The Evolution of the Terrestrial Vertebrates: Environmental and Physiological Considerations [and Discussion]

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The evolution of the terrestrial vertebrates: environmental and physiological considerations

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Physiological evidence has long been used to suggest that the gnathostomous vertebrates (those possessing jaws) were primitively fresh water. The same was also the case for the Osteichthyes (bony fish) and the Tetrapoda (Amphibia, Reptilia, Aves, Mammalia). However, the geological evidence favours a marine origin for the vertebrates as a whole, and, for the gnathostomes and the osteichthyans in particular. Some of the earliest amphibian remains may be associated with tidally influenced sediments. Furthermore, during the early part of the Devonian, fresh water chemistry may well have been different from that of today, lessening the divide between marine and non-marine environments.

Urea formation via the ornithine cycle, and urea retention in the body fluids, are useful adaptations for terrestrial life. They prevent excessive water loss associated with the elimination of nitrogenous waste. These abilities may have been primitive for the gnathostomes, and were developed in the marine environment to reduce osmotic dehydration.

In the aqueous medium, gaseous exchange is effected by the gills. These organs are, on the whole, useless in air. For vertebrates, air-breathing is effected by an inflatable sac, with moist linings, and an internal location. Some form of air-breathing sac was primitive for the osteichthyans, and may have been primitive for the gnathostomes. Again, this adaptation for terrestrial life developed in response to conditions experienced in the marine, aquatic environment.

A new model of tetrapod evolution is proposed in the light of the basic marine origin and character of the ancestors of the tetrapods.

1. Introduction

Two major groups of vertebrates can be recognized, the fish, with their predominantly aquatic mode of life, and the tetrapods (amphibians, reptiles, birds, and mammals), with a largely terrestrial mode of life.

The transition from fish to tetrapod has had a long history of study. Many of the important selection pressures and the morphological adaptations to these pressures have already been identified and discussed with respect to the evolution of the terrestrial mode of life for vertebrates, and the origin of the tetrapods (Gregory 1915; Barrell 1916*b*; Westoll 1943, 1961, 1980; Orton 1954; Gunter 1956; Romer 1956, 1958; Cowles 1958; Eaton 1959; Olsen 1961; Parsons & Williams 1962, 1963; Szarski 1963, 1967; Thomson 1966, 1971, 1972; Panchen 1967, 1977; Rackoff 1980). Some of the ecological aspects involved in the transition from aquatic to terrestrial habits have been stressed by Inger (1957), Thomson (1969*a*, 1980*a*) and Spjaelnaes (1982).

Physiological adaptations necessitated by the change are touched upon in some of these reviews. There have been numerous considerations of the adaptive changes that may have occurred in separate physiological systems. Osmoregulatory (that is, water–electrolyte balance) adaptations, including nitrogenous waste regulation, have been discussed by Marshall & Smith (1930); Smith (1932, 1953); Needham (1938); Florkin & Duchateau (1943); Brown & Stein (1960); Cohen & Brown (1960); Shaw (1960); Forster & Goldstein (1969); Hickman & Trump (1969); and Maetz (1971). Respiratory (CO_2–O_2 balance) changes have been dealt with by Atz (1952); Hughes & Shelton (1962); Cox (1967); McMahon (1969) and Packard (1974).

These physiological studies generally use information on living fish and tetrapods and extrapolate back. Emphasis is placed on the physiological adaptations observed in the extant bony fish (osteichthyans) – the coelacanth (*Latimeria*), the dipnoans (*Protopterus*, *Lepidosiren*, and *Neoceratodus*), various actinopterygians which show terrestrial habits (*Anguilla anguilla*, the European eel; *Periophthalmus* spp., the mudskippers) – and the extant amphibians. These studies are usually conducted within the context that the crossopterygian fish were ancestral to the amphibians, and that the transition from fish to tetrapod occurred in a fresh water environment during the Devonian. Important exceptions to the rule are the works of Packard (1974) and Thomson (1980*a*), who suggest that a marine setting cannot be ruled out for the origin of the amphibians.

The historical background to the consensus opinion on the evolution of the tetrapods is briefly outlined in §2. The geological and physiological information regarding the environment in which the tetrapods originally evolved is re-examined in §§3 and 4 and a new model is suggested in §5.

2. Historical background

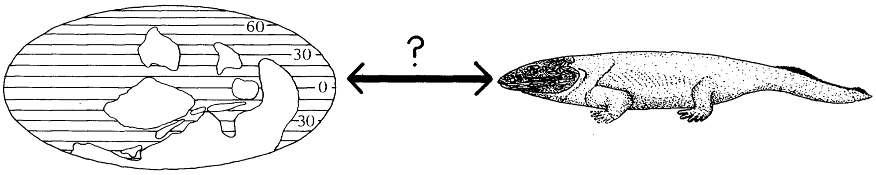
2*a*. *Origin of the tetrapods*; *timing*

A Siluro-Devonian setting for evolution of the terrestrial vertebrates and evolution of the tetrapods (see figure 1) was first proposed in the early part of this century (Barrell 1916*b*). Evidence for the timing of tetrapod origins came from three sources. Firstly, that the oldest known amphibian skeletal remains were reported from the Lower Carboniferous (Dawson 1863). Second, that amphibian footprints had been described in the Upper Devonian of Pennsylvania (Marsh 1896; Willard 1935). Third, that the Devonian Old Red Sandstone (O.R.S.) yielded the remains of possible piscine ancestors.

Since that time Upper Devonian amphibian skeletal remains have been discovered in the East Greenland Basin (Säve-Söderbergh 1932; Jarvik 1952; 1955*a*, *b*, 1964, 1980) and in eastern Australia (Campbell & Bell 1977). The trackways in the Upper Devonian of Pennsylvania have been shown to be those of a xiphosuran limulid (Caster 1938). However, Upper Devonian amphibian tracks have subsequently been reported from eastern Australia (Warren & Wakefield 1972) and Brazil (Leonardi 1983). From the evidence of the earliest amphibian remains it is apparent that the tetrapods evolved in the upper Middle or the Upper Devonian (Rackoff 1980). Groups possibly closely related to the tetrapods (crossopterygians and dipnoans) first occur in the Lower Devonian (Denison 1968*a*, *b*; Jessen 1975; Miman & Xiaobo 1981). In this review it will be shown that some of the physiological adaptations for terrestrial life were initiated in Silurian and Devonian fish.

