in more detail to the suite of characters used to generate hypotheses, as a result of improved resolution in understanding its structure. Features of the braincase and otic region anatomy are at present not well represented in such analyses, but should in the future be more clearly definable and thus more useful as characters. Thus, the ear region might regain its place as a phylogenetically significant area.

## SUMMARY

This article has shown some of the fundamental changes that occurred to the ear region during the fish–tetrapod transition. Some of these preceded, some accompanied, and some followed the transition from water dwelling to land dwelling, that is to say, the "fish–tetrapod" transition does not equate exactly with the water–land transition. Some of the changes to the ear region, although not all, were directly connected with changes to acoustic sensitivity with the shift from audition in water to audition in air, but others were affected by modifications to breathing and feeding systems that occurred to skull and muscular structure. As tetrapods evolved into a diverse array of body forms and ecologic niches, they solved the problems of audition in many different ways, some of which have no modern analogs.

## REFERENCES

- Ahlberg PE. 1991. A re-examination of sarcopterygian interrelationships, with special reference to the Porolepiformes. *Zool J Linn Soc* 103:241–287.
- Ahlberg PE, Johanson A. 1997. Second tristichopterid (Sarcopterygii, Osteolepiformes) from the Upper Devonian of Canowindra, New South Wales, Australia, and phylogeny of the Tristichopteridae. *J Vertebrate Palaeontol* 17: 653–673.
- Ahlberg PE, Clack JA, Luksevics E. 1996. Rapid braincase evolution between *Panderichthys* and the earliest tetrapods. *Nature* 381:61–64.
- Ahlberg PE, Luksevics E, Mark-Kurik E. 2000. A near-tetrapod from the Baltic Middle Devonian. *Palaeontology* 43:533–548.
- Allin EF, Hopson JA. 1992. Evolution of the auditory system in Synapsida ("mammal-like reptiles") as seen in the fossil record. In: Webster DB, Popper AN, Fay RR, editors. *The evolutionary biology of hearing*. New York: Springer-Verlag, p 587–614.
- Bernacsek GM, Carroll RL. 1981. Semicircular canal size in fossil fishes and amphibians. *Can J Earth Sci* 18:150–156.
- Bolt JR, Lombard RE. 1985. Evolution of the amphibian tympanic ear and the origin of frogs. *Biol J Linn Soc* 24:83–99.
- Brainerd EL, Ditelberg JS, Bramble DM. 1993. Lung ventilation in salamanders and the evolution of vertebrate air-breathing mechanisms. *Biol J Linn Soc* 49:16–183.
- Carroll RL. 1969. A middle Pennsylvanian captorhinomorph, and the interrelationships of primitive reptiles. *J Paleontol* 43:151–170.
- Carroll RL. 1986. The skeletal anatomy and some aspects of the physiology of primitive reptiles. In: Hotton N, editor. *The ecology and biology of mammal-like reptiles*. Washington, DC: Smithsonian Institution Press, p 25–45.
- Carroll RL, Gaskill P. 1978. The order Microsauria. *Mem Am Philos Soc* 126:1–211.
- Carroll RL, Bossy KA, Milner AC, Andrews SM, Wellstead CF. 1998. *Handbuch der Paläoherpetologie, Teil 1, Lepospondyli*. München: Verlag Dr Friedrich Pfeil.
- Clack JA. 1983. The stapes of the Coal Measures embolomere *Pholiderpeton scutigerum* Huxley (Amphibia: Anthracosauria) and otic evolution in early tetrapods. *Zool J Linn Soc* 79:121–148.
- Clack JA. 1987. *Pholiderpeton scutigerum* Huxley, an amphibian from the Yorkshire coal measures. *Philos Trans R Soc Lond Ser B* 318:1–107.
- Clack JA. 1989. Discovery of the earliest-known tetrapod stapes. *Nature* 342:425–427.
- Clack JA. 1992. The stapes of *Acanthostega gunnari* and the role of the stapes in early tetrapods. In: Webster DB, Fay RR, Popper AN, editors. *Evolutionary biology of hearing*. New York: Springer-Verlag, p 405–420.
- Clack JA. 1993. Homologies in the fossil record—the middle ear as a test case. In: Dübbedam JL, Goodwin BC, & Kortmulder K, editors. *Evolution, development and be-*



