

Modes of ventilation in early tetrapods: Costal aspiration as a key feature of amniotes

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The key difference between amniotes (reptiles, birds and mammals) and anamniotes (amphibians in the broadest sense of the word) is usually considered to be the amniotic egg, or a skin impermeable to water. We propose that the change in the mode of lung ventilation from buccal pumping to costal (rib-based) ventilation was equally, if not more important, in the evolution of tetrapod independence from the water. Costal ventilation would enable superior loss of carbon dioxide via the lungs: only then could cutaneous respiration be abandoned and the skin made impermeable to water. Additionally efficient carbon dioxide loss might be essential for the greater level of activity of amniotes. We examine aspects of the morphology of the heads, necks and ribs that correlate with the mode of ventilation. Anamniotes, living and fossil, have relatively broad heads and short necks, correlating with buccal pumping, and have immobile ribs. In contrast, amniotes have narrower, deeper heads, may have longer necks, and have mobile ribs, in correlation with costal ventilation. The stem amniote *Diadectes* is more like true amniotes in most respects, and we propose that the changes in the mode of ventilation occurred in a stepwise fashion among the stem amniotes. We also argue that the change in ventilatory mode in amniotes related to changes in the postural role of the epaxial muscles, and can be correlated with the evolution of herbivory.

Key words: Amniotes, amphibians, skull, ribs, ventilation, carbon dioxide, Palaeozoic, herbivory.

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Introduction

The anamniote/amniote transition was a key feature in tetrapod evolution, and one that has attracted a considerable amount of recent attention (e.g., Sumida & Martin 1997). One issue that has not received much recent attention, however, is that of the mode of ventilation in these early tetrapods and the role of changes in ventilation at the anamniote/amniote transition.

There is a distinct difference in the mode of ventilation between living anamniotes (amphibians) and amniotes. Amphibians have relatively small lungs that they fill via buccal pumping – raising and lowering the floor of the buccal cavity. Some salamanders lack lungs entirely. Almost all amphibians (with the exception of a few specialised frogs) rely extensively on the skin for the exchange of respiratory gases, and the skin is especially important for the loss of carbon dioxide. In contrast amniotes have larger, more complex lungs. Although a variety of modes of ventilation exist among extant amniotes, most use the ribs to change the pressure within the thoracic cavity, and draw in air by aspiration. The exceptions here are turtles, which have incorporated the ribs into the shell, but they still rely on intrathoracic pressure changes generated by movements of the two halves of the shell for respiration.

A critical evolutionary issue is as follows: which method of ventilation is primitive for tetrapods and which is derived? In the past, the idea that early tetrapods might have used buccal pumping, or even cutaneous gas exchange, has been strongly disputed. Two respected authorities advocated the use of ribs in costal ventilation from the earliest phase of tetrapod evolution (Gans 1970a; Romer 1972). Their opinions were based on two main premises which may not be entirely valid, as discussed below. Additionally, they made the tacit assumption that atmospheric levels of oxygen and carbon dioxide were similar in the late Palaeozoic to the levels of the present day, which we now know not to be the case (see Graham *et al.* 1997). However, more recent opinions tend towards considering buccal pumping to be the primitive tetrapod condition, based on the similarity between buccal pumping in modern amphibians and pulse pumping in lungfishes (e.g., Brainerd *et al.* 1993).

In this paper we address the question of when in tetrapod evolution the shift occurred from buccal pumping to costal ventilation, and the role that this may have played in the evolution of independence from the water. We investigate aspects of morphology that may correlate with ventilatory mode in both extant and fossil tetrapods: head shape, neck length, and rib shape. We also consider how these morphological changes might relate to other aspects of tetrapod biology, such as the loss of a larval stage, the postural role of the axial musculature, and the evolution of herbivory.

Note that we restrict the use of the term ‘amphibian’ in this paper to the modern, lissamphibian representatives. There is some debate about whether lissamphibians form a natural group, although there is none about the monophyly of amniotes. However, there is little doubt that a large component of the extinct Palaeozoic anamniote tetrapods are paraphyletic with respect to both modern anamniote and amniote tetrapods. The relationships of some of these groups to each other and to Crown Group tetrapods remain controversial (see e.g., Laurin & Reisz 1997).

Modern amniotes and lissamphibians are both highly derived animals. While amphibians are usually regarded as primitive with respect to their mode of reproduction (at least in the laying of an anamniote egg), it would be highly misleading to assume that other aspects of their physiology also represent the primitive tetrapod condition. Thus, referring to Palaeozoic anamniotes such as *Eryops* as ‘amphibians’, although commonly seen in print, may give a misleading impression as to the possible biology of such animals. Assuming that *Eryops* possessed the thin, permeable skin of modern amphibians might be as inappropriate as assuming that it hopped like a frog, although in the latter case we have the benefit of the osteology to show that it did not possess this

mode of locomotion. However, if the hypothesis of a relationship between temnospondyls and lissamphibians is accepted (e.g., Trueb & Cloutier 1991; Milner 1988, 1993), *Eryops* would belong to the stem lineage of lissamphibians.

In the past, the term 'labyrinthodont' was used to include many of the larger Palaeozoic tetrapods that form much of the subject of this investigation. The group is now recognised as paraphyletic, whichever phylogeny of early tetrapods is accepted. Furthermore it has the disadvantage of 'lumping' together forms which may, according to some phylogenies, belong on the one hand to the stem lineage of lissamphibians (such as temnospondyls) and on the other to the stem lineage of amniotes (such as anthracosaurs). This premise is accepted here. If this phylogeny is correct (or even it is not), these two stem lineages may have shown the beginnings of the differences in physiology seen in the modern crown groups. These differences may be disguised or overlooked if they are treated as a unit.

Abbreviation. — MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA.

Issues in early tetrapod respiration

The nature of the problem. — Although many accounts of tetrapod evolution consider the acquisition of oxygen to be the critical feature of respiration in the transition from water to land, in fact a much more important issue is that of carbon dioxide loss (Ultsch 1996; Janis & Farmer 1999).

In fishes, both O₂ and CO₂ are exchanged over the gills and, to a certain extent, over the skin, especially in air-breathing fishes (Feder & Burggren 1985). Oxygen is in scarce abundance in water in comparison to its availability on land, being around 30 times more abundant in air at sea level at 15°C. The scarcity of oxygen in water means that a large amount of water must be flushed over the gills to obtain sufficient quantities. With this large flux of water there is no problem with sufficient flux for CO₂ loss. Additionally, CO₂ is much more diffusible in water than is O₂, again facilitating its loss (Feder & Burggren 1985; Shoemaker *et al.* 1992). However, air breathers have to ventilate their respiratory surfaces with a much smaller volume of air in order to obtain the same amount of O₂ as a water breather. As air and water both hold equal volumes of CO₂ (at any given partial pressure of CO₂), this reduced amount of ventilation on land has important consequences for CO₂ loss and, accordingly, for acid/base balance (Shoemaker *et al.* 1992).

The sensory mode of determining the concentration of blood gases is different between fishes and tetrapods. In both fishes and amphibians a decrease in O₂ and/or an increase in CO₂ results in an increased rate of ventilation (Boutilier *et al.* 1992), suggesting that the blood levels of both gases are monitored. The primary sensory mode for controlling the rate of ventilation in fishes is the monitoring of O₂ levels by receptors on the gills (Randall 1990). Although a few fishes have some form of peripheral receptors for the monitoring of CO₂ levels, there is an increase in the sensitivity and variety of such receptors in tetrapods, emphasising the importance of the monitoring of CO₂ in aerial ventilation (Milsom 1995).

Thus, while O₂ uptake is of primary importance in the water, CO₂ loss is of critical importance on land. The problem with CO₂ loss on land is illustrated by the fact that all tetrapods are habituated to a certain degree of respiratory acidosis which they counteract by production of bicarbonate ions (Shoemaker *et al.* 1992). Tetrapods face particular problems of blood acid/base balance because of this problem of CO₂ build up, although the fish ancestors of tetrapods may have inhabited a hypercapnic aquatic environment and thus have been preadapted for the problems of terrestrial respiratory acidosis (Ultsch 1996).

Skin breathing. — Modern amphibians rely to a large extent on gaseous exchange via a moist skin; indeed, some terrestrial plethodontid salamanders lack lungs and rely entirely on the skin for gaseous exchange. However, the role of the skin is different with regards to O₂ gain and CO₂ loss. While all amphibians gain a minority of their O₂ via the skin, the great majority of amphibians lose the majority of their CO₂ via the skin (some specialised exceptions to this are discussed below). The very thin, glandular skin of modern amphibians which, along with a specialised cutaneous artery and vein, facilitates cutaneous gas exchange, may well be a derived feature in comparison with early tetrapods. However, many modern fishes and reptiles also employ a significant amount of cutaneous respiration (Feder & Burggren 1985), with the implication that this mode of respiration is primitive for tetrapods.

A significant problem with cutaneous respiration is that a skin that is permeable to gases is also permeable to water. This coupling of gas exchange and water loss limits the independence of modern amphibians from the water (Shoemaker *et al.* 1992). A few modern amphibians, including some tree frogs (e.g., *Hyla cinera* and *Chiromantis xerampelina*) and frogs found in arid environments (e.g., *Hyperolius nasua* and *Litoria gracilentia*), have mimicked reptiles in the use of lipids to waterproof their skin. These frogs have minimal cutaneous gas exchange, and are the only frogs to actively drink water. They also excrete nitrogen in the form of uric acid, rather than urea, again mimicking the reptilian condition (Shoemaker *et al.* 1992). However, these modern, highly specialised amphibians cannot be taken as representative of the primitive tetrapod condition. Additionally, these frogs may have limited capacity for increasing their metabolic rate (see discussion below).

Reliance on cutaneous respiration may also limit body size on land, due to the negative scaling of surface area to volume ratio. The rate of gaseous exchange via the skin is a function of the body surface area, while the use or production of respiratory gases is related to body volume. Thus, larger skin-breathing animals would be expected to have greater problems with CO₂ loss on land. This may limit the body size of terrestrial amphibians, although a slightly larger size might be permissible with a more elongated, eel-like shape, as this would afford a greater amount of skin surface area for a given body mass (Feder & Burggren 1985). The large aquatic salamanders *Cryptobranchus* and *Andrias* increase their surface to volume ratio by being flattened and such a strategy seems likely for some of the large aquatic temnospondyls (J.A. Clack personal communication). A flattened body form may also have been similarly important in some of the semi-terrestrial temnospondyls.

Lung breathing. — The earliest tetrapods most likely already had lungs, probably a common character of bony vertebrates (osteichthyans) (see discussion in Farmer 1997). Lungfish, the extant sister taxon to tetrapods, inhale air by a highly specialised

form of air gulping, and the muscular action employed is very similar to that of the buccal pumping mode used by modern salamanders (Brainerd *et al.* 1993).

Living amphibians also resemble lungfishes in having the hypaxial muscles divided into external oblique and internal oblique layers, with no further differentiation of these layers into intercostal musculature. However, all tetrapods possess a third, inner layer of hypaxial musculature, the transversus abdominus, which is used in exhalation. As a unique tetrapod feature, this muscle must have been acquired at least in the common ancestor of the Crown Group Tetrapoda (Brainerd *et al.* 1993). It may have evolved with the origin of tetrapods in the Late Devonian, or with the acquisition of greater terrestriality in the Early Carboniferous. All extant tetrapods also possess a ventral rectus abdominus portion of the hypaxial musculature, probably important in the early terrestrial tetrapods for postural support on land.

The most parsimonious interpretation of the similarities between lungfish and salamanders in the muscular control of lung ventilation is that this was the mode of ventilation possessed by the earliest tetrapods, first developed in the lunged sarcopterygian fishes, and retained in salamanders (and, by inference, in other modern amphibians). Other similarities in the sequence of movements in buccal pumping found between amphibians and ray-finned fishes suggest that this mechanism was primitive not only for lobe-finned vertebrates but also for bony vertebrates in general (Lauder 1985).