2*b*. *Origin of the tetrapods*: *environment*

The separate identity of the Silurian, Devonian, and Carboniferous Systems was only conclusively demonstrated in the 1840s (Murchison & de Verneuil 1841) after a long and



The Lower Devonian world (after Tarling & Turner 1982)

Ichthyostega — an Upper Devonian amphibian (after Jarvik 1980)

FIGURE 1. Is there a relation between the Siluro-Devonian environment and the evolution of the amphibians?

acrimonious conflict (see Rudwick 1979). Even then the debate did not finish in some areas. In Ireland, for instance, there was a strong tide of opinion that the O.R.S. (Devonian) was merely the basal formation of the Carboniferous (Kelly 1856, 1857; Jukes 1866; Kinahan 1880). Much of the work of this period was therefore concerned with proving the existence, or otherwise, of these systems. The boundaries are still subject to change locally (Allen & Williams 1982; Paproth *et al.* 1983).

Little consideration was given in early works to the depositional environments that the sediments represented. The general view, following Lyell, was that the bulk of the sedimentary geological record represented marine depositional environments (for example, Darwin 1977, p. 300). In particular, the O.R.S. of the British Isles was thought to have been deposited in a shallow, stormy, sea (Jukes 1866; Miller 1889, p. 223, p. 235). However, Godwin-Austin (1856) suggested that the O.R.S. was formed in large fresh water lakes or inland seas. He was followed in this interpretation by Geikie (1879). Goodchild (1904) proposed that the O.R.S. had a more eclectic origin, being formed in a variety of situations, including fluvial, lacustrine, and desert environments.

In 1916 two important papers by Barrell were published. In the first (Barrell 1916*a*) he argued that the O.R.S. was deposited primarily under the influence of fluvial conditions which operated in a semi-arid environment subject to seasonal rainfall. In the second (Barrell 1916*b*) he suggested that such conditions would provide the ideal milieu for the early evolution of the amphibians. His considerations derived from his work on the Devonian and Carboniferous of the Appalachian region of North America (Barrell 1913, 1914*a*, *b*). He believed that the character and disposition of the O.R.S. sediments in the Appalachian area were indicative of a large delta prograding into a marine basin to the west.

When Barrell's work was published the principle Middle and Upper Devonian fish faunas came from O.R.S. type sediments (for example, Dura Den, Orcadian Basin, Catskills). These faunas included forms whose nearest extant relatives lived in tropical rivers that showed a tendency towards periodical fouling. Several of these living relatives showed adaptations to terrestrial conditions, such as air-breathing. It was thus natural that the environments represented by the O.R.S. were considered to be those in which the terrestrial vertebrates first evolved. The vertebrates were thought to have moved onto land from the fresh water. This was linked to the process of periodic water fouling (Barrell 1916*b*; Westoll 1961; Romer 1966). This scenario is best summarized by Romer (1966, p. 86):

> the Devonian, during which land adaptations originated, was a time of seasonal droughts when life in fresh waters must have been difficult.... The fish, incapable of land locomotion,

> would be, literally, stuck in the mud...but the amphibian, with his [*sic*] short and clumsy but effective limbs, could crawl out of the pool and walk overland...and reach the next pool where water still remained'.

Since the early part of this century, however, the number of Devonian marine vertebrate faunas has increased substantially. Important marine localities are known in Germany (Ørvig 1961), the Middle East (Janvier 1977, 1980; Blieck *et al.* 1980), and Australia (Gardiner & Miles 1975). Groups possibly ancestral to the tetrapods, and showing adaptations to life on land, occur in these faunas. Furthermore, there is increasing evidence that the very earliest tetrapods were associated with marginal marine conditions, rather than the upland areas as envisaged by Barrell (1916*b*). In this review the environment in which land adaptations evolved is reassessed by using the geological and comparative physiological evidence. Both these strands of evidence have been left in the shadow of the morphological evidence as regards this phase of vertebrate evolution.

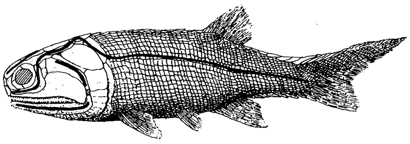
Recent studies (for example, Allen *et al.* 1968; Allen & Friend 1968; Woodrow *et al.* 1973; Allen 1979; Graham 1983; Allen & Crowley 1983) have upheld Barrell's views regarding the environment represented by the O.R.S., although the delta model has generally been replaced by models that recognize the evolution of sedimentary basin infills from fanglomerate and alluvial fan sediments to alluvial plain sediments. There has been a tendency to interpret all O.R.S. sequences in terms of fluvial processes. However, Allen & Williams (1981) and Allen (this symposium) show that in one of the classic O.R.S. areas, South Wales, it is difficult to differentiate between alluvial and tidal plain sediments in some instances. Tidally influenced sediments could be more common than previously appreciated, especially in areas known to be laterally continuous with marine environments. The wholesale application of alluvial fan and fluvial floodplain models should therefore be questioned. Perhaps the delta model originally proposed by Barrell, involving some marine influences, has more validity than has recently been granted.

In most other reviews on the early evolution of the amphibians it is assumed that water chemistry in the late Silurian–early Devonian was basically comparable to that of the present day. However, since that time the vascular plants have colonized the land. The effects on continental water chemistry may have been considerable, and will be considered in this review.

2*c*. *Origin of the tetrapods*: *ancestry*

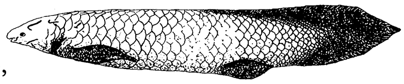
The ancestors of the tetrapods have been sought mainly within the dipnoan and crossopterygian fish. The dipnoans have living representatives that inhabit fresh water streams and lakes in tropical areas of Africa, South America, and Australia. Presence of paired lungs in these fish was reported by Bischoff (1840) and considered to be indicative of the tetrapod nature of these animals. The original description of the Australian dipnoan, *Neoceratodus*, by Krefft (1870) suggested that this animal was an amphibian that resembled the dipnoans. However, Gunther (1872) determined that *Neoceratodus* was a dipnoan, that the dipnoans included the Devonian form *Dipterus*, and that these animals were fish.