- haviour. In search of generative orders of biological form and process. *Acta Biotheoretica*. 41:391–410.
- Clack JA. 1994a. Earliest known tetrapod braincase and the evolution of the stapes and fenestra ovalis. *Nature* 369: 392–394.
- Clack JA. 1994b. *Acanthostega gunnari*, a Devonian tetrapod from Greenland; the snout, palate and ventral parts of the braincase, with a discussion of their significance. *Meddelelser om Grønland. Geoscience* 31:1–24.
- Clack JA. 1997. The evolution of tetrapod ears and the fossil record. *Brain Behav Evolut* 50:198–212.
- Clack JA. 1998. The neurocranium of *Acanthostega gunnari* and the evolution of the otic region in tetrapods. *Zool J Linn Soc* 122:61–97.
- Clack JA. 2001. The otoccipital region—origin, ontogeny and the fish-tetrapod transition. In: Ahlberg PE, editor. *Major events in early vertebrate evolution*. London: Systematics Association Symposium Volume, p 392–505.
- Clack JA. 2002a. Gaining ground: the origin and evolution of tetrapods. Bloomington, IN: Indiana University Press.
- Clack JA. 2002b. The dermal skull roof of *Acanthostega*, an early tetrapod from the late Devonian. *Trans R Soc Edinb Earth Sci*. 93:17–33.
- Clack, JA. 2002c. An early tetrapod from Romer's Gap. *Nature* 418:72–76.
- Clack JA. in press. A new baphetid (stem tetrapod) from Tyne and Wear, and the evolution of the tetrapod occiput. *Can J Earth Sci*.
- Clack JA, Ahlberg PE. 1997. A reinterpretation of the braincase of *Ichthyostega stensioei*. *J Vert Pal* 17:38A.
- Clack JA, Ahlberg PE, Ketcham, R, Dominguez Alonso P. 2002 The braincase and ear region of *Ichthyostega*: a uniquely specialised ear in an exceptionally primitive tetrapod braincase. *IPC 2002 Geol Soc Aust Abstr* 68:34.
- Coates MI, Clack JA. 1995. Romer's Gap—tetrapod origins and terrestriality. In: Arsenault M, Lelièvre H, Janvier P, editors. *Studies on early vertebrates*. Miguasha, Quebec: Bulletin du Muséum national d'histoire naturelle, Paris, p 373–388.
- Coates MI, Ruta M. 2002. New data and new trees: early tetrapod relationships revisited. *IPC 2002 Geol Soc Aust Abstr* 68:36.
- Couly GF, Coltey PM, Le Douarin NM. 1993. The triple origin of skull in higher vertebrates: a study in quail-chick chimeras. *Development* 117:409–429.
- Evans SE. 1986. The braincase of *Prolacerta broomi* (Reptilia: Triassic). *Neues Jahrb Geol Palaont Abh* 173:181–200.
- Gaffney ES. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bull Am Mus Nat Hist* 194:1–263.
- Godfrey SJ. 1989. Ontogenetic changes in the skull of the Carboniferous tetrapod *Greererepton burkemorani* Romer, 1969. *Philos Trans R Soc B* 323:135–153.
- Godfrey SJ, Fiorillo AR, Carroll RL. 1987. A newly discovered skull of the temnospondyl amphibian *Dendrerpeton acadianum* Owen. *Can J Earth Sci* 24:796–805.
- Goodrich ES. 1930. *Studies on the structure and development of vertebrates*. London: Macmillan.
- Gow CE. 1975. The morphology and relationships of *Yungina capensis* Broom and *Prolacerta broomi* Parrington. *Paleont Afr* 18:89–131.
- Heaton MJ. 1979. The cranial anatomy of primitive captorhinid reptiles from the Pennsylvanian and Permian of Oklahoma and Texas. *Bull Okla Geol Surv* 127:1–84.
- Hook RW. 1983. *Colosteus scutellatus* (Newberry) a primitive temnospondyl amphibian from the Middle Pennsylvanian of Linton, Ohio. *Am Mus Novitates* 2770:1–41.
- Janis C, Keller J. 2001. Modes of ventilation in early tetrapods: costal aspiration as a key feature of amniotes. *Acta Palaeont Polonica* 46:137–170.
- Jarvik E. 1980. *Basic structure and evolution of vertebrates*, vols. 1 and 2. New York: Academic Press.
- Johanson Z, Ahlberg PE. 1997. A new tristichopterid (Osteolepiformes: Sarcopterygii) from the Mandagery Sandstone (Late Devonian, Famennian) near Canowindra, NSW, Australia. *Trans R Soc Edinb: Earth Sci* 88:39–68.
- Johanson Z, Ahlberg PE, Ritchie A. in press. The braincase and palate of the tetrapodomorph sarcopterygian *Mandageria fairfaxi*: morphological variability near the fish-tetrapod transition. *Palaeontology*.
- Laurin M. 1996. A redescription of the cranial anatomy of *Seymouria baylorensis*, the best known seymouriamorph (Vertebrata: Seymouriamorpha). *Paleobios* 17:1–16.
- Laurin M. 1998. The importance of global parsimony and historical bias in understanding tetrapod evolution. Part I. Systematics, middle ear evolution and jaw suspension. *Ann Sci Nat* 1:1–42.
- Laurin M, Reisz R. 1997. A new perspective on tetrapod phylogeny. In: Sumida S, Martin KL, editors. *Amniote origins—completing the transition to land*. London: Academic Press, p 9–59.
- Laurin M, Reisz RR. 1999. A new study of *Solendonsaurus janenschi*, and a reconsideration of amniote origins and stegocephalian evolution. *Can J Earth Sci* 36:1239–12155.
- Lebedev OA, Coates MI. 1995. The postcranial skeleton of the Devonian tetrapod *Tulerpeton curtum* Lebedev. *Zool J Linn Soc* 114:307–348.
- Lombard RE, Bolt JR. 1979. Evolution of the tetrapod ear: an analysis and reinterpretation. *Biol J Linn Soc* 11:19–76.
- Lombard RE, Bolt JR. 1995. A new primitive tetrapod, *Whatcheeria deltae*, from the Lower Carboniferous of Iowa. *Palaeontology* 38:471–494.
- Long JA. 1990. Heterochrony and the origin of tetrapods. *Lethaia* 23:157–166.
- Mathiesen C, Popper AN. 1987. The ultrastructure and innervation of the ear of the gar, *Lepisosteus osseus*. *J Morphol* 194:129–142.
- Milner AR. 1988. The relationships and origin of the living amphibians. In: Benton MJ, editor. *The phylogeny and classification of the tetrapods*. Oxford: Clarendon Press.
- Milner AR, Sequeira SEK. 1994. The temnospondyl amphibians from the Viséan of East Kirkton, West Lothian, Scotland. *Trans R Soc Edinb Earth Sci* 84:331–362.