Buccal pumping is a relatively inefficient method of lung ventilation, as several buccal volumes of air must be pumped from the mouth into the thorax in order to fill the lungs. In contrast, costal aspiration involves a change in shape of the thorax, creating a potential negative pressure and sucking in air via aspiration to fill the lungs with a single breath. Thus faster rates of ventilation and gas exchange are possible with costal ventilation than can be achieved via buccal pumping. However, although the majority of CO₂ is lost over the skin in amphibians, as previously discussed, lung breathing (at least in frogs) is still important for ridding the body of excess CO₂ (Boutilier 1990). If this was also the case for the early tetrapods, as seems plausible, then the capacity for lung ventilation could set limits on the amount of additional metabolic CO₂ that the animal could handle, and hence set limits on the capacity for increasing its metabolic rate (see later discussion).

Evolutionary considerations

Discussion of previous ideas. — There were two main features of early tetrapods that originally led to the view that they would have engaged in costal ventilation rather than buccal pumping.

Firstly, most early tetrapods were thought to have had substantial rib cages, in which the ribs surrounded the body cavity more or less fully. Gans (1970a) considered that the large, overlapping ribs of early tetrapods such as *Ichthyostega* would prevent expansion of the lungs by the efforts of buccal pumping. However, this would not have been true unless the ribs formed a completely solid abdominal wall (Beth Brainerd personal communication), which was not in fact the case. Gans (1970b) also considered that the broad head shape and buccal pumping mode of ventilation of modern frogs represents a derived condition, related to their mode of vocalisation.

Secondly, both Gans (1970a) and Romer (1972) perceived a problem concerning the large body size of many 'labyrinthodonts' – an order of magnitude larger than modern amphibians (*Eryops* was the size of a large crocodile). They expressed doubts that such large animals could have lost sufficient CO₂ on land without the efficient mode of lung ventilation provided by costal aspiration. They suggested that the large size of these animals would have resulted in a relatively small surface area for cutaneous gaseous exchange. Additionally, many early tetrapods had bony scutes on the external surface of their skins, and they thought that these would have rendered the skin impermeable. Thus the presence of dermal scutes was argued to be incompatible with cutaneous respiration. Ultsch (1996) and Graham *et al.* (1997) also consider that early tetrapods would have been limited in their use of cutaneous respiration. It is appropriate to revisit these views, now that a great deal more is known about very early tetrapods.

With regards to the issue of early tetrapod ribs, the taxa that were used as examples in such studies were *Ichthyostega* (Late Devonian) and *Eryops* (Early Permian). Both animals are now known to be atypical in the form of the ribs, *Ichthyostega* for early tetrapods generally, and *Eryops* for temnospondyls in particular. It has been suggested that the ribs in *Ichthyostega* may have had a supporting role in locomotion (Thomson 1980). Certainly the contrast could hardly be greater than with *Acanthostega* (also Late Devonian), whose ribs have only recently been described (Coates 1996). Its short straight ribs appear most unlikely to have formed part of a ventilatory mechanism.

In temnospondyls, the ribs are straight and relatively short (Milner 1988, 1993) and, in this fashion, similar to those of *Acanthostega*. There seems to be no evidence in most of them of cartilaginous extensions carrying the rib ends round under the body so that they could meet each other or contact any midline structures (as is also true for *Eryops*, as later described). In order to function in costal ventilation, such extensions appear to be necessary and are found in modern animals where the ribs have this role. In *Ichthyostega*, *Acanthostega*, most of the Early Carboniferous tetrapods, and temnospondyls in general, the ribs have tapering ends 'finished' in smooth periosteal bone.

In contrast, some of the anthracosaurs, such as *Pholiderpeton* (Late Carboniferous), have relatively much longer ribs that are curved (Clack 1987), with ends bearing an unfinished facet suggestive of a cartilaginous end (J.A. Clack personal communication). If any early tetrapods had begun to employ the ribs in ventilatory movements, it was likely to have been these animals, considered as stem amniotes here. Other animals such as the more terrestrial microsaurids might also have begun this process independently of the amniote lineage, although the small size of most microsaurids would have made it easier for them to lose CO₂ via the skin.

Temnospondyls may have elaborated the buccal pumping mechanism by the development of the palatal vacuities (Clack 1992). Modern amphibians assist the mechanism of buccal pumping by lowering the eyeball into the buccal space, depressing the skin covering the palatal vacuity. Not only does their mode of lung ventilation not involve the use of ribs, but in most frogs the ribs have been lost altogether.

In amniotes, in contrast with temnospondyls, the ribs are usually quite long and curved. Ribs may have become in some way involved in breathing among amniotes at an early stage in their evolution, bearing opposing sets of muscles (i.e., the hypaxial intercostal muscles) to open and close the rib cage as they do in modern mammals. However, modern amniote groups, lizards, crocodiles, turtles, birds, and mammals, all use

rather different methods of lung ventilation. These differences suggest that their common ancestor was not reliant on costal ventilation alone for gaseous exchange. In turtles for example, the ribs have become incorporated into the shell internally, so it is hard to see how the turtles' ancestors could have done this if the lungs had been ventilated exclusively by rib movements. It may be that early tetrapods were using all possible means by which to aid gas exchange – air-gulping, buccal pumping and skin breathing, with rib movements being added at some stage in the ancestors of amniotes.

With regards to the issue of 'bony scales', it is important to realise that the gastralia (ventral scales) were dermal in origin. Thus, these scales would have had blood vessels running through them to the overlying epidermis. Pores in the bones and vascular spaces throughout the dermal bone provide evidence of such a blood supply (Bystrow 1947). Grooves for blood vessels are sometimes visible as well, but even without this, the structure and tissue relations of the dermal bones and scales imply that epidermal tissue lay external to them (J.A. Clack personal communication). This means that capillaries must have carried blood close to the surface for oxygenation. The thickness of the epidermis is unknown and therefore cannot be dismissed as 'too thick' (e.g., Ultsch 1997). In the case of heavily ornamented dermal bone the epidermis may have followed the ornament pattern quite closely, and where the ornament was reduced, skin folds may have hung from it, as suggested for *Crassigyrinus* (Clack 1998). It is known that the palate of *Ichthyostega* bore large blood vessels running over it (Jarvik 1996).

The scales of early tetrapods were not similar to the cosmine-covered ones of primitive osteolepiform fishes; they apparently were not covered by enameloid of any kind, and in this sense were not unlike the thinner scales of other tetrapodomorph fishes such as *Eusthenopteron*. Note that even heavily-scaled fishes such as the polypterid *Calamoichthyes* are still able to exchange 30% of their O₂ via their skin, as the scales are covered by non-keratinised dermal cells (Feder & Burggren 1985).

However, the skin of an early tetrapod would not have been like that of a modern amniote. Amniotes have incorporated the structural protein keratin into their epidermis which, along with the presence of lipids, means that the skin is 'waterproof', and thus less suitable for gaseous exchange than the thin, moist skin of modern amphibians. However, lizards and snakes may still perform a substantial part of their gas exchange through the skin, using the thin skin between the scales to do so (Feder & Burggren 1985). Turtles may exchange 30% of their CO₂ and 20% of their O₂ through the skin (although this is in the aquatic environment, and occurs largely through the cloaca, and so is not directly comparable with the situation in other tetrapods). Even humans lose around 1.5% of their CO₂ via their skin (Feder & Burggren 1985).

The elevated oxygen levels that pertained in the Late Carboniferous and Early Permian, 50 to 100% above present-day levels (Berner & Canfield 1989), must have had profound effects on the physiology of early tetrapods. These atmospheric concentrations would have resulted in a higher gradient between the air and the body. It would have been much easier to uptake O₂ through the skin as well as via the lungs. However, while such elevated O₂ levels would have made the obtaining of O₂ via the skin or lungs an easier proposition than under present day conditions, they would have exacerbated the problem of CO₂ loss. Higher levels of atmospheric O₂ would mean that the early tetrapods would be able to have lower rates of lung ventilation, with the result that a greater amount CO₂ loss would have to occur via the skin than under present-day

conditions. Fortunately, during that same time period atmospheric CO₂ levels were relatively low (similar to present-day levels; Berner 1993), so that the diffusion gradient for CO₂ loss would still have been relatively favourable.

New hypotheses. — Evidence from both modern animals and the fossil record leads us to the following hypotheses about the respiratory biology of early tetrapods. As with their fish ancestors, both aquatic and terrestrial early tetrapods would have relied on both the lungs and the skin for gaseous exchange. There is good evidence to suggest that they ventilated their lungs with a similar buccal-pumping motion to that seen in both living lungfishes and lissamphibians, and the fossil record evidence does not support the contention that the ribs were initially used in ventilation.

For the terrestrial tetrapods, CO₂ loss would have been of critical importance. The greater availability of O₂ in air would mean that lung ventilation rates could be relatively low, all the more so in the later Palaeozoic (Late Carboniferous–Early Permian) when levels of atmospheric O₂ were greatly elevated. These low rates of lung ventilation, sufficient for O₂ gain, would have been insufficient for all of the metabolic CO₂ loss. As in modern lissamphibians the majority of CO₂ loss was probably via the skin and, as in all extant tetrapods, these animals were probably adapted to a certain degree of respiratory acidosis. Note that there is no reason to assume that the dermal armour of some of the early tetrapods would have prevented cutaneous gas exchange, although the large size of many of these animals would have resulted in a less than favourable surface area to volume ratio for cutaneous gas exchange.

While this mode of respiratory biology may have been sufficient for these early tetrapods, the retention of a moist skin (essential for cutaneous respiration) would have limited them to near-water habitats. A few specialised modern frogs have ‘water-proofed’ their skin with lipids in a fashion analogous to amniotes, and are able to get rid of most or all of their CO₂ via their lungs. However, it seems unlikely that the relatively inefficient ventilatory mode of buccal pumping would be able to support amniote levels of metabolic rate.

In order for a tetrapod to assume an amniote-like biology, with independence from the water and a higher metabolic rate than seen in modern lissamphibians, a more efficient mode of lung ventilation would be necessary to ensure adequate rates of CO₂ loss. The way in which the capacity for a greater metabolic rate relates to the efficient excretion of CO₂ via the lungs is a complex one, relating to acid/base regulation. This physiological system is outlined below.

Intense exercise in amphibians and reptiles is carried out largely by anaerobic metabolism. Anaerobic metabolism is not sustainable, because it results in the production of lactic acid and a hence in a decrease in blood pH. The resulting acidosis is buffered by the production of bicarbonate ions, which in turn result in high levels of blood CO₂. Following activity, ectothermic tetrapods must have a period of inactivity during which the resulting acidosis is corrected. Birds and mammals do not encounter this problem because, as endotherms, they can engage in sustained aerobic activity.

Modern amphibians use several systems to deal with blood acidosis. These include using the skin to excrete hydrogen ions, the lungs to excrete CO₂, and the kidney and other structures (e.g., the bladder and the cloaca) to excrete acid (Jackson 1986; Boutilier 1992). However, when the skin of amniotes becomes impermeable to water it would also have a reduced ability to function in acid/base regulation. Thus ectothermic

amniotes would have to assume more of these functions via the kidney and the lungs. Extant reptiles that engage in sustained activity can have amounts CO_2 to excrete that are considerably greater than the amounts of O_2 that they take in to fuel this activity (Jim Hicks personal communication).

We propose that the evolution of costal ventilation would have enabled amniotes to be much more efficient at excreting CO_2 via the lungs, because it would allow for much greater rates of lung ventilation than buccal pumping. The evolution of costal ventilation, because of this role in acid/base regulation following activity, may have allowed amniotes to achieve higher levels of activity than possible in anamniotes.

Hypotheses of the osteological correlates of ventilation

We consider four key morphological features, and formulate specific hypotheses about the observable changes in these systems that would support or refute our major hypothesis about a change in ventilatory mode at the anamniote/amniote transition.