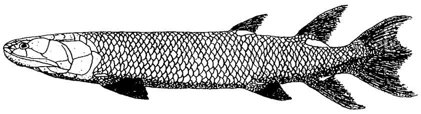
The work of both Baur (1896) and Dollo (1896) indicated that the dipnoans were not the ancestors of the tetrapods but that this position was held by the crossopterygians. At that time the crossopterygians were thought to include living representatives in *Calamoichthyes* and *Polypterus*, which inhabited tropical streams in Africa, and possibly had a limited ability to use



(*a*) actinopterygian
Moythomasia nitidus
(after Jessen 1968),
Middle Devonian,
Germany

(*b*) dipnoan
Neoceratodus forsteri
(after Jarvik 1980, fig. 336A),
Recent Australia





(*c*) crossopterygian
Eusthenopteron foordi
(after Jarvik 1980, fig. 72A),
Upper Devonian,
Canada

(*d*) amphibian
Ichthyostega
(after Jarvik 1980, fig. 170),
Upper Devonian–
Lower Carboniferous,
Greenland

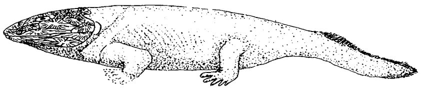


Figure 2. Representatives of the three major subdivisions of the Osteichthyes (Actinopterygii, Crossopterygii, and Dipnoi), and a primitive amphibian.

their air-bladder for respiration (Pollard 1891). The crossopterygians also included a variety of Devonian forms (Woodward 1891). In describing *Sauripterus* from the O.R.S. of Pennsylvania, Hall (1843) homologized the proximal pectoral fin elements of the crossopterygians with the proximal elements of the tetrapod forelimb. The work of Hall was extended by Gregory (1911, 1915) who, apart from homologizing pectoral fin elements, also homologized crossopterygian and tetrapod cranial elements. *Sauripterus* was used by Broom (1913) as the possible ancestor of the tetrapods in his review of vertebrate limb structure.

Goodrich (1908, 1928) has shown that the genera *Calamoichthyes* and *Polypterus* are not crossopterygians. He has suggested that they are primitive actinopterygians and is supported in this view by Gardiner (1963, 1967). Several other authors have expressed the view that these fish are a completely separate group (Daget *et al.* 1964; Lehmann 1966; Nelson 1969; Jessen 1973; Nyebelin 1976; and Jarvik 1980). Either way, they are removed from consideration as possible tetrapod ancestors (Schaeffer 1965).

With this change it appeared that the crossopterygians had become extinct during the Cretaceous. However, in 1938 a possible living representative – the coelacanth *Latimeria* – was discovered in the seas off East Africa (Smith 1939). Since then further specimens of this fish have been caught and a great deal of anatomical information is now available (Millot &

Anthony 1958, 1965; Millot *et al.* 1978. Certain fundamental differences in the endocranial anatomy of the coelacanths and the crossopterygians have been demonstrated (Bjerring 1967, 1973; Jarvik 1968*b*, 1980). The exocranial anatomy, though, has been shown to be related to that of the porolepiform crossopterygians (Andrews 1973). Doubt has been cast on the systematic position of the coelacanths by the work of Miles (1977), Wiley (1979), Gardiner (1980), and Forey (1984).

Many authors have accepted or added to the suggestion (Baur 1896; Dollo 1896) that the crossopterygians were ancestral to the tetrapods (for example, Watson 1926; Jarvik 1942, 1972, 1980, 1981; Westoll 1938, 1943, 1961; Romer 1966; Panchen 1967, 1977; Bertmar 1968; Thomson 1968). This has been based on the considerable increase in our knowledge of crossopterygian anatomy, particularly through the meticulous work of Erik Jarvik (1942, 1944*a*, *b*, 1948, 1949, 1950*a*, *b*, *c*, 1954, 1966, 1972, 1975, 1980). Important contributions have also been made by Säve-Söderbergh (1933, 1941); Westoll (1936, 1937*a*); Jessen (1966, 1967, 1975); Andrews & Westoll (1970); Andrews (1973); Vorobyeva (1975, 1977); and Miman & Xiaoba (1981).

Several studies have indicated a close relationship between the crossoterygians and the dipnoans (Denison 1968*a*, *b*; Thomson & Campbell 1971; Miles 1975). If the crossopterygians are also considered to be closely related to the tetrapods, then cladistically speaking they may be a paraphyletic group (Patterson 1980). The dipnoans, crossopterygians and actinopterygians are all grouped together in the higher level group Osteichthyes. The dipnoans and crossopterygians are considered to be more closely related to one another than either is to the actinopterygians (Schaeffer 1968; Gardiner 1973).

So, despite the wealth of detailed anatomical information and the exciting discoveries of the past 70 years since the publication of Barrell's work (1916*a*, *b*), we appear to be further than ever from a concensus on the interrelations of the fish and the tetrapods. A majority verdict would probably find in favour of the osteolepiform crossopterygians being the closest relatives (or ancestors) of the tetrapods (for example, Panchen 1967, 1977; Schultze 1977; Szarski 1967). Within the osteolepiforms it is the osteolepidids that appear to be the most closely related family (Vorobyeva 1977; Rackoff 1980, pp. 282–288; Thomson 1980*a*, p. 192; Westoll 1980). A close relationship between the crossopterygians and the dipnoans would also be supported, these probably having arisen from a common ancestor (Schaeffer 1968). The crossopterygians, dipnoans, coelacanths, and actinopterygians together constitute a monophyletic assemblage, the Osteichthyes (Schaeffer 1968; Gardiner 1973; Forey 1984).

The extant primitive actinopterygians and dipnoans show physiological adaptations to the terrestrial environment. This has been used to support claims for a close relationship between these groups and the tetrapods. Physiological adaptation to life on land is inferred for the crossopterygians owing to their close relationship with the tetrapods. In this review the development of physiological adaptation to terrestrial life in the osteichthyan groups will be considered. Did the actinopterygians and dipnoans adapt to the terrestrial environment to the same extent as the crossopterygians? If not, why not? These questions will be considered. The answers may provide further information which may help to resolve the question of tetrapod ancestry.