- Olson EC. 1947. The family Diadectidae and its bearing on the classification of reptiles. *Fieldiana, Geol* 11:1–53.
- Olson EC. 1961. Jaw mechanisms: rhipidistians, amphibians, reptiles. *Am Zool* 1:205–215.
- Olson EC. 1966. The relationships of *Diadectes*. *Fieldiana, Geol* 14:199–227.
- Platt C. 1983. The peripheral vestibular system of fishes. In: Northcutt G, Davis RE, editors. *Fish neurobiology*. Ann Arbor: University of Michigan Press, p 89–123.
- Popper A, Platt C. 1996. Sensory hair cell arrays in lungfish inner ears suggest retention of the primitive patterns for bony fishes. In: *Society for Neuroscience abstracts*, vol 22. Washington, DC: Society for Neuroscience, p 1819.
- Popper AN. 1978. Scanning electron microscope study of the otolith organs in the bichir (*Polypterus bichir*) and shovel-nosed sturgeon (*Scaphirhynchus platyrhynchus*). *J Comp Neurol* 181:117–128.
- Popper AN, Northcutt RG. 1983. Structure and innervation of the inner ear of the bowfin, *Amia calva*. *J Comp Neurol* 213:279–286.
- Popper AN, Platt C. 1993. Inner ear and lateral line. In: Evans DH, editors. *The physiology of fishes*. Boca Raton, FL: CRC Press, p 99–135.
- Popper AN, Rogers PH, Saidel WM, Cox M. 1988. Role of the fish ear in sound processing. In: Atema J, Fay RR, Popper AN, Tavolga WN, editors. *Sensory biology of aquatic animals*. New York: Springer-Verlag, p 687–710.
- Retzius G. 1881. Das Gehörorgan der Wirbelthiere. Morphologisch-histologische Studien. I. Das Gehörorgan der Fische und Amphibien. Stockholm, Sweden. Centraldruckerei.
- Romer AS. 1937. The braincase of the Carboniferous crossopterygian *Megalichthys nitidus*. *Bull Mus Comp Anat, Harvard* 82:1–73.
- Romer AS, Price LI. 1940. Review of the Pelycosauria. *Geol Soc Am Spec Pap* 28:1–538.
- Ruta M, Coates MI, Quicke, DLJ. in press. Early tetrapod relationships revisited. *Biol Rev*.
- Schoch RR, Milner AR. 2000. *Handbuch der Paläoherpetologie Teil 3B Stereospondyli*. München: Verlag Dr Friedrich Pfeil.
- Smithson TR. 1982. The cranial morphology of *Greererpeton burkemorani* (Amphibia: Temnospondyli). *Zool J Linn Soc* 76:29–90.
- Smithson TR, Thomson KS. 1982. The hyomandibula of *Eusthenopteron foordi* Whiteaves (Pisces: Crossopterygii) and the early evolution of the tetrapod stapes. *Zool J Linn Soc* 74:93–103.
- Vorobyeva EI, Schultze H-P. 1991. Description and systematics of panderichthyid fishes with comments on their relationship to tetrapods. In: Schultze H-P, Truab L, editors. *Origins of the higher groups of tetrapods*. Ithaca, NY: Comstock Publishing Associates, p 68–109.