



Proposed habitats of early tetrapods: gills, kidneys, and the water–land transition

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Received April 1996; accepted for publication January 1998

Recent finds of early tetrapods have established that the most primitive form, *Acanthostega*, retained internal gills and other fish-like features; this has led to the conclusion that it was a primarily aquatic animal. Other Late Devonian tetrapods, such as *Ichthyostega* and *Tulerpeton*, provide no evidence of internal gills, but have also been interpreted as inhabiting an aquatic environment. The probable aquatic habits of a diversity of Devonian tetrapods has led to the suggestion that the entire early tetrapod radiation may have been an aquatic one, with terrestriality having evolved in later forms. However, consideration of the physiology of living amphibious vertebrates suggests that this scenario is unlikely. The use of the gills for the excretion of carbon dioxide and ammonia appears to be a fundamental feature of all primarily aquatic vertebrates. No living fish loses its internal gills, even if it excretes a significant portion of its nitrogenous waste as urea via the kidney in the water. Gills are simply too valuable to be lost by an aquatic animal, even in those air-breathing fishes that no longer use the gills for oxygen uptake. We suggest that the apparent loss of the gills in tetrapods more derived than *Acanthostega* signals their descent from a more terrestrial phase in tetrapod evolution, following the primary assumption by the kidney of the excretion of nitrogenous wastes. Without this new role of the kidney, loss of the gills would have been impossible. With this new kidney role, loss of the gills may have been advantageous in reducing desiccation on land.

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ADDITIONAL KEY WORDS:—evolution of terrestriality – amphibians – carbon dioxide excretion–nitrogen excretion.

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INTRODUCTION

Recent discoveries of the Late Devonian tetrapod *Acanthostega* have led to a reinterpretation of the habitat of this taxon, and to the conditions under which tetrapods first evolved. *Acanthostega* appears to have been a primarily aquatic animal, and tetrapod innovations such as legs with digits are now assumed to have been evolved within an aquatic environment (Clack, 1988, 1989; Clack & Coates, 1995; Coates & Clack, 1990, 1991, 1995; Daeschler & Shubin 1995). Two significant features of *Acanthostega* are the presence of large, ventrally grooved ceratobranchials, and a postbranchial lamina along the anterior margin of the shoulder girdle, suggesting the retention of functional internal gills and an open opercular chamber for aquatic respiration (Coates & Clack, 1991; Clack & Coates, 1995).

Re-evaluation of the postcranial skeleton of the other Late Devonian tetrapod known from Greenland, *Ichthyostega* (which was, until recently, the only well-known early tetrapod), has shown that it, like *Acanthostega*, is polydactylous, and that the hind limb (the number of digits in the forelimb is unknown) is more paddle-like than a leg designed primarily for terrestrial locomotion (Coates & Clack, 1990, 1995). However, *Ichthyostega* has skeletal features that suggest a greater degree of terrestriality (or at least of a terrestrial inheritance) than *Acanthostega*, and also lacks evidence of retained internal gills (Clack & Coates, 1995; Coates & Clack, 1995). Both *Acanthostega* and *Ichthyostega* share an apparent aquatic adaptation in the retention of lepidotrichia (fin rays) in the tail fin, but these are relatively more reduced in *Ichthyostega* (Clack & Coates, 1995).

Another recently described genus of Late Devonian tetrapods, the Russian *Tulerpeton*, reveals that it was also polydactylous and apparently adapted for an aquatic lifestyle (being found in a marine environment) (Lebedev & Coates, 1995). However, *Tulerpeton* possesses a more derived postcranial skeleton than either *Acanthostega* or *Ichthyostega*, suggestive of a greater degree of terrestrial adaptation (Lebedev & Coates, 1995). Other Late Devonian tetrapods are known only from fragmentary material, and the limb elements are unknown. Partial shoulder girdles of a North American form, *Hynierpeton*, is suggestive of robust forelimb musculature, possibly for terrestrial locomotion (Daeschler *et al.*, 1994). *Ventastega*, from Latvia, is known primarily from cranial material (Ahlberg, Luksevics & Lebedev, 1994). The other known taxa were originally described as fishes, or considered to be fishes by some workers: they include *Obruchevichthys* (from Latvia), *Elginerpeton* (from Scotland), and *Metaxygnathus* (from Australia). These fragmentary tetrapods, with the possible exception of *Hynierpeton*, are considered to be more primitive than *Acanthostega* (Clack, 1997). All Late Devonian tetrapods are found in association with fishes, indicating that they were at least preserved in an aquatic habitat (Clack, 1997).