3. ENVIRONMENTAL CONSIDERATIONS

3a. *Introduction*

Analysis of the distributions of the Palaeozoic sarcopterygians (Dipnoi plus Crossopterygii) (Thomson 1969*b*, 1980*a*) has shown that these fish inhabited both marine and fresh water environments. The same appears to be true for the Devonian actinopterygians. Very few osteichthyan genera appear to have been restricted to fresh water (Table 1). The majority of Devonian crossopterygians and dipnoans are found in either marine and continental sediments, or in just marine sediments. This raises questions regarding the fresh water origin of the tetrapods. Considerations of the environments inhabited by the osteichthyans and primitive amphibians have rested heavily on the assumptions that atmospheric and water chemistries were broadly comparable to those of the present day. Some general aspects of the Devonian physical environment are outlined in the next section.

3b. *The Devonian physical environment*

3b. i. *The Devonian atmosphere*

The level of carbon dioxide in the Devonian environment was similar to that of the present (Frakes 1979). The amount of oxygen in the atmosphere has been linked to plant photosynthesis, with an increase in photosynthesis leading to an increase in the level of oxygen (Berkner & Marshall 1965; Cloud 1976). The spread of the vascular plants on to land during the Devonian may have contributed to a substantial enrichment of atmospheric oxygen. Berkner & Marshall (1965) suggested that the Carboniferous atmosphere had at least as much oxygen as the present day atmosphere, if not more. In the early part of the Devonian the oxygen level in the atmosphere was low, probably only a third of the present value (Cope & Chaloner 1980). The rise of land-living vertebrates in the Devonian may reflect the vast increase in oxygen within the atmosphere that occurred at this time. However, the aquisition of air-breathing organs by the vertebrates predates the dramatic oxygen level increase and these organs had their origin in a different environment to that which they became so eminently suited.

3b. ii. *Devonian water chemistry*

Ocean water salinity is thought to have been closely comparable to that of the present during the Devonian (Burton & Wright 1979). Clearly though, the amount of dissolved oxygen in the seas, and indeed in continental waters, would have been much lower at the beginning of the Devonian. There appears to have been no prior consideration as to the composition of fresh waters during the Devonian. To effect a full and detailed review of this topic would require the reassessment of all Devonian geochemical data that may have some bearing on this question, which would be a complete study in itself. I shall consider some general points.

Vascular land plants, although known at this period (Banks 1980; Edwards 1980*a*, *b*, and this symposium) appear to have been restricted to the vicinity of water bodies. There is little evidence for extensive protective floras having been developed at any distance from fluvial systems. Obviously, a great deal of bias exists in that much of the O.R.S. sedimentary record is so intimately related to fluvial conditions. Evidence for presence of extensive land floras away from rivers, if such existed, might be expected in distal and late stage sheetflood sediments, like those described from the late Lower Devonian of South Wales (Tunbridge 1981). Even in these sediments there is the possibility that the plant material might be derived from near-fluvial

TABLE 1. THE DISTRIBUTION OF SILURIAN AND DEVONIAN OSTEICHTHYANS WITH RESPECT TO ENVIRONMENT

Actinopterygii	age	environment
Andreolepis	U.S.	M
Dialipina	L.D.	M
Ligulalepis	L.D.	M
Orvikuina	M.D.	M
Stegotrachelus	M.D.	C (?In)
Cheirolepis	M.D., U.D.	C (?In)
Moythomasia	M.D., U.D.	M
Osorioichthys	U.D.	M
Tegeolepis	U.D.	M
Dipnoi		
Uranolophus	L.D.	M
Dipnorhynchus	L.D., M.D.	M
Melanognathus	M.D.	M
Pentlandia	M.D.	C (?In)
Stomiahykus	M.D.	M
Conchodus	M.D., U.D.	M, C (Ex)
Dipterus	M.D., U.D.	M. C (Ex, ?In, In)
Ganorhynchus	M.D., U.D.	M
Rhinodipterus	M.D., U.D.	M, C (Ex)
Chirodipterus	U.D.	M
Devonosteus	U.D.	M
Fleurantia	U.D.	C (?In)
Griphognathus	U.D.	M
Grossipterus	U.D.	M, C (Ex)
Holodipterus	U.D.	M
Jarvikia	U.D.	C (?In)
Oervigia	U.D.	C (?In)
Palaeadaphus	U.D.	M, C (Ex)
Phaneropleuron	U.D.	C (Ex)
Rhynchodipterus	U.D.	C (Ex)
Soederberghia	U.D.	C (Ex, ?In)
Crossopterygii		
Powichthys	L.D.	M
Youngolepis	L.D.	C (Ex)
Porolepis	L.D., M.D.	M. C (Ex)
Onychodus	L.D., M.D., U.D.	M
Gyroptychius	M.D.	M, C (Ex, ?In)
Hamodus	M.D.	M, C (Ex)
Heimenia	M.D.	C (Ex)
Latvius	M.D.	M, C (Ex)
Osteolepis	M.D.	M, C (Ex, ?In, In)
Thursius	M.D.	M, C (Ex, ?In)
Tristichopterus	M.D.	C (?In)
Glyptolepis	M.D., U.D.	M, C (Ex, ?In)
Holoptychius	M.D., U.D.	M, C (Ex, ?In, In)
Panderichthys	M.D., U.D.	C (Ex, ?In)
Strunius	M.D., U.D.	M
Bogdanovia	U.D.	C (Ex)
Callistiopterus	U.D.	C (?In)
Chagrinia	U.D.	M
Dictyonosteus	U.D.	C (Ex)
Diplocercides	U.D.	M
Elpistostege	U.D.	C (?In)
Euporosteus	U.D.	M
Eusthenodon	U.D.	C (Ex, ?In)
Eusthenopteron	U.D.	M, C (Ex, ?In)
Hyneria	U.D.	C (Ex)
Laccognathus	U.D.	C (Ex)

TABLE 1 (*cont.*)

Litoptychius	U.D.	M
Megalichthys	U.D.	C (Ex)
Megistolepis	U.D.	C (Ex)
Nesides	U.D.	M
Platycephalichthys	U.D.	C (Ex)
Polyplocodus	U.D.	C (Ex)
Pseudosauripterus	U.D.	C (Ex)
Rhizodopsis	U.D.	C (Ex, ?In)
Sauripterus	U.D.	C (Ex)
Sterropterygion	U.D.	C (Ex)
Thaumatolepis	U.D.	C (ex)

U.S., Upper Silurian; L.D., Lower Devonian; M.D., Middle Devonian; U.D., Upper Devonian; M, marine; C, continental; Ex, external basin; In, internal basin; ?In, internal basin with possible connection to other basins.