Firstly, we examine head shape. Szarski (1962) originally commented on the 'bellows-like' head shape of 'labyrinthodonts', and suggested that the wide and relatively flat nature of their heads reflected their use in buccal pumping. This head shape would also increase the surface to volume ratio of the head, important in any cutaneous component of gas exchange. Buccal pumping is achieved by lowering and raising the floor of the buccal cavity. A maximum change of the volume within the buccal cavity would thus be achieved with a head that was both broad in comparison with its length and relatively shallow dorsoventrally, as in the design of a pair of bellows.

Modern frogs have heads of this general shape, although their snouts are short in comparison with most Palaeozoic anamniotes. In contrast, most amniotes have heads that are both narrower and deeper than those of frogs and early anamniote tetrapods such as the Devonian forms, temnospondyls, and baphetids. Relatively narrower heads are seen in extant salamanders and caecilians, and also among the Palaeozoic 'lepospondyl' groups such as microsaur, aistopods, adelogyrinids, and early nectrideans. However, most of these animals are relatively small (with a few exceptions such as the microsauro *Pantylus*, they have a snout-vent length of around 10 cm), though some eel-like or fully aquatic forms are longer. Like the extant amphibians, lepospondyls could have relied on cutaneous gas exchange. It is notable however that some microsaur have long, slender, curved ribs. Some phylogenies suggest that microsaur are closely related to amniotes; thus these ribs may either represent a shared derived feature with amniotes or may be an independent acquisition.

We predict that head shape should be quantifiably different between modern frogs and modern amniotes, and that these differences should also be applicable to Palaeozoic amniotes and early anamniote tetrapods. Our hypothesis here is that buccal pumping constrains head shape to a wide and shallow morphology, and that only when costal ventilation has evolved can head shape be 'released' from ventilation. We propose that the narrow and deep skull is correlated with the adoption of costal ventilation.

Note that the adoption of costal ventilation would not mandate a change in head shape, but would allow for its evolution. Thus it is not necessary to demonstrate that every amniote has a narrow, deep head in order for our hypothesis to be supported (although we

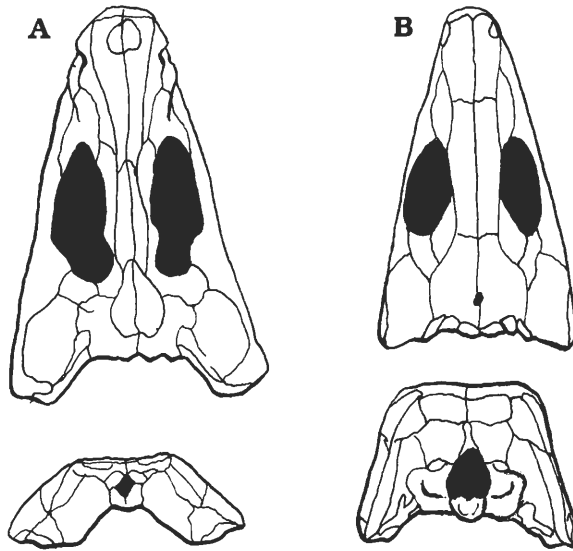


Fig. 1. Schematic views of head proportions in Paleozoic tetrapods (modified from Carroll 1988). Dorsal and occipital views of anamniote (*Megalocephalus*) (A) and amniote (*Paleothyris*) (B).

later discuss possible advantages of this head shape for the realignment of jaw adductor musculature, and the impact this had on the evolution of herbivory). In other words, our hypothesis would be refuted if any large terrestrial anamniote had a narrow, amniote-like head, but it would not be refuted if an early amniote retained a broader head.

Our second hypothesis concerns the size of the head in relation to the size of the body. We propose that buccal pumpers will have relatively large heads in comparison to their body lengths. A large head will result in a relatively large buccal volume, thus a large head would be able to fill the lungs with fewer efforts of pumping than a head with a smaller buccal capacity.

Frogs appear to have relatively larger heads in comparison with body length than amniotes, although we argue below that both a large head and a short body may be the result of other design constraints in frogs besides ventilation. However, many early tetrapods such as *Acanthostega*, *Eucritta* (a basal baphetid: no other baphetid postcranial skeleton is known from articulated remains), colosteids and temnospondyls (including early forms such as *Balanerpeton* and *Dendrerpeton*) also appear to have relatively large heads (J.A. Clack personal communication). Thus the specific hypothesis in this case is that buccal pumping constrains relative head size, and that a smaller head size (in large, terrestrial tetrapods) can only be achieved following the evolution of costal ventilation.

We make the hypothesis that Palaeozoic amniotes will have smaller heads than those early tetrapods noted above, including stem tetrapods and those on the lissamphibian stem lineage. Note, again, that it is not essential for all amniotes to have small heads. Costal ventilation would allow for a reduction in relative head size, but would not mandate a reduction. However, our hypothesis would be refuted if any large, terrestrial anamniote had a head comparable in proportions to that seen in modern amniotes. We would ideally like to show that this change happened during the evolution of amniotes, but this is not essential to the argument.

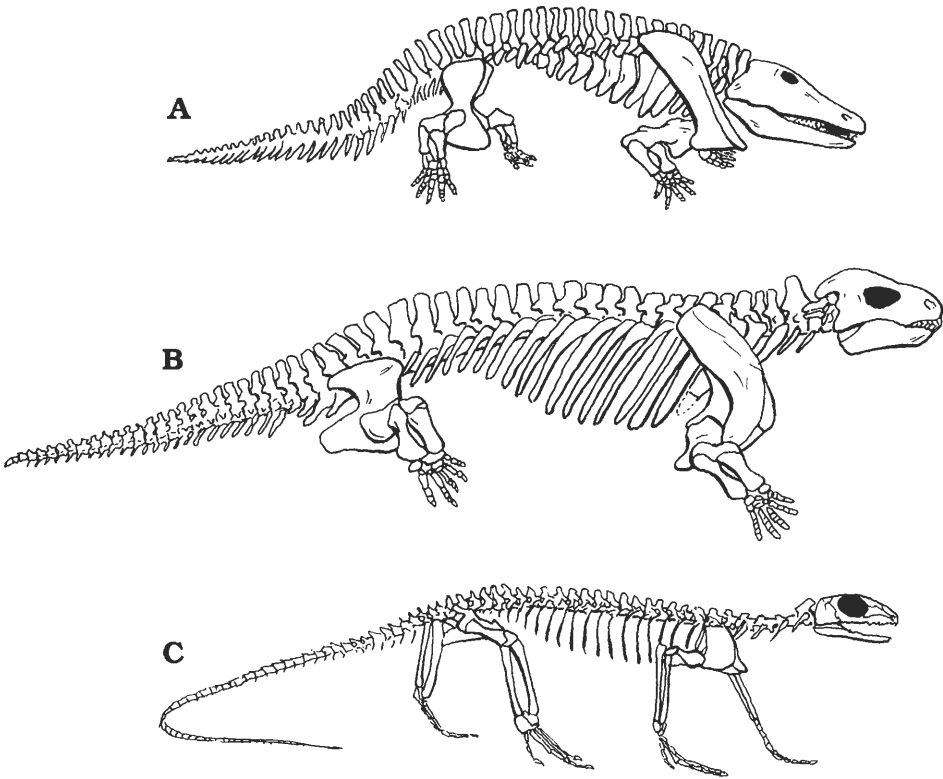


Fig. 2. Schematic views of whole body proportions in Palaeozoic tetrapods (modified from Carroll 1988). A. Anamniote (*Eryops*). B. Stem amniote (*Diadectes*). C. Amniote (*Petrolacosaurus*); this is a primitive diapsid, showing the longer neck typical of certain amniotes.

Our third hypothesis relates to neck length. Modern amphibians (especially frogs) have short necks, and this also appeared to be the case among early tetrapods. Not all amniotes have long necks, but longer necks do appear to be an amniote feature, as seen in the supposed stem amniote *Westlothiana* (Smithson 1989). Internal features of the anatomy match these features. Modern amphibians lack a distinct trachea; they retain a more lungfish-like condition of having the lungs converge into a short, broad laryngo-tracheal chamber that opens into the pharynx via the glottis. In contrast, amniotes have a tube-like trachea, with cartilaginous rings to maintain patency that branches ventrally into two bronchi leading to each lung. Additionally, the lungs of amniotes are more complexly internally subdivided than the lungs of most amphibians. Note, however, that while some frogs have fairly complexly divided lungs, the extant basal lepidosaur *Sphenodon* has simple, sac-like lungs (Hughes 1963). This suggests that the common ancestor of lissamphibians and amniotes also had simple, undivided lungs.

We propose that the short, broad entrance to the lungs is functionally correlated with a buccal-pumping mode of lung ventilation, and that it would be difficult to fill the lungs through a long, narrow, tube-like trachea without the more efficient mode of costal aspiration. Thus we advance the specific hypothesis that anamniotes should have short necks, reflecting the absence of a trachea. Long necks, with five or more

cervical vertebrae (that mandate the possession of a trachea or a similar structure) should only be seen in amniotes or their immediate relatives. Our hypothesis predicts that the stem tetrapods and stem lissamphibians would retain the primitive, short cervical region, and would be refuted by the discovery of one of these forms in which five or more obviously differentiated cervical vertebrae were present.

Our final hypothesis concerns the nature and shape of the ribs. Modern amphibians have very short ribs, whereas modern amniotes have a relatively robust rib cage, connecting ventrally (via cartilaginous rib extensions) to a sternum (the derived condition in turtles is an exception here). The condition in modern amphibians is clearly a derived one, as relatively robust ribs are a feature of most Palaeozoic tetrapods more derived than *Acanthostega*, an animal that was probably primarily aquatic (Coates & Clack 1995). However, as discussed below, it is not clear that the original function of tetrapod ribs was for ventilation: the broad, flat, overlapping ribs of animals such as *Ichthyostega* and *Eryops* suggest an immobile rib cage, possibly used in postural support on land. Coates & Clack (1995) point out the similarity of the rib cage in these early tetrapods to the condition in the silky anteater (*Cyclopes didactylus*), where the rib cage clearly plays a postural role in arboreal locomotion. Perhaps the additional possession of a diaphragm for lung ventilation allows for the specialisation of the rib cage in this animal.

An amniote-like sternum, which forms a component of the ventrally complete rib cage of modern amniotes, is probably not a primitive tetrapod feature. Sterna are often cartilaginous, and it is difficult to determine their presence in fossils. However, the 'sternal' elements of modern amphibians are probably not homologous with the amniote sternum (Zug 1979). The amniote type of sternum can be inferred to be present in most Palaeozoic amniotes (i.e., Crown Group Amniota) by the use of Witmer's (1995) Extant Phylogenetic Bracket, as the modern synapsid (mammal) and sauropsid (reptile and bird) amniote lineages have their divergence in the Late Carboniferous (Carroll 1988).

For tetrapods that precede the synapsid/sauropsid split, the presence of a sternum might be inferred from rib anatomy; that is, from the possession of ribs with distal articulatory surfaces for cartilaginous extensions that would connect to a ventral sternum. Ribs used in costal ventilation would have to be mobile. Mobility would be indicated by the articulation with the vertebral column, by the development of rib heads with a distinctly separated tuberculum and capitulum, allowing for rotation during rib abduction and adduction. Additionally, the ribs would have to be relatively narrow, rounded, and non-overlapping, to allow space for intercostal musculature (derived from the hypaxial musculature) to both attach to the ribs and to move them. Finally, the ribs would be expected to have a degree of mesiodistal curvature; adduction of curved ribs would result in a relatively greater expansion of the pleuroperitoneal cavity than the same degree of abduction of flat ribs.

Thus we can make some specific predictions about the morphology of ribs of tetrapods with costal ventilation. Costal aspirators should have non-overlapping ribs with relatively tubular shaft proportions and a degree of mesiodistal curvature; the shape of the distal ends should be suggestive of an articulation with cartilaginous rib extensions; and the rib heads should have a distinct tuberculum and capitulum. Our hypothesis would be supported if such a change in rib morphology was coincident with the anamniote/amniote transition, or was acquired within the stem amniote lineage. Our hypothesis would be falsified if early amniotes did not have ribs of this morphology, or if other anamniotes (i.e., those other than stem amniotes) did possess ribs of this morphology.