In a phylogenetic analysis of early tetrapods Lebedev and Coates (1995) concluded that *Tulerpeton* is significantly more derived than the other two well-known Devonian

tetrapods, *Acanthostega* and *Ichthyostega*; they placed *Tulerpeton* as the sister-taxon to the Reptiliomorpha (a group that includes the extant amniotes). The other tetrapod clade, the Batrachomorpha, contains the extant amphibians. Although *Tulerpeton* itself lacks any evidence for the retention of an operculum or internal gills, Lebedev and Coates (1995) considered that the emphasis on air breathing may have been evolved independently within the amniote and batrachomorph stem-groups. They arrived at this conclusion based in part on the aquatic environment of *Tulerpeton*, suggesting that full terrestriality was not yet attained by the division of reptiliomorph and batrachomorph tetrapod clades, and in part because they considered that the colosteids (primitive batrachomorphs) *Greererpeton* and *Colosteus* show evidence of the retention of the gill-breathing condition. The notion that the entire radiation of Devonian tetrapods may have been a primarily aquatic one is also expressed in Coates and Clack (1995).

We propose here that there are some serious flaws with this 'aquatic tetrapod evolution' scenario when the physiological requirements of these early tetrapods are considered. We have no objections to the specific phylogeny of Lebedev and Coates (1995), nor do we question the likelihood that *Acanthostega* was a primarily aquatic animal, and that the origins of tetrapod innovations may have been initially for an aquatic lifestyle. However, despite the fact that *Ichthyostega* and *Tulerpeton* may have been aquatic in their habits, we argue that the apparent loss of the internal gills in the adults of these animals requires that they had their origins in a (as yet undiscovered) more terrestrial ancestor.

EVIDENCE FOR THE ABSENCE OF GILLS IN MOST EARLY TETRAPODS

The principal assertion expressed above, that tetrapods more derived than *Acanthostega* are not primarily aquatic animals, rests on the interpretation of the available evidence that internal gills are absent in these animals. This argument does, of course, rely on negative evidence, and this is admittedly problematical. The main reason why other Devonian tetrapods such as *Ichthyostega*, *Hynerpeton* and *Tulerpeton* are assumed to lack internal gills, apart from the lack of ossified gill bar elements (which could easily be lost in fossils), is because of the loss or reduction of the post-branchial lamina in the shoulder girdle (suggesting the absence of an opercular chamber). It has been pointed out that some eusthenopterid fish also lacked post-branchial laminae, yet were obviously in possession of gills (Jenny Clack, pers. comm.) On the other hand, the Early Carboniferous primitive aquatic tetrapod *Whatcheeria* does possess a post-branchial lamina yet lacks any evidence of ossified internal gill elements, despite extensive searching among "numerous articulated cranial remains, including several nearly complete skulls" (Lombard & Bolt, 1995). Thus the retention of a post-branchial lamina in *Greererpeton* (Lebedev & Coates, 1995) cannot be taken as confirmatory evidence of retained internal gills.