Based largely on Thomson (1969*b*, table 1), with supplementary information from Jessen (1966), Gross (1968), Schultze (1968).

conditions. As yet, though, there are no reports of plant material in such sequences. Lack of an extensive land flora allowed an increased effect of weathering and leaching of source rocks and sediments. This, in turn, may have led to an increase in the ion concentration of 'fresh water'. Such effects may have been increased because of the relatively low oxygen levels in the atmosphere.

Livingstone (1963) reviewed the present day fresh water chemistry of all parts of the world and the data used here is taken from his work. The climate of most of the areas under consideration has been claimed to be tropical (House 1975*a*, *b*; Frakes 1979; Heckel & Witzke 1979). The global mean ion content of fresh water is $120/10^6$. Tropical areas generally have lower salinity waters, presumably because these areas support high density ecosystems which act as 'ion sponges'. During the earlier part of the Devonian this effect would have been minimal. In desert areas total ion content of water varies from $300/10^6$ to $300000/10^6$ (Goudie & Wilkinson 1977, p. 68). In comparison, average sea water ion content is $35000/10^6$ (Mason 1958). Rivers in arid regions (for example, Somalia, Middle East) attain concentrations of up to $5000/10^6$ during the dry season. Exceptionally high values can develop in enclosed lakes in arid regions. For example, Lake Eyre in Australia reaches salinities of up to $240000/10^6$. The Middle Devonian Orcadian Basin lakes of northern Scotland have been interpreted as having suffered seasonal salinity variations (Donovan 1980).

With regard to specific ions, marine waters show fairly consistent compositions (Mason 1958; see table 2). Continental waters are more variable (Livingstone 1963; see table 3). However,

TABLE 2. AVERAGE PERCENTAGE IONIC COMPOSITION OF SEA WATER ($35000/10^6$)
(After Mason 1958.)

ion	percentage
Cl^-	55.0
Na^+	30.5
SO_4^{2-}	7.5
Mg^{2+}	3.5
Ca^{2+}	1.0
K^+	1.0
HCO_3^-	0.5
Br^-	tr.
F^-	tr.
$H_3BO_3^-$	tr.
Sr^{2+}	tr.

tr., Trace

TABLE 3. PERCENTAGE IONIC COMPOSITION OF NON-MARINE WATERS OVER A RANGE OF SALINITIES (35.2 to 352000.0/10^6).

(Data from Livingstone (1963, tables 8G, 16G, 23N, 34D, 35A, 38D, 41L, 43F, 50C, and 57K).)

	35.2	35.4	346.0	353.0	3550.0	3673.0	32300.0	40300.0	352000.0
ion									
Cl^-	3.1	2.0	2.9	2.1	0.1	20.5	56.7	37.7	39.1
Na^+	6.2	4.5	4.6	2.1	—	13.3	31.8	27.5	27.6†
SO_4^{2-}	3.1	15.5	6.9	6.2	79.4	44.1	5.9	24.4	27.0
Mg^{2+}	0.2	5.6	0.9	0.4	7.5	3.5	2.4	3.7	5.4
Ca^{2+}	12.2	20.3	19.6	21.0	10.6	13.5	1.9	1.3	Tr.
K^+	4.3	4.5	—	0.6	—	0.2	0.7	—	
HCO_3^-	60.5	32.8	59.0	57.2	—	3.8	0.6	5.2	0.7

† Includes K^+.

continental waters in present day arid regions attain compositions comparable to marine waters. The main ions in high salinity fresh waters are commonly sodium and chloride.

In addition, account must be taken of the clear evidence for high levels of volcanic activity in some areas, which might have contributed to the ionic enrichment of continental waters (Thomson & Keith 1984). For instance, in South Wales the Lower O.R.S. contains an abundance of tuff beds: the deposits of explosive volcanic events (Allen & Williams 1981, 1982). Between the base of the Townsend Tuff Bed (which has been taken as the local base of the Devonian (Allen & Williams 1981)) and the top of the Picard Bay Tuff Bed (a thickness of less than 50 m) there is evidence for at least eleven ash falls. The period of time represented by this package of sediments has been calculated to be, at most, 65000 years (Allen & Williams 1982). These tuff beds were subsequently eroded by streams in the Lower Devonian, or indeed were deposited directly into water bodies (Allen & Williams 1982).

So, it is possible that early Devonian continental drainage systems were characterized by waters with higher ionic concentrations than those of present day continental drainage systems. However (if present day arid regions represent a viable analogue) these waters would still have been dilute in comparison with sea water. Only in enclosed drainage basins would exceptionally high salinites, comparable to those of marine basins, have occurred. In the alternating wet-season–dry-season climate of the tropics there may have been a seasonal variation in fresh water salinity, with higher salinity generally being developed during the dry-season. Livingstone (1963, table 54) has indicated an interesting phenomenon. Streams entering a lake in the arid region of Australia have high salinities even when a drought has finished, so that high salinity conditions persist into the wet-season. This is presumably due to these post-drought fluvial systems tapping areas of high salinity developed during the drought. This effect may have also been important in the Devonian.

In considering the physiological adaptations of the Devonian osteichthyans with respect to their ability to colonize the terrestrial environment, the possibility that the fresh water aquatic environment was of higher salinity than that of the present may be of direct relevance. Certainly this factor is important for the colonization of fresh water environments, and yet it appears to have been ignored.