Figs. 1 and 2 illustrate representative examples of skulls and postcranial skeletons, and show that the above predictions are generally true. That is, that anamniotes ('labyrinthodonts') have skulls that are broader, flatter, and larger in respect to their body length than amniotes; that only amniotes have long necks; and that ribs in anamniotes are short, broad and flat whereas those of amniote are long, rounded and curved. Additionally, the derived anamniote *Diadectes*, the sister taxon to amniotes, is somewhat intermediate in the possession of these features. However, in order to fully support our hypothesis it is necessary to examine a large range of taxa and to provide some quantification of the data.

Materials and methods

Head length in relation to head width. — We included frogs among amphibians, and lizards (primarily from the families Iguanidae and Varanidae) for modern amniotes (the taxa measured are listed in the appendix). We additionally included some alligators for comparison with the lizard data. The reasons for restricting our choice of taxa to these tetrapod groups were as follows.

Firstly, an overwhelming important issue was related to the statistical design of the study. In order to make a meaningful comparison with the available data on fossil tetrapods, it was important to select extant taxa in this same general size range; this excluded the majority of species of modern amphibians. We also selected taxa on the basis of their respiration mode. Although some salamanders were large enough for consideration in the sample, these taxa were all exclusively or primarily aquatic taxa, relying on the skin and/or external gills for gas exchange. Thus they would not serve as a good model for an animal whose head shape was expected to reflect its mode of lung ventilation on land. Likewise, fully aquatic frogs (e.g., *Xenopus*) were also excluded. Lizards were the obvious choice to represent the primitive amniote condition, as they have not augmented their costal ventilation with any type of diaphragm, as seen in both crocodylians and mammals. However, to counteract the possible criticism that primitive tetrapods had broad, flat heads because of a supposed 'crocodile-like' mode of life, several crocodylians (represented by 15 individuals of various sizes of *Alligator mississippiensis*) were included for comparison.

Measurements of the modern taxa were made from the collections at the Museum of Comparative Zoology (Harvard University) and the American Museum of Natural History (New York). Skull length was measured from the tip of the snout to the end of the basioccipital bone at the foramen magnum. Skull width was measured as the distance between quadrate jaw articulations, taken from the lateral border of the condyles. We also measured the skull occipital height for some taxa, in order to distinguish between the flatter heads of amphibians and the deeper heads of amniotes. However, as these data were virtually impossible to obtain in the fossils we did not include this measurement in the analyses. All data points are from single individuals. In the few instances where we had data from more than one individual of the same species, these measurements were not averaged because these individuals were often of different sizes (a problem when dealing with average measurements from species with indeterminate growth). The data set included measurements from 89 frogs, 96 lizards, and the sphenodontid *Sphenodon punctatus* (skull from the Brown University teaching collections).

In our measurements of fossil taxa, we also excluded a number of types of primitive tetrapods from the data set. Among the anamniotes, we excluded those taxa that had been determined to be secondarily fully aquatic (see e.g., Carroll 1988; Benton 1997), for similar reasons as for the exclusion of the aquatic lissamphibians: this included both broad-headed brachyopids and plagiosaurs, and narrow-headed trematosaurs. Among the 'lepospondyls', only microsaur were included. Long, snake-like taxa such as lysorophids and aistopods would have had a very high surface area to volume ratio, and may have relied extensively on cutaneous respiration. The nectrideans were also probably fully aquatic (and the head shape of many defied measurement!) Among the amniotes we excluded taxa with extensive head ornamentation in the form of knobs and skull projections, such as pareiasaurs and procolophonids, which might have resulted in head shapes uncharacteristic of the majority of amniotes. However, we note that while these taxa have skulls that are uncharacteristically wide for amniotes, they also have relatively deep skulls, rather than the flat skulls typical of anamniotes.

The fossil taxa were measured in a similar fashion to the living ones, with the exception that skull width was occasionally estimated from doubling the distance from the jaw joint to the skull midline in an incomplete skull. Only skulls that were uncrushed in the lateral dimension were measured. The data at the same institutions as for the living taxa, and additionally at the Field Museum of Natural History (Chicago), the University Museum of Zoology, Cambridge (UK), and the Natural History Museum, London (UK). The fossil data set included measurements from 71 anamniotes and 8 amniotes. We also included a couple of taxa whose taxonomic position could be considered as 'intermediate' with respect to amniote status (see Lee & Spencer 1997): *Diadectes* and *Limnoscelis*. Unfortunately, the amniote data proved very difficult to obtain. None of the collections that we were able to visit had skull material from early primitive amniotes, such as protorothyridids. With the exception of a measurement from the captorhinomorph *Captorhinus* our amniotes are all synapsids. However, we note that all of the available illustrations of more primitive amniotes depict the skulls as being long, narrow, and deep in comparison with contemporaneous anamniotes. The complete list of taxa measured is presented in Appendix 1.

Statistical analyses. — The data were entered into the statistical package Data Desk, which was employed for the initial plotting and analyses. In order to determine whether the various groups were statistically different from each other in slope and/or intercept the reduced major axis regression lines were calculated and the statistical parameters estimated following Plotnick (1989).

The ideal measure to plot would have been some indication of ratio of head length to head width against body mass, or some estimate of body mass. However, independent data on body mass were difficult to obtain for the living specimens, and impossible for the fossils. It might have been possible to obtain a proxy of body mass, such as femur cross-sectional area, for some of the living taxa. But this would have been almost impossible for the fossils, very few of which had postcranial material associated with the skulls. We could devise no measure from the skull alone that would serve as an independent estimate of body mass, especially one that we could be confident would hold true across the wide taxonomic range considered here. Instead we examined head shape by plotting head width against head length.

Head length in relation to body length. — These data were gathered from the literature, from papers that provided reconstructions of the complete skeleton of the animals (see Table 1). The length of the head was measured with callipers, and the length of the presacral vertebral column was measured with a flexible rule, to accommodate curvature of the column. The length of the head and the presacral vertebral column were added together to create the snout-vent length, and the relative head length was then calculated as a percentage of the snout-vent length.

Neck length. — Data were again obtained from the literature, from papers that provided a clear picture of the cervical region (and in some cases provided an actual count of the number of cervical vertebrae) (see Table 2). The data on *Eryops* were derived from the mounted museum specimen (see below).

Rib morphology. — All data collection on rib morphology was from mounted specimens on display at the MCZ. We measured the following complete, articulated specimens (all from the Early Permian of Texas): the temnospondyl labyrinthodont *Eryops megacephalus* (MCZ 1539); the amniote sister taxon *Diadectes tennitectus* (MCZ 1035); and the amniote pelycosaur *Ophiacodon uniformis* (MCZ 1366) and *Dimetrodon grandis* (MCZ 1366).

The following measurements were taken on each presacral rib (with the exception of the ribs underneath the pectoral girdle, which were inaccessible): rib length, maximum shaft width, the distance between the tuberculum and the capitulum, and the degree of rib curvature (the rib cord ratio) (see Table 3). The rib width, and the tuberculum/capitulum distance were made using dial callipers. The rib length was measured by the use of a flexible rule laid along the rib surface. This rule was also used to estimate rib curvature; after the rule had been bent so as to lie along the outer surface of the rib the shape of the rule was traced onto a piece of paper. The degree of rib curvature was estimated as the ratio of the cord length to the maximum cord width. To envisage these measurements: if the rib is thought of as a curved bow (as used with arrows), the cord length is the length of the string that would connect the ends of the bow, and the maximum cord width is the maximum distance between the string and the body of the bow (the more curved the bow, the greater the cord width).

Results

Head length in relation to head width. — The results of the statistical analysis are shown in Fig. 3. There is a clear difference between the distribution of lizards and frogs on the plot: for any given head length frogs have heads that are much broader than those of lizards. The frog and lizard regression lines are significantly different from each other in both slope and intercept (there is no statistical difference between the lizards and the alligators). We had predicted that the frogs' heads might scale with positive allometry and the lizards' heads with isometry, given the potential surface area (= floor of mouth) to volume (= lung volume) parameters involved. However, while there is a difference in allometric scaling in the direction that we predicted, in fact frogs' heads scale isometrically and lizards' heads scale with negative allometry.

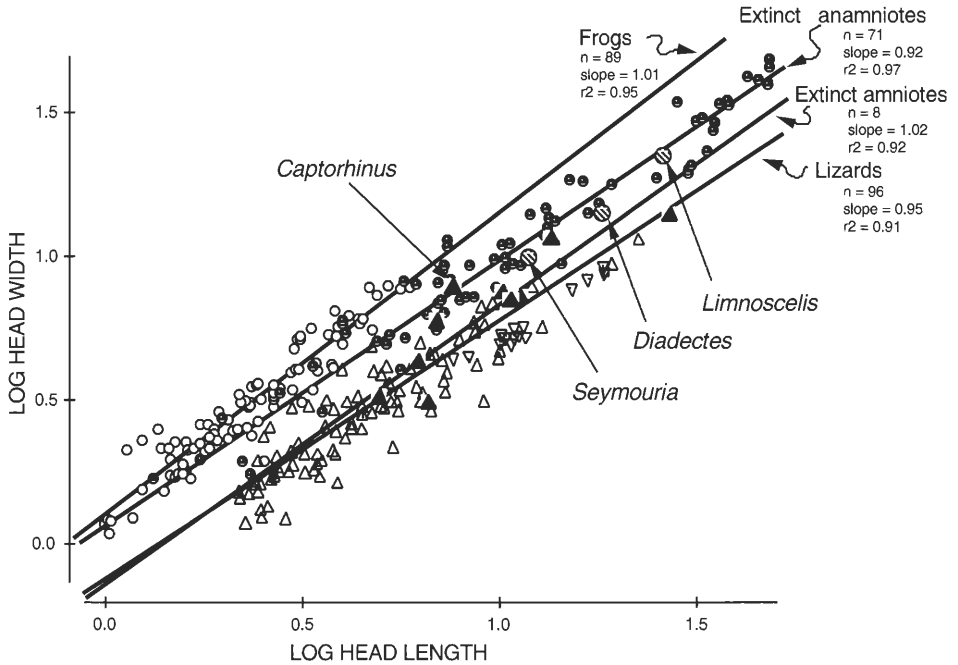


Fig. 3. Scaling of head width to head length in tetrapods. Key to symbols: open circles, frogs; solid circles, the majority of fossil anamniotes; hatched circles, stem amniotes; open triangles, lizards (inc. *Sphenodon*); inverted open triangles, alligators; solid triangles, fossil amniotes.

When the fossil data are entered the general pattern is as predicted: anamniotes tend to cluster with the frogs and amniotes with the lizards. However, the detailed pattern and the statistical analyses do not yield as clear-cut a picture. Given the nature of the data, this is hardly surprising. The very clear difference between the two modern groups must come in part from the fact that the data are drawn from two rather narrow taxonomic groupings, essentially from two discrete orders at a single point in time. In contrast, the fossil data represent a highly paraphyletic grouping and from a wide range of times, ranging from Late Devonian to mid Triassic, and would be expected to have a greater degree of variation.

The fossil anamniotes cluster closer to the frogs than to the lizards. The intercept of the regression line for fossil anamniotes is statistically indistinguishable from that of the frogs, and statistically different from that of the lizards. However, the points representing the fossil anamniotes generally lie below those of the frogs, and the slope of the line is significantly different from frogs (and indistinguishable from that of the lizards). These differences hold true even if only the smaller fossil non-amniotes (i.e., those whose head lengths fall in the same size range as the frogs) are considered.

Thus fossil anamniotes are statistically distinguishable from extant amniotes with regards to their head shape (head length *versus* width). They have heads that are relatively wider than those of modern amniotes, even though their heads are slightly narrower than those of frogs. Additionally, the head shape of fossil anamniotes scales with negative isometry (as in amniotes) rather than with allometry (as in frogs). The relatively wider heads of modern frogs may be related to their very short snout; frog head

shape may additionally be influenced by demands of vocalisation as well as by lung ventilation (Gans 1970b).