Ossified branchial elements are known from a number of primitive tetrapods, mainly temnospondyls (Berman, 1973; Milner, 1982), but they are also seen in *Colosteus* (Hook, 1983), and in one microsauro (Milner, 1982). These elements, however, do not appear to be similar structures to the branchial ossifications of *Acanthostega*, which appear to be functionally equivalent to fish internal branchial arches (Coates & Clack, 1991). The elements in other tetrapods represent tooth-bearing ceratobranchial elements (dental ossicles), probably used in aquatic filter

feeding. They are found only in small individuals (presumed larvae), and occasionally in neotonous adults, such as the temnospondyls *Gerrothorax*, *Dvinosaurus*, and *Trimerorhachis*. The presence of these elements cannot be used to infer the presence of internal gills (Berman, 1973; Milner, 1982).

Would our argument be invalidated if it were subsequently shown that Devonian tetrapods such as *Ichthyostega* actually did possess *Acanthostega*-like internal gills? The particular argument concerning the Devonian taxa, based on negative evidence for gills in these early tetrapods, would be invalidated, but our general point would not. Our main argument is that the loss of the internal gills would not occur in an aquatic environment, and that the absence of gills, at whatever evolutionary level, signifies a more terrestrial ancestry. In this paper we take the fossil evidence at face value, and assume that gill loss in adult tetrapods occurred at the evolutionary transition between *Acanthostega* and more derived taxa.

THE PHYSIOLOGY OF LIVING AQUATIC AND AMPHIBIOUS VERTEBRATES

The possession of a lung is usually seen as an important preadaptation in tetrapods, enabling terrestrial respiration. Gills are perceived as devices for aquatic respiration, so their loss in tetrapods (at least in terrestrial adults) is rarely questioned. However, gills serve a number of other important functions in fish besides gas exchange, primarily in nitrogen excretion, ionic regulation, and acid-base regulation (see Evans, 1993; Wood, 1993; Heisler, 1993); thus their loss in tetrapods poses a number of physiological problems. We will focus here primarily on the excretion of nitrogen, and the switch in tetrapods from the use of the gills to the use of the kidney for this function.

Physiology of fishes

The consumption and breakdown of proteins in fishes produces two major waste molecules, ammonia (NH₃) and urea (a molecule that is synthesized from ammonia primarily by the ornithine urea cycle). Elimination of these nitrogenous wastes can take place across the gills, across the skin, through the kidney, and through the intestines (reviewed Wood, 1993). Mapping the site of excretion of nitrogenous wastes onto the vertebrate phylogeny suggests a historical precedence for removal primarily via the gills. Gills are the principal site of nitrogen excretion in Agnatha (95%), Chondrichthyes (73–93%), and in the majority of Osteichthyes (both Sarcopterygii and Actinopterygii) that have been studied (reviewed in Wood, 1993).

There are several features of fish gills that make them highly suitable for the transfer of molecules from the internal to the external environment. They have an extremely large surface area and the epithelium is in direct contact with the external environment. The rate of water flow across gill epithelium is around two orders of magnitude greater than the rate of urine flow from the kidney in fishes or in mammals (Heisler, 1993). Thus molecules are rapidly transferred from organism to environment without the need for large concentration gradients, as is necessary in the kidney.

Although gills are the most important site of nitrogenous waste excretion in almost

all fishes studied, there are circumstances that can influence the rate of excretion at the various sites. Examples include an alkaline environment, prolonged blood acidosis, and osmotic stress (reviewed in Wood, 1993). The reduction in gill surface area that usually accompanies aerial respiration in fishes also could lead to selection for increased use of the kidney, skin, or intestines for nitrogenous waste excretion. Although this seems to be the case in the obligate air-breathing osteoglossid teleost *Arapaima* (Hochachka *et al.*, 1978), no such trend is found in the facultative air-breathing erythrinid teleost *Hoplerythrinus unitaeniatus* (Cameron & Wood, 1978). In the African and South American lungfishes (*Protopterus* and *Lepidosiren*, respectively), gills have little or no importance for oxygen absorption, yet are retained for carbon dioxide and nitrogenous waste excretion (Johansen & Lenfant, 1968; Lenfant & Johansen, 1968; Wood, 1993). Hence consideration of situations that promote the use of skin, intestines, and kidneys for functions that were ancestrally carried out by the gills do not result in the complete loss of gills among extant primarily aquatic vertebrates.