3c. *Devonian sedimentary basins*

Three broad facies (sedimentary environment) associations have been established for the Devonian (see figure 3) (House 1975*b*): the O.R.S. magnafacies (continental, fluvio-clastics

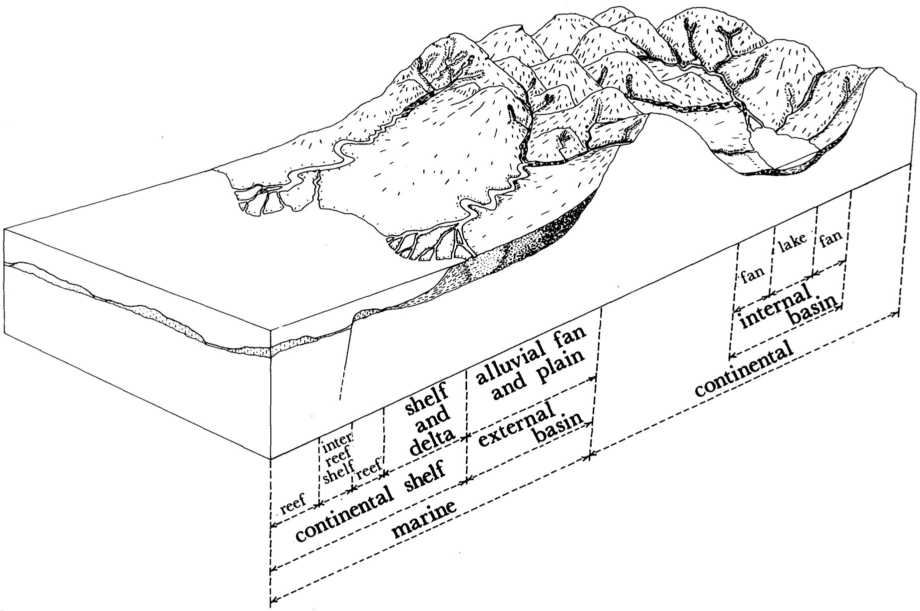


FIGURE 3. Devonian sedimentary basins, showing relations and broad outlines of the magnafacies infill. Silurian and Devonian osteichthyans and the earliest amphibians occur predominantly in shallow marine (continental shelf – Rhenish magnafacies) and continental (Old Red Sandstone magnafacies) environments.

(Barrell 1916*a*; Allen 1962, 1979)); the Rhenish magnafacies (near-shore, marine clastics, plus carbonates and reefs (Schmidt 1926; Rabein 1956; Goldring & Langenstrassen 1979)); and the Hercynian magnafacies (bathyal pelagics, plus carbonates and reefs (Goldring 1962; Erben 1964; Krebs 1979)). Osteichthyans generally occur in the O.R.S. and Rhenish magnafacies, that is, continental and shallow marine sediments. This broad distinction of Devonian marine and non-marine sedimentary basins is made on the basis of the tectonic setting of the basins, coupled with the nature of the sedimentary infill and the fossil biota.

The predominantly continental O.R.S. magnafacies is the product of erosion of upland areas (Allen 1962) formed largely by the processes of ocean closure and granite batholith emplacement (Leeder 1976). O.R.S. sediments are generally thought to have accumulated in two tectonic settings (Allen *et al.* 1968; Allen & Friend 1968; Allen 1979; Dineley 1979). The major site of accumulation is in basins that fringe continents. These external or extramontane basins are laterally continuous with marine basins. The other site of deposition is in basins that are surrounded by the continent, sometimes being located in the continental interior. These internal or intermontane basins are commonly associated with large-scale tectonic features, such as rifts or strike-slip faults. Internal basins may appear to be isolated from contact with other basins. It has been suggested that this particular type of basin is characterized by fresh water drainage systems (Thomson 1980*a*).

The sedimentary infill of both types of O.R.S. basin is generally interpreted in terms of fluvial sedimentation (for example, Allen 1979). As previously mentioned (§2), it can prove difficult to distinguish, on sedimentological grounds, between fluvially and tidally influenced sediments in red bed sequences of coastal areas. Unfortunately these sequences frequently lack good palaeontological control on the environment. Marine influences on O.R.S. sedimentation may be more important than is recognized at present. In view of the fact that external O.R.S. sequences are laterally continuous with marine basins it is strange that more successions have not been interpreted in the light of deltaic models of sedimentation.

Thomson (1969*b*, 1980*a*) conducted his analyses of the environments inhabited by the sauropterygian fish within this framework of sedimentary basins, recognizing marine and non-marine basins. Non-marine basins are divided into those having contacts with marine basins (external basins) and those lacking such contacts (internal basins). Internal basins are considered by Thomson to have been fresh water drainage systems.

3*c*. i. *Shallow marine and external O.R.S. basins*

The studies of Thomson (1969*b*, 1980*a*) clearly recognize that the external O.R.S. and shallow marine basins were in lateral continuity, and furthermore correctly identify external O.R.S. and shallow marine basins. Only a few points need to be added at the present time on this aspect, particularly relating to the earliest amphibians.

Thomson (1980*a*) considered that *Melanognathus*, a dipnoan, from the Lower Devonian of Canada (Jarvik 1967), was found in a non-internal setting. The sequence in which this fish occurs has been identified as being part of a shallow marine shelf area (Norris 1968). The earliest osteolepiform crossopterygians, from the Lower Devonian of China (Miman & Xiaoba 1981), probably occur in an external O.R.S. sequence (Y. Liu, personal communication). Amphibian trackways (Warren & Wakefield 1972) and remains (Campbell & Bell 1977) in the Upper Devonian of Eastern Australia are from an external O.R.S. sequence (Hill 1968). Recently reported amphibian trackways from the Upper Devonian of the Parana Basin in Brazil (Leonardi 1983) also occur in an external O.R.S. sequence, which shows the effects of tidal influence.