A comparable pattern is seen for the fossil amniotes, in that they tend to cluster with their modern relatives. Both the slope and the intercept of the regression line of fossil amniote head shape are indistinguishable from that of the lizards, and both are statistically different from those of the frogs. Thus the fossil amniotes show a statistical difference from both modern amphibians (in both the slope and intercept of the regression line), and from fossil anamniotes (in the intercept only). Fossil amniotes have significantly narrower heads for any given head length than anamniotes.

These results support our general hypothesis (or, at least, fail to refute it): that amniotes have narrower heads than anamniotes. However, in considering where particular fossil data points fall we still lack strong confirmation that this head shape change was coincident with the anamniote/amniote transition. The Early Permian stem amniote anthracosaurs, *Seymouria*, *Limnoscelis*, and *Diadectes*, fall on, or slightly below, the regression line for the general anamniote condition, whereas one might expect them to be more intermediate in position, or even amniote-like. The only anapsid amniote in our data (the remainder are synapsids), *Captorhinus*, has a rather broad head, falling outside of the range of lizard head shapes. However, remember that our hypothesis would only be falsified had any anamniote been found to have a narrow, lizard-like head, which is not the case. Our hypothesis is not falsified by the fact that head shape is still relatively wide in some primitive amniotes. In later discussion we note that *Diadectes* has a relatively deep, amniote-like skull in comparison with other stem amniotes, despite the retention of a relatively broad skull.

Head length in relation to body length. — All non-anthracosaurian anamniotes have head lengths that are at least 30% of their snout-vent length (average 34.5%), with the greatest percentage being 44% (see Table 1). The amniotes mostly have head lengths below 27% of their snout-vent length (average 25.5%). The exceptions are with the captorhinids (*Eocaptorhinus* being the only taxon to overlap in relative head length with the non-anthracosaurian anamniotes) and with the archosaur *Protosuchus*. The condition in *Protosuchus* is clearly a derived one. The condition in the captorhinids is probably also derived: note that other primitive ‘anapsids’ such as *Paleothyris* and *Hylonomus*, animals that lie more basal on the amniote cladogram than *Captorhinus* (Gauthier 1994), have relatively smaller heads (22 and 24% of snout-vent length, respectively). The heads of the anthracosaurian anamniotes are similar in proportions to those of the amniotes (average = 24% snout-vent length).

Neck length. — Of the taxa surveyed, all non-anthracosaurian anamniotes, with the exception of some lepospondyls, have four or fewer cervical vertebrae, while most amniotes have four or more cervical vertebrae (the exception being the pareiasaur *Scutosaurus*) (see Table 2). Some lepospondyl anamniotes may have a greater number of cervical vertebrae; for example, the microsaur *Pantylus* has eight (Carroll 1968). However, as previously discussed, lepospondyls were in general small and probably reliant on cutaneous gas exchange and microsaurians may conceivably have evolved costal ventilation convergently with amniotes. Slightly longer necks (5–6 cervical vertebrae) are seen in the anthracosaurian anamniotes, which are a paraphyletic assem-

Table 1. Head/snout-vent length proportions in early tetrapods.

Taxon	Head length (mm)	Body length (mm)	S/V length (mm)	Head to total length ratio	Ref. (see Appendix 2)
Non-anthracosaur anamniotes					
<i>Acanihostega gunnari</i>	95.5	195.9	291.4	33%	6
<i>Balanerpeton woodi</i>	40.5	99.6	140.1	30%	17
<i>Cacops</i> sp.	180.5	510	690.5	35%	27
<i>Caerhachis bairdi</i>	53.8	147.8	201.6	36%	13
<i>Dendrerpeton obtusum</i>	10.5	23.7	34.2	30%	16
<i>Dendrerpeton acadianum</i>	79.6	166.3	245.9	32%	14
<i>Eoscopus lockardi</i>	39.9	67.8	107.7	37%	7
<i>Eryops</i> *	25.9	54.3	80.2	32%	10
<i>Eupelor</i>	238	523	761	31%	24
<i>Peltobatrachus pustulatus</i> *	84	232.8	316.8	38%	20
Permian taxon	5.3	12.1	17.5	44%	15
<i>Trematops</i> *	45.2	71.6	116.8	39%	10
Anthracosaurian anamniotes					
<i>Brukerpeton</i> *	15.5	50.2	65.7	24%	3
<i>Diadectes</i> *	21	91.7	112.7	19%	3
<i>Gephyrostegus bohemicus</i>	52.1	130.3	182.4	28.5%	2
<i>Limnoscelis</i> *	15.7	40.8	56.5	28%	3
<i>Proterogyrinus scheeli</i>	136.4	524.5	660.9	21%	12
<i>Seymouria baylorensis</i> *	19	64.3	83.3	23%	3
Amniotes					
<i>Captorhinus</i> *	35	94.5	129.5	27%	10
<i>Dimetrodon grandis</i> *	17.4	53.5	70.9	25%	3
<i>Eocaptorhinus laticeps</i> *	18	39.7	57.7	31%	3
<i>Euparkeria</i> *	19	53	72	26.5%	3
<i>Haptodus</i> *	17.9	49.2	67.1	26.5%	3
<i>Hylonomus lyelli</i> *	15.7	49.6	65.3	24%	3
<i>Lycanops</i> *	36.3	116	152.3	24%	10
<i>Paleothyris</i>	26.3	93.6	119.9	22%	2
<i>Pantelosaurus saxonicus</i> *	17.1	47.3	64.4	26.5%	10
<i>Pareiasaurus karpinskyi</i>	23.8	72.2	96	25%	10
<i>Petalacosaurus</i> *	16.4	67.6	84	24.5%	21
<i>Planocephalosaurus</i> *	20.4	51.8	72.2	28.5%	3
<i>Procolophon</i> *	20.7	69.5	90.2	23%	3
<i>Protosuchus</i> *	20.7	50.9	71.6	29%	3
<i>Scuteosaurus</i> *	12.4	45.9	58.3	19.5%	3
<i>Sphenodon punctatus</i> *#	15.6	46	61.6	25.5%	10
<i>Spinoaequalis schultzei</i>	30.3	93	123.4	24.5%	8
<i>Thrinaxodon</i> *	25.8	91.3	117.1	22%	3
<i>Varanops brevirostris</i> *	17.5	49	66.5	26.5%	10

* Unmodified measurement from literature, not scaled to actual length (otherwise = measurement scaled to actual length).

Extant taxon.

blage of sister taxa to the amniotes, and thus might be expected to display an intermediate condition.

Thus these data fail to refute our hypothesis: they show that no large, terrestrial anamniote has a long neck, whereas long necks are present among the amniotes. A survey of any palaeontology text (e.g., Carroll 1988) will confirm this impression that

Table 2. Neck lengths of early tetrapods.

Taxon	No. of cervical vertebrae	Reference (see Appendix 2)
Non-anthracosaur anamniotes		
<i>Amphibamus lyelli</i>	2	1
<i>Apidosaurus novomexicanus</i>	1	1
<i>Broillielus brevis</i>	3	1
<i>Cacops aspiderphorus</i>	2	27
<i>Caerorachis bairdi</i>	4	5
<i>Crassigyrinus scoticus</i> *	3	20
<i>Dissorophus angustus</i> *	2	1
<i>Eryops megacephalus</i> #	4	#
<i>Greererpton burkemorani</i>	4	9
<i>Micropholis stowi</i>	2	25
<i>Paracyclotus davidi</i>	2	26
<i>Pholidogaster pisciformis</i>	3	23
Anthracosaurian anamniotes		
<i>Gephyrostegus bohemicus</i>	5	2
<i>Diadectes</i> sp.	6	4
Anniotes		
<i>Araeoscelis</i>	8	22
<i>Cephalerpeton ventriarmatum</i>	3	3
<i>Cotylorhynchus hancocki</i>	7	18
<i>Dimetrodon angelensis</i>	4	18
<i>Dolissaurus adamanteus</i>	4	18
<i>Eocaptorhinus laticeps</i> *	5	11
<i>Paleothyris acadiana</i> *		2
<i>Petrolacosaurus</i>	5	21
<i>Procolophon</i> sp.	6	4
<i>Scutosaurus</i> sp.	3	4

* Number of cervical vertebrae provided by author. Otherwise estimated from illustrations.

Museum specimen (MCZ 1539).

anamniotes have very short necks while many anniiotes have longer necks (i.e., necks at least as long as in a modern lizard).

Rib morphology. — The temnospondyl anamniote *Eryops*, has flanged, imbricating ribs in the anterior portion of the rib cage. Ribs 2–12 (total rib number is 20) all have large, distal flanges that overlap with the rib posterior to them (see Fig. 4). The tuberculum and capitulum are conjoined, leaving the diapophysis and parapophysis facets almost directly together. The ribs are very flat and show little curvature; the average cord ratio is 0.06, and the maximum cord ratio of any one rib is 0.13 (see Table 3). Additionally, the ribs are relatively short, and the distal ends are thin-edged and expanded, showing no evidence of attachment of cartilaginous rib extensions.

In contrast the anniiote *Ophiacodon*, a relatively primitive synapsid, has rounded ribs that show minimal flanging, except for a slight degree of non-imbricating expansion in the dorsal portion of the more anterior ribs (ribs 1–17 out of a total of 27 ribs). The rib heads have a distinctly separated tuberculum and capitulum, with widely separated diapophyseal and parapophyseal facets. The ribs are more highly curved than in *Eryops*, with an average cord ratio of 0.10, and a maximum cord ratio of 0.14 (see Ta-

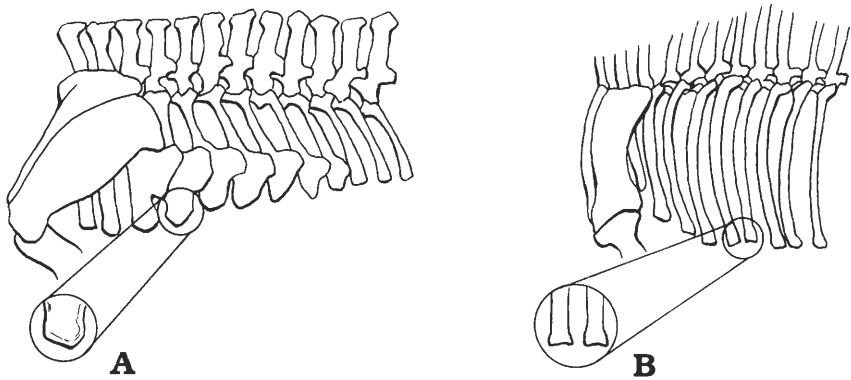


Fig. 4. Rib cage anatomy of *Eryops* (anamniote) (A) and *Dimetrodon* (amniote) (B).

ble 3). The distal ends of the ribs are blunted and of the same diameter as the rib shafts, with slightly concave ventral surfaces (see Fig. 4). This resembles the morphology of the ribs in extant amniotes that bear a cartilaginous rib extension.

The more derived synapsid, *Dimetrodon*, shows a similar, but more derived, condition of the rib cage to *Ophiacodon*. All of the ribs are rounded, and of uniform thickness; all evidence of flanging is lost. The rib heads have an even greater separation of tuberculum and capitulum than in *Ophiacodon*. The ribs are also more highly curved than in *Ophiacodon*, with an average cord ratio of 0.15 and a maximum cord ratio for any single rib of 0.20 (see Table 3). The distal ends of the ribs have a similar morphology to *Ophiacodon*.

The morphology of the rib cage of *Diadectes* bears greater resemblance to the amniote condition than to that of *Eryops*. The ribs are rounded, rather than broad and flat, but overlapping distal flanges are retained on ribs 5 and 6, just behind the shoulder girdle. The curvature of the ribs is similar to that in *Ophiacodon*: the average cord ratio is 0.10, and the maximum cord ratio for any one rib is 0.13. All of the ribs, with the exception of the last three (nos. 17–19, which are also shorter than the other ribs), show a distal morphology similar to that of the amniotes, suggestive of the attachment of cartilaginous rib extensions. However, *Diadectes* shows a more primitive condition in the morphology of the rib heads. The tuberculum and capitulum, although more widely separated than in *Eryops*, are conjoined by a web of bone, rather than forming two separate heads as in the amniotes.