The ability to convert ammonia to urea via the ornithine urea cycle is probably primitive for gnathostomes and is retained by sarcopterygians. The ornithine urea cycle is found in chondrichthyans, coelacanth, lungfishes, and tetrapods (reviewed in Bray, 1985; Graham, 1997). Because the body fluids of primitive gnathostomes had ionic concentrations that were more dilute than sea water, the ability to convert ammonia into urea prevented osmotic dehydration, as seen today in chondrichthyans and coelacanth. Chondrichthyans that inhabit freshwater (e.g. the stingray *Potamotrygon*) are ammoniotelic: that is, they excrete nitrogenous wastes primarily as ammonia (Gerst & Thorson, 1977). Osmotic stress in the freshwater environment promotes neither urea production nor rectal gland function; over evolutionary time the enzymes of the ornithine urea cycle might become dysfunctional in such circumstances (Gerst & Thorson, 1977). The loss of a functional ornithine urea cycle in the majority of teleosts (Wood, 1993) suggests a long evolutionary history in freshwater. Information on nitrogen metabolism is sorely lacking in more primitive actinopterygians (e.g. polypterids, chondrosteans, lepisosteans).

In some air-breathing fishes, and in intertidal fishes exposed to air, nitrogenous waste excretion is reduced and waste products accumulate in the body. There is evidence that a very few species of teleosts possess a functional ornithine urea cycle; for example *Heteropneustes fossilis* and the mudskippers *Periophthalmus* and *Boleophthalmus*. In these fishes air exposure results in a reduction in ammonia excretion and a buildup of urea, although experiments looking at pre- and post-emersion nitrogen excretion have yielded highly variable results (Gordon *et al.*, 1969; Gordon, Fischer, & Tarifeno, 1970; Gordon, Ng, & Yip, 1978; Morii, Nishikata & Tamura, 1978; Saha & Ratha, 1989; Graham, 1997). Conversion of ammonia to urea would be advantageous for emersed fishes for several reasons: ammonia is toxic and can only be tolerated in dilute concentrations, while urea is less toxic and can therefore be stored in high concentrations in the body. Hence considerably less water is required to eliminate nitrogenous waste as urea than as ammonia.

Lungfishes, as the extant sister-taxon to tetrapods, are of special interest in this respect, possibly representing the ancestral tetrapod condition. In an aquatic (freshwater) environment lungfish eliminate nitrogenous waste as ammonia over the gills, but during aestivation on land they convert the ammonia to urea and retain it in the body fluids (Smith, 1930). Like other fishes they are not known to excrete nitrogenous end-products on land. Upon its return to water, the African lungfish

(*Protopterus aethiopicus*) excretes large amounts of urea, although the site of excretion is not known.

These living air-breathing fishes provide some insights as to how the kidney might have assumed increasing functions in proto-tetrapods in an aquatic environment, functions that would be preadaptive for a terrestrial existence. Note, however, that no fish excretes urea via the kidney while on land. Observation on living animals clearly show that as long as fishes are primarily aquatic animals, the gills remain an important site for the excretion of nitrogen and carbon dioxide, and for ion regulation. Gills are simply too valuable in an aquatic environment to be readily lost.

Physiology of modern amphibians

The gills of larval amphibians act like fish gills as the site of excretion of nitrogen (as ammonia) and carbon dioxide, plus regulation of monovalent ions. However, at metamorphosis the gills are usually lost, and these functions are taken over by the lungs (some carbon dioxide excretion), kidneys (nitrogen excretion in the form of urea), and the skin (monovalent ion regulation, plus some excretion of both carbon dioxide and nitrogenous waste in the form of ammonia) (Rahn & Howell, 1976; Maetz, Payan & de Renzis, 1976; Gordon & Olson, 1995).