3*c*. ii. *Internal O.R.S. basins*

The Laurentian continent (North America, Greenland, northwest Europe) is the best known Devonian area, and several internal basin O.R.S. sequences have been described for the Laurentian area (Orcadian Basin, Midland Valley, East Greenland, Western Norway, Spitzbergen, Escuminac). These basins all yield osteichthyans and the East Greenland Basin is the site of finds of Upper Devonian amphibian remains. Is it correct to assume that these basins were characterized by fresh water? For instance, the Spitzbergen Basin, while considered to have an internal setting, is influenced by marine transgression. Harland (1961) and Allen & Friend (1968) have suggested that this basin was a gulf-like feature that opened northwards into a marine basin. The Munster Basin of southern Ireland has been interpreted as both an external (Allen 1979) and an internal basin (Gardiner & MacCarthy 1981). A gulf-like interpretation may help to resolve this problem. In the Upper Devonian the Munster Basin is affected by a marine transgression which comes from the south (Clayton *et al.* 1979; Holland 1979), the direction in which the basin may have opened.

It has been suggested (Spjeldnaes 1982) that the East Greenland Basin was affected by marine conditions during the Upper Devonian. The ichthyostegalid amphibians reported from this basin (Säve-Söderbergh 1933; Jarvik 1952, 1955*a*, *b*, 1961, 1980) may be associated with tidal flat environments. However, reconstructions of the O.R.S. continent (Dineley 1979) place the East Greenland Basin within the continental interior. This problem might be resolved by reference to the major wrench fault system which may have transected the Laurentian continent (Ziegler 1981, 1982). The East Greenland Basin was probably associated with this tectonic regime. Marine conditions could possibly be introduced via this major wrench faulting system.

Both the Midland Valley and the Northumberland Basins are affected by marine transgressions

(Browne 1980; Leeder 1974) and appear to have opened to marine conditions to the east. Pennington (1975) has described Middle Devonian marginal marine facies in the Argyll field of the North Sea. Recently, Ziegler (1981) has proposed that a sea-arm, possibly fault-controlled, extended up into the central North Sea area from the Rhenish Basin to the south. This arm is thought to have also been connected with the Orcadian and Western Norwegian Basins (Ziegler 1981). Such a feature could have been the route by which the osteichthyans entered these basins, coming from the Rhenish Basin area to the south. No marine facies are known within either the Orcadian Basin or the Western Norwegian basins. However, external O.R.S. and shallow marine facies have been reported in the Lower Devonian Ringerike Series of southern Norway (Nilsen 1973).

The southern end of the major wrench fault system which may have transected the Laurentian continent is placed in the eastern American area and the Escuminac Basin of eastern Canada might have also been associated with this regime. No marine facies have been reported in the Escuminac Basin. However, the upper part of the sequence of this basin has been removed by a Carboniferous transgressive event (Dineley & Williams 1968). The internal basin sediments are preceded by external O.R.S. facies (Dineley & Williams 1968). Devonian sediments in Manitoba and Saskatchewan have been interpreted as having been deposited in a gulf-like basin, enclosed by land on three sides but opening to the northwest into marine environments (Kent 1968).

Internal basins have been recognized on other Devonian continents. In the Kazakstan area of the Siberian continent internal basins have been described (Predtechensky & Krasnov 1968). These internal facies appear to have been geographically adjacent to external and marginal marine conditions, and in the Givetian and Famennian were affected by marine transgressions. Bony fish are associated with both continental and marine facies. It is possible that the Kazakstani basins were also gulf-like in form and had permanent or near-permanent contacts with marine basins.

Several Devonian basins in the Western Australian region of Gondwana are thought to represent gulf-like internal basins and exhibit a mixture of continental and marine facies (Johnstone *et al.* 1968). The Canning Basin, which includes the Frasnian Gogo Formation, with its exquisitely preserved osteichthyans, is one of these.

3*d*. *Conclusions*

A brief consideration of the Devonian physical environment indicates that the atmosphere may have been different from that of the present day, having low oxygen partial pressure in the early Devonian. It is possible that early Devonian continental waters were somewhat more saline owing to the general lack of a plant cover, localized enhancement of salinity by volcanic material, and the high partial pressure of carbon dioxide with respect to oxygen.

Given that many of the areas inhabited by the osteichthyan fish were probably in the tropical belt, there would have been a seasonal variation in continental water salinity, with increases during the dry season and decreases during the wet season, as is seen for modern arid and semi-arid rivers. This may have facilitated the movement of marine fish (such as the osteichthyans) into continental drainage systems. Subsequently some osteichthyans may have adapted to the lower salinity waters of the continents. It is shown in the next section that it is physiologically easier for marine fish to colonize the terrestrial environment than it is for fresh water fish. The ability of the essentially marine osteichthyans to inhabit the possibly high salinity Devonian fluvial systems may have been an important stage in the development of terrestriality in the vertebrates. Normally the fluvial environment has a more intimate relationship with the terrestrial environment than does the shallow marine environment. However, some areas of the shallow marine environment are also associated with terrestrial environments, notably, the littoral and tidal flat areas of coasts, and emergent parts of reefs.

Considerations of the environmental settings of the fossil osteichthyans and amphibians are necessarily reliant upon the interpretation of the sedimentary environments in which they occur. During the Devonian the osteichthyans and amphibians are, in the main, associated with shallow marine and continental facies. The continental sedimentary sequences that accumulated in internal basins did not necessarily lack contact with either external or marine basins. Indeed many internal basins appear to have been gulf-like in form and to have made contact with the marine environment. Marine facies occur in some internal basins. Thomson (1969*a*, 1980*a*). in his analyses of the environments inhabited by the lobe-finned osteichthyans (generally agreed to be closer to the tetrapods than the actinopterygian osteichthyans), took the internal basin environment to be synonymous with a fresh water environment. Even withstanding comments made in this paper as to the possible Devonian water chemistry, it is clear that the internal basin environment is not synonymous with fresh water. When this is taken into account Devonian osteichthyans and amphibians show an even more marked association with marine or marginal marine environments, or with continental environments in direct lateral continuity with the marine environment.

4. PHYSIOLOGICAL CONSIDERATIONS

4*a*. *Physiology of the primitive vertebrates*

Despite the poor general agreement on the nature of lower vertebrate interrelations (see §2*c*) it is possible, in a broad manner, to reconstruct primitive vertebrate physiology.