Discussion

Our data show that modern amphibians have heads that are relatively broader than those of modern reptiles, and we propose that this correlates with their buccal pumping mode of lung ventilation. Paleozoic anamniotes also have relatively broad heads, whereas most Paleozoic amniotes have narrower ones, supporting our hypothesis that this transition in mode of lung ventilation took place close to the anamniote/amniote transition. In addition, these amniotes have relatively smaller heads and longer necks than anamniotes, features also related to the mode of lung ventilation. Only amniotes

Table 3. Rib measurements of early tetrapods (all measurements in mm, from specimens in the Museum of Comparative Zoology). Rib counts commence at first accessible rib behind shoulder girdle.

rib no.	rib length	basal shaft width	max shaft width	rib cord ratio	rib no.	rib length	basal shaft width	max shaft width	rib cord ratio
<i>Eryops</i>					<i>Diadectes</i>				
7	168	30.3	51.9	0.12	5	NM	19.4	67.5	NM
8	160	26.2	50.5	0.13	6	NM	19.4	NM	NM
9	157	23.8	49.7	0.11	7	300	20.7	20.7	0.10
10	147	19.1	42.3	0.07	8	318	16.5	19.2	0.13
11	138	19.7	36.5	0.05	9	318	16.7	18.0	0.10
12	130	21.3	32.2	0.02	10	332	19.1	19.1	0.10
13	123	18.7	18.7	0.02	11	316	19.0	19.0	0.12
14	106	15.4	15.4	0.02	12	208	18.3	18.3	0.10
15	95	13.6	13.6	0.02	13	278	18.1	18.1	0.10
16	85	7.9	7.9	0.02	14	258	18.1	18.1	0.09
17	78	6.6	6.6	0.04	15	228	15.5	15.5	0.12
18	68	5.9	5.9	0.06	16	193	12.5	14.6	0.09
19	58	4.4	4.9	0.02	17	148	10.2	13.8	0.08
20	53	5.8	5.8	0.08	18	105	11.8	11.8	0.07
					19	58	10.3	11.7	0.05
<i>Ophiacodon</i>					<i>Dimetrodon</i>				
9	138	8.2	14.0	0.10	7	168	4.7	4.7	0.17
10	145	6.3	16.0	0.10	8	188	10.8	10.8	0.15
11	148	6.8	12.7	0.13	9	213	7.5	7.5	0.15
12	159	6.3	15.6	0.13	10	217	7.8	7.8	0.14
13	165	7.4	13.5	0.13	11	223	6.0	6.0	0.15
14	168	7.6	NM	0.14	12	225	5.8	5.8	0.15
15	171	6.4	13.7	0.14	13	227	6.6	6.6	0.14
16	163	6.3	NM	0.12	14	241	5.0	5.5	0.17
17	143	5.9	14.4	0.09	15	240	5.1	5.5	0.17
18	145	5.9	11.1	0.10	16	239	7.0	7.0	0.17
19	137	5.4	10.4	0.10	17	235	5.8	5.8	0.19
20	110	5.9	NM	0.09	18	227	5.3	5.3	0.19
21	97	NM	5.3	0.08	19	210	5.0	5.8	0.20
22	86	NM	5.5	0.08	20	185	5.8	5.8	0.15
23	68	NM	5.1	0.07	21	156	5.5	5.5	0.20
24	55	NM	5.9	0.07	22	131	2.5	4.8	0.18
25	43	NM	4.8	0.03	23	103	2.7	4.6	0.13
26	25	NM	4.4	0	24	82	2.2	4.3	0.15
27	15	NM	4.3	0	25	42	3.1	4.4	0.05
					26	22	2.3	3.6	0.05

NM – not measurable (hidden behind shoulder girdle or plaster reconstruction).

possess long necks, and the possession of ribcage morphology suitable for costal ventilation is absent from large temnospondyl anamniotes such as *Eryops*. These morphological features are in support of the hypothesis that buccal pumping was the primitive tetrapod condition, and that costal ventilation is a derived feature of amniotes, occurring at or near the anamniote/amniote transition.

Brainerd and co-workers (personal communication, and see Owerkowicz *et al.* 1999) have suggested that the gular pumping seen in some present-day lepidosaurs, such as *Varanus*, is a holdover of the early tetrapod buccal pumping mechanism. *Varanus* appears to use this pumping as a means of obtaining additional oxygen, especially during

locomotion when costal ventilation is impaired. Brainerd (personal communication) suggested that protoamniotes might have been able to free their head from the constraints of buccal pumping by evolving a longer neck and moving the pump to the throat, perhaps employing a mixture of gular pumping and costal ventilation as an intermediary condition. However, our data on neck length (Table 2) show that longer necks, at least of the length seen in modern lizards, were not gained until the fully amniote condition, making this scenario unlikely. We would suggest that gular pumping is a derived feature among certain amniotes, not a primitive, protoamniote one. However, we discuss later the possibility of some intermediate condition among the anthracosaurs.

In the remainder of this section we will consider some other features of early tetrapod biology that are interrelated to our conclusion that only amniotes possess costal ventilation. These include considerations of the following issues. (1) The mode of carbon dioxide loss in early anamniote tetrapods. (2) The changes in the relative roles of axial skeleton and musculature in postural support in amniotes. (3) The evolution of herbivory in amniotes. (4) The possible transitional steps towards the amniote condition of costal ventilation among the derived anthracosaurian anamniotes (i.e., stem amniotes).

Early tetrapods and carbon dioxide loss. — Other workers (e.g., Packard 1976; Ultsch 1996) have also considered this issue of carbon dioxide loss and the problem with cutaneous gaseous exchange in early tetrapods. But, unlike Gans (1970a) and Romer (1972), they did not conclude that the low surface area to volume ratio of large tetrapods would mandate costal aspiration. Instead, they speculated that early tetrapods developed tolerance of high blood levels of carbon dioxide. Ultsch (1996) noted that current evolutionary scenarios of tetrapod origins depict the osteolepiform ancestors of tetrapods as being large fishes inhabiting warm, shallow aquatic environments. If this were true, then these fishes would have had problems with both hypoxia (low oxygen levels) and hypercapnia (high carbon dioxide levels, because of the carbon dioxide produced by the aquatic vegetation). Modern fishes in such environments have adapted to metabolic tolerance of hypercapnia, and early tetrapods may have inherited such a tolerance that was preadaptive for the terrestrial environment.

Ultsch (1996) considered that early tetrapods probably relied heavily on the skin for carbon dioxide loss, despite the problem of the dermal ossifications, an opinion with which we concur. The potential limitation imposed by dermal scutes depends whether or not the covering epidermis was vascularized, as previously discussed. It seems likely that the very thin, glandular skin of modern amphibians is a derived lissamphibian feature (Feder & Burggren 1985). However, it would not be impossible for early tetrapods to have substantial carbon dioxide loss via a less specialised skin that lacked the keratinised layer of epidermis typical of amniotes. Indeed, a fully keratinised epidermis is probably a derived amniote feature, as it is achieved in a slightly different way between synapsids (using α keratin only) and sauropsids (= reptiles plus birds, using primarily β keratin). Perhaps these early tetrapods would tolerate hypercapnia on land, and return to the water at frequent intervals for the bulk of their carbon dioxide loss.

This mode of hypercapnia tolerance might have been a 'good enough' solution for most Palaeozoic lifestyles. However, it may have been prohibitive not only to independence from the water but also to the development of greater levels of terrestrial activity. The small size and specialised skin of modern amphibians might be an adaptive response to the problem of hypercapnia, derived quite independently to the amniote solution of

costal ventilation. With regards to the issue of body size and the unfavourable surface area to volume ratio in many Palaeozoic anamniotes, we note an interesting fact about atmospheric conditions in the Palaeozoic. During the later half of the Carboniferous and the earlier half of the Permian atmospheric carbon dioxide levels were extremely low (Berner 1993) while oxygen levels were high (Berner & Canfield 1989).

Graham *et al.* (1995, 1997) commented on the potential significance of these elevated levels of atmospheric oxygen in the evolution of tetrapods, but failed to note the importance of the lowered levels of carbon dioxide. With low environmental carbon dioxide there would be a more favourable diffusion gradient for its loss, perhaps enabling larger animals to rely on diffusion on land. We note that this Permo-Carboniferous interval of lowered carbon dioxide appears to match the time of the known ranges of larger, terrestrial anamniote tetrapods, such as the eryopids (see e.g., Carroll 1988; Benton 1997).

Rib cage morphology and the evolution of trunk postural support. — Ribs in (gnathostome) fishes have a primarily locomotor function. They are embedded in the hypaxial musculature in the myosepta between segmental myomeres, bolstering the attachments of the myomeres to each other and enabling greater contractile force of the axial musculature (Wake 1979). Appendicular muscles have little function in propulsion in most fishes.

Ribs in amniote tetrapods have a triple function. They retain a locomotor function for the attachment of the hypaxial musculature, but the locomotory role of the appendicular muscles becomes increasingly important, especially in tetrapods with an upright posture such as birds and mammals. Ribs also play a role in costal ventilation, with the differentiation of hypaxial muscles to form the intercostal musculature. The roles of the hypaxial musculature in both locomotion and ventilation are incompatible to a certain extent, and the evolution of upright posture within synapsids and archosaurs may have been in order to reduce the mobility of the trunk during rapid locomotion, allowing simultaneous running and breathing (Carrier 1987).

The third role of the ribs in amniotes is for postural support. The ribs and the axial musculature act together to suspend the viscera under the effects of gravitational forces on land, and prevent the trunk from collapsing between the limb girdles. This postural role of the rib cage must have been a feature of the earliest terrestrial tetrapods, as evidenced by the robust, imbricating ribs of *Ichthyostega*. The highly robust rib cage of *Eryops*, described here, is not typical of all early tetrapods, many of which have fairly short ribs, as previously discussed. Further work is necessary to see if there is a size component in the type of rib morphology in these taxa. It might be expected that larger animals would need relatively more robust ribs. Note that the possible plagiosaur *Peltobatrachus*, a large-sized semi-terrestrial Late Permian taxon (although not quite as big as *Eryops*) has ribs with a very *Eryops*-like morphology (Panchen 1959).

Modern amphibians have reduced ribs, and they clearly rely less upon the rib cage for postural support. However, frogs have an exceedingly short trunk, in correlation with their saltatory mode of locomotion, and terrestrial salamanders and caecilians are all of small body size (an order of magnitude smaller than the known Devonian tetrapods) with a tubular body shape. Thus postural support from the ribs is less essential in these animals.

Note that, while the role of postural support by the rib cage must have been assumed with the first terrestrial tetrapods, there is no such mandate for the use of the ribs

for ventilation at this evolutionary transition. We can deduce from the application of the Extant Phylogenetic Bracket (Witmer 1995) that costal ventilation must have been a feature of virtually all extinct amniotes (i.e., all members of crown group Amniota). However, we must use osteological evidence to infer if costal ventilation was first acquired earlier in tetrapod history.

As would be expected, the rib morphology of the fossil amniotes resembles that of extant amniotes, meeting all of the expected requirements for costal ventilation (see earlier discussion). In contrast, the rib morphology of *Eryops* is not compatible with the function of costal ventilation. The conjoined tuberculum and capitulum of the rib heads do not indicate that the rib was mobile on the vertebral column. The ribs were flat, with little curvature, and would not have produced much expansion of the pleuroperitoneal cavity, even if they were capable of abduction. The broad, overlapping ribs would have allowed for little space for intercostal musculature. And, finally, the distal morphology of the ribs is incompatible with the presence of cartilaginous rib extensions connecting to a sternum.

The broad surface provided by the overlapping ribs in *Eryops* most likely provided a surface for the insertion of hypaxial and shoulder musculature to aid in trunk stabilisation. It is perhaps significant that the rib flanging is most prominent in the region of the pectoral girdle, which is the area that would be expected to undergo the most extreme shear forces during terrestrial locomotion.