Aquatic amphibians, both larvae and adults, produce ammonia as the major end product of nitrogenous excretion, while urea is the main product in terrestrial animals (Goldstein, 1972). Studies on some species of aquatic anuran tadpoles show that they are initially incapable of producing urea, but gain the enzymes necessary for urea synthesis during metamorphosis (Boutilier, Stiffler & Toews, 1992). Urea is an appropriate excretory product in the terrestrial environment not only because it is less toxic, but also because it requires less water for elimination than ammonia (Forster & Goldstein, 1969), thus reducing the amount of excretory water loss. Thus amphibians are able to cope with the problem of nitrogenous waste on land in a manner that seems impossible for fishes; the production of urea and its excretion by the kidney in the urine without the need to return to water.

Some highly specialized living amphibians, such as the frog *Xenopus*, are able to be aquatic as adults without functional gills, and conduct much of their excretion of carbon dioxide and nitrogenous waste through the skin. But the thin, permeable skin of living amphibians is highly specialized, and there is considerable fossil evidence to suggest that early tetrapods had dermal scales (reviewed in Ultsch, 1996). Living amphibians, especially frogs, are poor models for the physiology of early tetrapods (Gans, 1970).

IMPLICATIONS FOR THE PHYSIOLOGY OF EARLY TETRAPODS

The apparent lack of gills (their presumed loss in the adult form) in the Devonian tetrapods *Ichthyostega* and *Tulerpeton* implies not only the assumption of respiratory gas exchange via the lungs and skin, but also the assumption of all of nitrogenous waste excretion in the form of urea by the kidney. Yet if these tetrapods had been primarily aquatic, as suggested (Coates & Clack, 1995; Lebedev & Coates, 1995),

there would have been no reason for the gills to be lost. Based on numerous examples from living air-breathing fishes, both aquatic and semi-terrestrial, we conclude that the loss of gills in early tetrapods must be indicative of a phase of predominant terrestriality.

In considering likely events in tetrapod evolution, it is most important to note that no fish loses the gills entirely, even though the gills may be reduced. The retention of gills in aquatic, obligate air-breathing fishes, such as certain lungfishes and osteoglossid teleosts, appears to reflect their necessity in carbon dioxide excretion. The retention of the gills in amphibious fish such as mudskippers, which rely extensively on the skin for the exchange of respiratory gases, may reflect their necessity in the function of aquatic nitrogen excretion. Also note that in cases where retention of the larval gills is an option for an aquatic adult tetrapod, the gills are usually retained. Neotinous adult salamanders retain the gills for the excretion of carbon dioxide and ammonia (neotony does not appear to be a developmental option for frogs).

It is not known why fish may be able to use the kidney to excrete urea in water, but are unable to do so on land. All that can be known is that no living fish does this, out of a large variety of possible candidates where one might imagine that this would be adaptatively advantageous. The only conclusion must be that this change in kidney function is not an easy one to achieve, in physiological and evolutionary terms, considering that it has happened only once, in the ancestor of extant tetrapods. It is conceivable that an aquatic tetrapod could have evolved a kidney that excreted all its nitrogenous wastes as urea under all conditions, preadapted for a transition to excreting urea on land. Given the previous discussions of the physiological advantages of the excretion of nitrogenous wastes as ammonia over the gills, however, it is difficult to conceive of an adaptive scenario whereby this derived type of kidney would have arisen in the aquatic environment.

A remaining problem is the issue of why gills should have been lost at all in early tetrapods, even amphibious (as opposed to fully aquatic) ones. Gill retention would be useful for the excretion of nitrogen and carbon dioxide on the return to the water. Indeed, Romer (1972) considered that early tetrapods might well have retained their gills for the purpose of carbon dioxide loss (he did not consider the problem of nitrogen excretion). However, note that while no amphibious fish loses the gills entirely, the degree of gill reduction in amphibious fish does correlate with their degree of terrestriality (Gordon & Olson, 1995), suggesting that gills are in some fashion disadvantageous on land. The loss of the gills in early tetrapods would have been advantageous in the avoidance of desiccation, as gills would have presented a potential surface for water loss on land, although the skin would presumably also remain as a (smaller) site of water loss.

CONCLUSIONS

Most scenarios of the physiology of the transition from water to land in the evolution of tetrapods have focused on the changes in respiration, from a gill-based mode of oxygen acquisition to a lung-based one. It has long been acknowledged that lungs are a primitive feature for tetrapods and that air-breathing would have well preceded the water-land transition (e.g. Bray, 1985; Thomson, 1993). But less

attention has been focused on the issue of gill loss. Textbooks (e.g. Benton, 1997) and other general accounts of the fish-tetrapod transition only consider the issue of obtaining oxygen on land and the presence of lungs in early tetrapods; the problems with carbon dioxide loss and nitrogen excretion, and the issue of eventual gill loss are usually ignored. Even studies that have considered the use of the gills for functions other than oxygen uptake (e.g. Ultsch, 1996) have not considered the role of the gills in the excretion of nitrogenous wastes in this context, and how the loss of the gills must reflect the takeover of that function by the kidney. It is our aim in this paper to focus attention on the issues of the implications of gill loss, and the importance of the changing role of the kidney in early tetrapod evolution.

Although the gill-bearing early tetrapod *Acanthostega* may have been a primarily aquatic animal, and *Ichthyostega* and *Tulerpeton* may have been tetrapods that inhabited an aquatic environment, if the two latter taxa had indeed lost their gills this would strongly imply an ancestry from a more terrestrial form, perhaps an animal more terrestrial than any known amphibious teleost. Some extant frogs may be able to survive as aquatic adults without gills, but these represent specialized descendants of a gill-less ancestor (no frog retains gills in the adult stage). This modern amphibian example has little bearing on evolutionary scenarios for gill loss in early tetrapods: the fact that a tetrapod can survive in an aquatic environment without gills is not sufficient reason to suppose that there would have been selection for gill loss under such conditions.

The physiology of extant fishes strongly contradicts the likelihood of gills being lost in an aquatic environment in early tetrapods, as gills remain useful for both carbon dioxide and nitrogen loss. Even if early aquatic tetrapods had been using the kidney primarily for urea excretion, as in some present day air-breathing teleosts, gill retention would still have been advantageous for carbon dioxide loss and for some excretion of nitrogen as ammonia. We are unable to devise a scenario whereby the loss of gills in a primarily aquatic animal would be adaptive: all the available evidence points to the contrary. The common ancestor of gill-less tetrapods would be more likely to experience selection for gill loss in the context of a committed terrestrial existence in order to avoid desiccation. With this loss of the gills the majority of carbon dioxide loss must now be via the lungs, and the majority of nitrogen loss via the kidney, with the skin perhaps playing a secondary role in both cases.

The above scenario would imply the adoption of a secondarily more aquatic habitat by the Devonian tetrapods that lack gills. However, this would not be at variance with their anatomy. Note also that secondarily aquatic adaptations are common in later (Permo-Carboniferous) primitive tetrapods (Ahlberg & Milner, 1994). *Ichthyostega* has numerous anatomical features that suggest greater adaptation for terrestriality than seen in *Acanthostega*: an elbow joint with an olecranon process, zygapophyseal articulations between the trunk vertebrae, more heavily ossified neural arches, and broad, overlapping ribs suggestive of a trunk-stiffening mechanism (Coates & Clack, 1995). *Tulerpeton* appears to have even more terrestrial adaptations (Lebedev & Coates, 1995).

We contend that the loss of adult gills in tetrapods may be used as an 'indicator' (in the sense of Daeschler & Shubin, 1995) of an initial primarily terrestrial stage in early tetrapod history. Although the fossil record evidence is for an aquatic radiation of Late Devonian tetrapods, if the gills have indeed been lost in those tetrapods

more derived than *Acanthostega*, then we conclude those tetrapods must have an ancestry in a more terrestrial form than is known at the present time.

ACKNOWLEDGEMENTS

We thank J. John Sepkoski Jr., Jenny Clack, and an anonymous reviewer for comments on the manuscript.

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