The most interesting result is the amniote-like nature of the rib cage of *Diadectes*, the sister-taxon to the amniotes. The major way in which this animal is more primitive than the synapsids investigated here is in the more conjoined nature of the rib head tuberculum and capitulum, suggesting slightly less mobility of the ribs. *Diadectes* also retains a slight degree of overlapping rib flanging in the region of the pectoral girdle. However, in other respects the morphology of *Diadectes* is fully compatible with costal ventilation. The rounded ribs, lacking flanges in most instances, would allow room for the placement and attachment of intercostal muscles. The considerable curvature of the ribs suggests an adaptation for greater expansion of the pleuroperitoneal cavity on abduction. The distal morphology of the ribs suggests the presence of cartilaginous rib extensions and, by inference, the presence of an amniote-like sternum.

If *Diadectes* has an amniote-like condition of the rib cage, what was the condition in the other amniote-related 'anthracosaurian' taxa? Laurin & Reisz (1997) code anthracosaurs as primitive as *Proterogyrinus* as having 'long and curved' ribs (as opposed to 'short and straight'), but do not cite sources for these data. Seymouriamorphs appear to have had some of the same features as *Diadectes*. The ribs of *Ariekanerpeton* are described as 'clearly double-headed' (Ivakhneko 1981), suggestive of rib mobility. However, the ribs under the shoulder girdle appear to have distinct broad flanges in both *Seymouria* (White 1939) and *Ariekanerpeton* (Ivakhneko 1981; Laurin 1996), although the ribs are also described as becoming more gracile posteriorly. A similar condition is apparent in gephyrostegids. Carroll (1969) describes *Gephyrostegus* as also having a distinct capitulum and tuberculum to the rib heads, with anteriorly flanged ribs. He also describes the morphology of the more posterior ribs as having narrow, blunt-ending shafts, perhaps indicative of cartilaginous extensions, and he considers that *Gephyrostegus* may have had cartilaginous sternal elements.

Thus at least the more derived anthracosaurid anamniotes appear to have had ribs capable of some mobility, perhaps with a degree of costal ventilation. The larger forms, seymouriamorphs and diadectomorphs, have expanded vertebrae, with 'swollen' neural arches, and this condition has generally been interpreted as an adaptive stage in the evolution of terrestrial locomotion (Romer 1956). Most amniotes lack this vertebral morphology, although it has been observed in some primitive amniotes, where it is most often expressed in the region of the limb girdles and may be related to stabilisation of rotary forces during limb-powered locomotion (Sumida 1997). This bolstered condition of the vertebral column may provide a greater supportive and postural role, perhaps allowing for some reduction in the extent of rib flanging, enabling the rib cage to be freed for a greater role in ventilation. The vertebral differences between derived anamniotes and the majority of amniotes may be related to differences in the morphology of the axial musculature.

Extant amniotes possess differentiated epaxial musculature, in contrast to the single dorsalis trunci epaxial mass of amphibians. Ritter (1995) notes that the epaxial musculature of lizards provides a primarily postural support, whereas in salamanders the epaxial muscles are primarily locomotor in function. He suggests that epaxial differentiation, and the role of these muscles in postural support, is a key innovation of amniotes, possible only with the loss of the larval phase with the necessity of using the axial musculature for swimming in the initial phase of the life cycle. Note that Olson (1936) reconstructed the epaxial musculature of some primitive tetrapods, examining the same taxa as we do here in relation to rib morphology. Although he concluded that the epaxial muscles of *Eryops* were more differentiated than in the modern amphibian condition, he interpreted them as being thick, fleshy, and segmental in structure. In contrast, *Dimetrodon* was interpreted as having thinner, tendinous epaxial muscles that were no longer segmentally divided. *Diadectes* was interpreted as possessing an intermediate condition.

This scenario for the change in function of epaxial musculature, from locomotion to postural control, may also relate to changes in the functional role of the rib cage. We suggest that only when the epaxial muscles could be differentiated for postural control, with the loss of the larval phase, could the ribcage be freed from its extent in maintaining trunk posture, and be utilised for other functions such as costal ventilation. Lack of fully differentiated epaxial musculature might also explain why the large, terrestrial anthracosaurian taxa (seymouriamorphs and diadectomorphs) had expanded vertebrae, presumably to aid in trunk support. The acquisition of postural control by differentiated epaxials would explain why the majority of amniotes do not possess such a bolstered vertebral column.

The evolution of head shape, static pressure feeding, and herbivory. — Sues & Reisz (1998) note that herbivory appears to be a purely amniote feature, with the possible exception of the diadectids (but see later discussion). They dismiss the explanation of Hotton *et al.* (1997) for the restriction of herbivory to amniotes (i.e., that only the amniotic reproductive mode allows for the transfer of cellulytic endosymbiont microbes), but do not provide an alternative hypothesis.

We suggest that the acquisition of static pressure feeding in amniotes was the critical feature, and discuss below how this mode of feeding would be impossible with the broad, flat head of most anamniotes. It would be impossible toprehend vegetation and to bite off portions with the anterior teeth without the ability to exert static pressure at

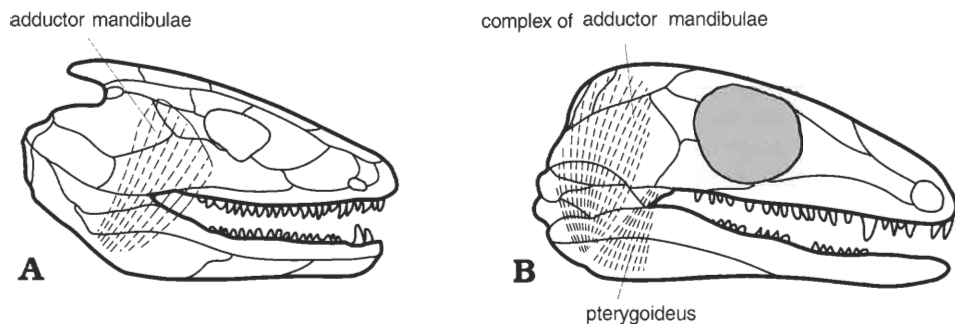


Fig. 5. Skulls of anamniote (*Palaeogyrinus*) (A) and amniote (*Paleothyris*) (B) tetrapods showing attachment of jaw adductor muscles.

the front of the jaw. We propose that, in order for a tetrapod to be herbivorous, it must first have acquired costal ventilation and freed its head from the constraints of buccal pumping. This hypothesis would explain why no anamniote is, or apparently was, herbivorous. Herbivory was possible for the first time in *Diadectes* due to its deeper head shape (see Fig. 7), which would have allowed for the development of the posteriorly positioned adductor mandibularis muscle (see below).

Olson (1961) noted that the jaw adductor arrangement of generalised amniotes allows for two types of feeding mode: an 'inertial' system, with the snapping of the jaws from an open position, and a 'static pressure' system whereby force can be exerted with the jaws closed. The pterygoideus muscle is best positioned to effect inertial feeding, as its line of action will be at right angles to the lower jaw when the mouth is open. However, the pterygoideus is at an acute angle to the lower jaw when the mouth is closed, poorly positioned to exert pressure. In contrast the more posteriorly positioned muscles, such as the adductor mandibularis, are in an advantaged position to exert this static pressure with a closed mouth, but are at an unfavourable angle when the jaw is depressed (see Fig. 5).

Frazetta (1968) noted that in the anamniote, flat-headed condition there is a less differentiated adductor mass, and that it would be impossible to attach a muscle in the position of the amniote posterior adductor mandibularis. The flat head would render the muscle fibres too short to allow for the jaw to be opened to any significant extent, given that muscles can stretch no more than one third of their resting length. The typical anamniote jaw adductor muscle arrangement, with the adductor mandibularis directed in a similar fashion to the amniote pterygoideus (i.e., running obliquely from an anterior origin to a posterior insertion) would only allow for inertial feeding. Static pressure feeding would be impossible until a deeper skull was acquired and more posteriorly positioned muscles could be developed.

Carroll (1969) took this idea several steps further, reconstructing the evolutionary sequence of this change in jaw musculature. He noted that a distinctive amniote feature is a pterygoid flange in the palate, which functions for the origin of the pterygoideus muscle, and proposed that the appearance of this flange signalled the amniote-like differentiation of the adductor muscles and the acquisition of static pressure feeding. Some evidence of a pterygoid flange is first seen in gephyrostegids (Laurin & Reisz 1997; Lee & Spencer 1997) although only diadectomorphs have a fully amniote-like condition (Carroll 1969).

Carroll (1969) also noted that amniotes lack the palatal tusks and labyrinthine folding of the tooth enamel of most labyrinthodonts, and suggested that this loss is related to their more derived, controlled jaw movements. Inertial feeding, with the jaws simply being snapped shut from an open-mouth position, would exert considerable stress on the teeth, reflected in their being strengthened with the labyrinthine enamel. Such bolstered teeth would be unnecessary with the finer control of jaw movements afforded by static pressure feeding. Likewise, palatal teeth would function toprehend food (probably by stabbing it) in an inertial feeding mode, but such prehension (with closed or partially closed jaws) would be better accomplished by the anterior dentition if static pressure feeding was a possibility. Thus the loss of both palatal tusks and labyrinthine enamel should be correlated with the acquisition of static pressure feeding.

This ability to employ static pressure feeding is clearly of great advantage to amniotes. Inertial feeding cannot be employed in applying pressure at the front of the jaw with the mouth closed, and the combination of inertial feeding and static pressure feeding allows for a greater range of feeding strategies. Modern frogs and salamanders have circumvented the lack of the precision afforded by static pressure feeding by the evolution of a projectile tongue for prey capture and prehension, a device not generally employed by amniotes (except for its convergent evolution in chameleons).

Transitional steps in stem amniote taxa. — Fig. 6 shows the acquisition of amniote-like features superimposed onto a cladogram (modified from Lee & Spencer 1997: note, however, that Berman *et al.* 1992, place diadectomorphs within the Amniota, as the sister taxon to synapsids). Although we were only able to observe the rib cage of *Diadectes* among the stem amniote taxa, data from the literature suggest that some degree of rib modification was present in all stem amniotes, suggesting that these taxa also possessed a degree of costal ventilation. The possession of slightly longer necks within this grouping also suggests that a trachea may have been present. These taxa also generally possess smaller heads than most anamniote tetrapods, of comparable proportions to the heads of amniotes, suggesting a lesser importance of the head in lung ventilation (see Table 1). But it is not until the level of *Diadectes* that there is good evidence for a change in head shape sufficient to allow for radical restructuring of the jaw adductor musculature. We contend that it is the evolution of costal respiration, freeing the head from its role in lung ventilation, that allows for this modification of head shape in amniotes.

We expressed the opinion above that only amniotes could be herbivorous, because of the necessity of the development of a static pressure system of feeding. However, diadectids have long been regarded as herbivores, because of their transversely expanded, molariform cheek teeth with evidence of fore and aft wear, incisor-like spatulate anterior teeth, and barrel-shaped rib cage suggestive of a large gut for fermentation (Hotton *et al.* 1997; Sues & Reisz 1998). They have often been touted as the 'only amphibian herbivores.' The herbivory of diadectids is strongly suggestive of the ability for static pressure feeding.

As noted previously, a incipient pterygoid flange indicating differentiation of the jaw adductors is first seen in gephyrostegids, but Carroll (1969) claims that this is not fully developed until the level of diadectomorphs. Carroll (1969) also notes that both gephyrostegids and seymouriamorphs retain infolded labyrinthine enamel of the teeth and large palatal tusks (although the large anterior tusks on the dentary are lost in seymouriamorphs; Lee & Spencer 1997). These features are suggestive of a primary

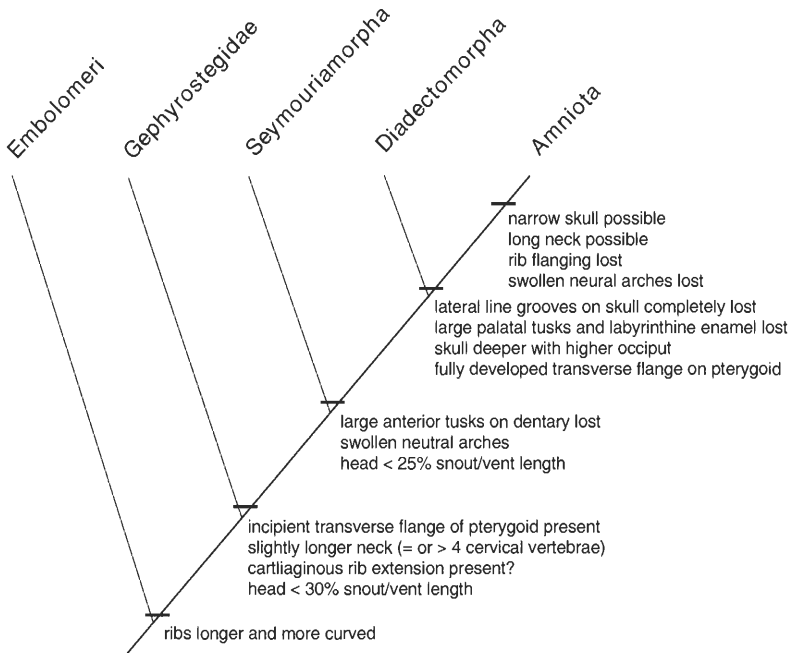


Fig. 6. Phylogeny of reptilomorph tetrapods, showing probable points of acquisition of key amniote characters (modified from Lee & Spencer 1997).

mode of inertial feeding. However, diadectomorphs have lost both palatal tusks (Lee & Spencer 1998) and labyrinthine enamel (Laurin & Reisz 1997), further suggesting the acquisition of static pressure feeding. Although *Diadectes* and *Seymouria* retain fairly broad skulls (see Fig. 3), *Diadectes* has a much deeper skull than *Seymouria*, approaching an amniote-like condition (see Fig. 7). (This similarity of the skull depth of *Diadectes* to the amniote condition can also be observed in Berman 2000, Fig. 3.) The combination of these various lines of evidence, derived pterygoid flange, deep skull, and inferred static pressure feeding, suggest that *Diadectes* had an amniote-like differentiation of the jaw adductor musculature.

Thus the evidence suggests that some degree of costal ventilation characterised all anthracosaurs, but that the head was not finally released from the constraints of buccal pumping until the level of *Diadectes*. Why should this be the case? We suggest that the answer may lie in the development of the postural role of the epaxial muscles, freeing the ribs from their greater role in postural maintenance, and the correlation of this feature with the mode of reproduction.

Following the hypothesis of Ritter (1995), it may be the case that epaxial muscles can only be co-opted for postural control once the swimming larval stage has been lost. As previously discussed, differentiated epaxial muscles may be an essential prerequisite for the release of ribs from a primary rigid postural function, and allow them to be lighter, and more mobile. If this correlation of reproductive mode, epaxial differentiation, and rib motility can be substantiated, we would expect to see full dependence on costal ventilation (with concurrent release of head shape and capacity for herbivorous feeding) only in an animal that had acquired the amniote egg. Lee & Spencer (1997) ar-

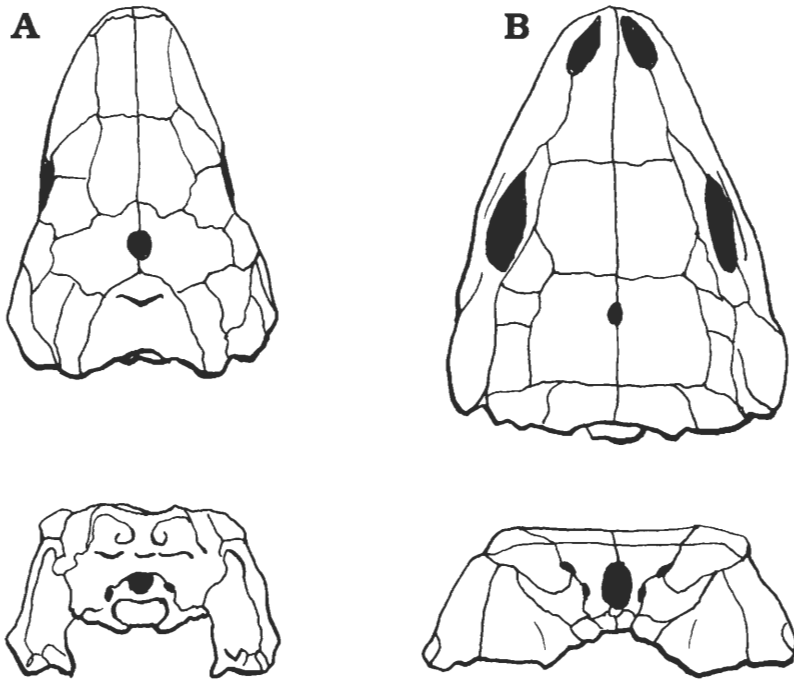


Fig. 7. Comparison of head shapes in *Diadectes* (A) and *Seymouria* (B), in dorsal and occipital views (modified from Romer 1956, 1966). Note that *Diadectes* has a higher occipital region than *Seymouria*. In this depiction it also appears to have a narrower skull, at least in the dorsal portion, although this is not reflected in our measured data (see Fig. 3).

gued that *Diadectes* might well have laid amniotic eggs, and note that all evidence of lateral lines (suggestive of aquatic larvae) are lost at the node uniting diadectids and the crown group Amniota.

We interpret these data to infer that it was the evolution of the amniote egg, and the concurrent loss of a larval locomotor role for the epaxial musculature, that was the final step in the evolution of costal ventilation. This change in epaxial muscle function, from locomotion to postural control, freed the ribs from the full extent of their postural role, and allowed for a change in head shape with the absence of the need for ancillary buccal pumping. Note that, although *Diadectes* has clearly evolved the capacity for static pressure feeding, it retains the swollen neural arches typical of seymouriamorphs and some early amniotes. This vertebral morphology may represent an intermediate condition in postural control, aiding the role of the rib cage but preceding the full differentiation of postural epaxial musculature.

Conclusion

The large, flat heads of the larger Palaeozoic anamniote tetrapods reflects the dependence of these animals on the primitive tetrapod mode of lung ventilation via buccal pumping. These animals would have been inefficient at carbon dioxide loss, but may have coped

with this problem by tolerating hypercapnia and/or returning frequently to the water where carbon dioxide could be lost more easily over the skin. Additionally, exceptionally low levels of atmospheric carbon dioxide and high levels of oxygen during the Late Carboniferous and Early Permian, coincident with the time of the first major radiation of terrestrial tetrapods, may have aided in the ability of these animals to survive on land.

We suggest that fully developed costal ventilation is a derived amniote feature, and may have been a key evolutionary adaptation of this group (and perhaps found among stem amniotes to a certain extent). Costal ventilation allows for higher rates of lung ventilation, thus enabling a faster means of correcting exercise induced acidosis, and perhaps allowing amniotes to assume greater levels of activity than anamniotes. With the lungs assuming a greater percentage of the burden of acid clearance, the skin could now become 'waterproofed', enabling amniotes to live in drier habitats, independent of the water.

Some evidence for a rib cage designed for costal ventilation is seen in the most primitive of the anamniotes forming the stem of the amniote lineage (i.e., 'anthracosaurs'). But evidence of the release of the head from a buccal-pumping role is not initially seen, suggesting that these animals may have been utilising both costal ventilation and buccal pumping. Only at the level of *Diadectes* do we see a morphological shift to a deeper skull, allowing realignment of the jaw musculature to allow static pressure feeding (evidenced by herbivory, and loss of labyrinthine enamel and palatal tusks).

Other evidence (loss of lateral line canals on the skull) suggests that *Diadectes* had lost the larval stage, and may have been functionally amniote-like in its reproductive physiology (whether or not its taxonomic position is within the crown group Amniota). We suggest, following Ritter (1995), that it is not until the larval stage has been lost that the epaxial musculature can assume a postural role. With the presence of postural epaxials, the rib cage could be released from some of its postural role, allowing for the full development of costal ventilation and the complete loss of ancillary buccal pumping.

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Appendix 1

Details of taxa measured for head length and head width (data used in Fig. 3).

Modern amphibian genera included (from a single species, unless otherwise specified; if from multiple species, number of species indicates number of individuals, unless otherwise specified): *Agalychnis*, *Anotheca*, *Aromobates*, *Astylosternus*, *Atelopus* (2 species), *Bombina*, *Bufo* (33 species, 35 individuals), *Callulops*, *Caudiverbera* (2 species), *Ceratobatrachus*, *Ceratophrys*, *Conraua*, *Cyclorana* (2 species), *Discodeles* (2 species), *Discoglossus*, *Eleutherodactylus*, *Gastrotheca* (2 species), *Hemiphractus*, *Hyla* (4 species), *Leptodactylus*, *Limnodynastes*, *Litoria* (2 species), *Megalophrys*, *Mixophyes*, *Nyctimystes*, *Pachymedusa*, *Pedostibes*, *Phyllomedusa*, *Pipa*, *Platymantis*, *Pyxicephalus* (2 species), and *Rana* (14 species).

Modern lizard genera included (same specifications as for the frogs): *Amblyrhynchus* (1 species, 2 individuals), *Ameiva*, *Amphibolurus* (3 species), *Anolis* (5 species), *Basiliscus* (3 species), *Brachylophys* (2 species), *Callopietes*, *Chamaeleo* (7 species), *Conolophus* (2 species), *Cordylus*, *Cnemidophorus*, *Crotaphytus*, *Ctenosaura* (7 species), *Cyclura* (3 species), *Dipsosaurus* (1 species, 2 individuals), *Dracaena* (2 species), *Eublepharis*, *Eugongylus*, *Eumeces*, *Gekko*, *Gerrhosaurus* (2 species), *Goniocephalus*, *Heloderma* (2 species), *Hydrosaurus*, *Iguana* (2 species, 3 individuals), *Lacerta* (2 species), *Laemactus*, *Leiocephalus* (2 species), *Macroscincus*, *Physignatus*, *Plica*, *Polychrus*, *Sauromalus* (4 species, 5 individuals), *Sceloporus*, *Tiliqua* (2 species), *Tropidurus*, *Tupinambis* (3 species), *Uranoscodon*, *Uromastix* (3 species), *Varanus* (11 species, 13 individuals), and *Zonosaurus*.

Fossil non-amniote taxa included (specifications as for the frogs): *Amphibamus*, *Acanthostega*, *Acanthostoma* (1 species, 2 individuals), *Archegosaurus*, *Batrachosuchus*, *Benthosuchus*, *Bothriceps*, *Branchiosaurus* (2 species), *Buettneria*, *Chigutisaurus*, *Coelelosaurus*, *Cyclotosaurus*, *Deltacephalus*, *Eucrinita*, *Dissorophus* (2 species), *Dvinosaurus*, *Edops* (1 species, 2 individuals), *Eryops* (3 species, 7 species), *Eupelor* (2 species, 4 individuals), *Greererpeton*, *Ichthyostega* (1 species, 2 individuals), *Isodectes*, *Lyderkkerina* (1 species, 7 individuals), *Megalocephalus*, *Microbrachis*, *Micropholis*, *Pantylus* (1 species, 2 individuals), *Pariotichus*, *Parioxys* (1 species, 2 individuals), *Parotosaurus* (2 species), *Rhinesuchoides* (1 species, 2 individuals), *Sclerocephalus*, *Seymouria*, *Silvanerpeton*, *Stegops* (1 species, 2 individuals), *Trimerorhachis* (1 species, 3 individuals), *Xenobrachyops*, and *Zatrachus* (3 species, 5 individuals).

Fossil amniote taxa included (specifications as for the frogs): *Captorhinus*, *Dimetrodon*, *Pristerodon*, *Probelosodon*, *Procynosuchus*, *Scaloposaurus*, *Scyalops*, and *Thrinaxodon*.

Appendix 2

Key to literature used in the construction of Tables 1 and 2.

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