The earliest vertebrates are thought to have been marine animals (Halstead, this symposium). Palaeontological evidence points to the shallow marine, continental platform having been the locus of evolution (Denison 1956; White 1958; Boucot & Janis 1983). The same is apparently true of the osteichthyan fish (table 1). However, the physiological evidence regarding the original environment of the two groups has proved somewhat more difficult to interpret.

Indeed, physiological evidence has been used to support a fresh water origin for both the vertebrates as a whole, and the osteichthyans in particular. Both the structure and function of the vertebrate kidney, and the ionic concentrations of the body fluids of vertebrates, have been thought to point towards fresh water origins (Marshall & Smith 1930; Smith 1932, 1953; Romer & Grove 1935; Romer 1966; Croghan 1983).

Among the fish, most of the extant forms (marine or otherwise) are hypo-osmotic in relation to sea water (body fluid ionic concentration below that of sea water). This was thought to indicate that the primitive vertebrates were fresh water animals, and that their body fluids underwent dilution as an adaptation to the low-salinity fresh water environment. However, this does not adequately explain why the most primitive vertebrates, the hagfish, are iso-osmotic to sea water (body fluid ionic concentration close to that of sea water) (Robertson 1963). Further support for fresh water origins was taken from studies of kidney structure and function. Fresh water teleost actinopterygian fish have body fluids that are hyperosmotic to fresh water (more concentrated). They are thus subject to water influx by osmosis. The kidney has complete nephrons and produces a dilute urine to maintain a relatively high body fluid concentration. All the extant marine teleosts are derived from fresh water forms. In the marine environment these fish are hypo-osmotic and suffer dehydration (water is removed by osmosis). To combat this, the rate of blood ultrafiltration is reduced by degeneration of the glomerulus, even to the point of complete absence (aglomerular state). This was thought to indicate that the vertebrate glomerular kidney originated in the fresh water environment, mainly as a body-fluid volume-controlling organ (Romer & Grove 1935).

In recent years alternative viewpoints have been expressed. With regard to the kidney, it has been suggested (Robertson 1957; Hickman & Trump 1969) that this organ originated as an ion rather than a water regulator. This is consonant with the ability of the hagfish to regulate certain ions (Robertson 1963). In particular, the kidney is considered to have originated to regulate divalent ions (for example, calcium, magnesium and sulphate) (Boucot & Janis 1983). Endodermally derived tissues (for example gills) of extant fish are involved in the transport of monovalent ions (sodium and chloride mainly) (Maetz 1971). Only the kidney can handle divalent ions, and this may be related to its derivation from mesodermal tissue. As Boucot & Janis (1983) suggest, the ability to control the concentrations of divalent ions may have been important with respect to increased muscular and neuronal activity necessary for an active way of life. The origin of the glomerular kidney may be linked to the change from the sluggish, benthonic, filter-feeding proto-chordate state to the active, possibly predaceous, vertebrate state. Development of a mineralized, bony skeleton as a calcium and phosphate store (Pautard 1961) could be an important corollary event. In the fresh water and terrestrial environments the kidney was preadapted to assume the role of a water and organic waste-regulating organ, taking over these functions from the gills and extra-renal organs (for example, anal glands).

It has been further suggested that the low body fluid ionic concentration present in the vast majority of fish represents a basic cellular physiological adaptation (Thomson 1980*b*), which occurred independent of the external salinity. Many of the basic vertebrate characters (muscular segmentation, tail, glomerular kidney, mineralized skeleton) have been related to the assumption of an active swimming mode of life. Is it possible that the adoption of a low body fluid concentration is also related to this change of life-style? A general lowering of the body ionic concentration may have led to the more efficent distinction of areas of high ionic activity (muscles and nerves) from the background 'noise', and thus to more efficient muscular activity, and control of this activity.

There is, therefore, no serious physiological bar to the suggestion that the first vertebrates were marine animals. Indeed, assumption of a marine origin for the vertebrates relates the origin of several organ systems to a common cause.

The fish are generally divided into two groups. Those that possess jaws (Gnathostomata) are more closely related to the tetrapods (Amphibia, Reptilia, Aves and Mammalia) than those fish without jaws (Agnatha). It is among the gnathostomes that we must look for the development of the physiological ability to cope with the terrestrial environment. Although, as has been previously discussed (§2*c*), there is no concensus on gnathostome interrelations, we can broadly reconstruct their primitive physiological state.

4*b*. *Physiology of the Gnathostomes*

The gnathostomes (Acanthodii, Actinopterygii, Chondrichthyes, Crossopterygii, Dipnoi, Placodermi) appeared first in shallow marine environments during the Upper Silurian

(Moy-Thomas & Miles 1971). Most gnathostome groups subsequently invaded the fresh water environment, and some also colonized the terrestrial environment. The primitive gnathostomes had body fluid ionic concentrations below those of the marine environment they inhabited (Thomson 1980*b*) and were thus subject to osmotic dehydration. In view of this a primitive mechanism for maintaining body fluid osmolarity should be expected among the gnathostomes.

The chondrichthyans maintain low concentrations of body fluid electrolytes in the marine environment by the retention of organic compounds derived from the metabolism of amino acids (Smith 1936). Amino acids are broken down via the purine cycle, and produce energy (Cohen & Brown 1960). This process also results in the production of ammonia. Ammonia is highly toxic (see, for example, Ball 1967) and extremely soluble, and is not a suitable compound to accumulate to maintain osmolarity. Instead, ammonia is converted to less toxic and less soluble nitrogenous compounds such as urea, uric acid and trimethylamine oxide (Forster & Goldstein 1969). These substances can be maintained at relatively high concentrations with no deleterious effects, and thus can be used to raise the total body osmolarity to a level comparable to that of sea water. Urea can be produced by both the purine and ornithine pathways. However, the ornithine pathway is some 50–100 times more efficient (Schooler *et al.* 1966). The process of producing and storing urea in the body fluids is referred to as uraemia. As a result of uraemia, low electrolyte concentrations can be maintained, with little or no water outflux. Uraemia has also been demonstrated in the dipnoans (Smith 1930*a*, *b*; Janssens 1964; Brown *et al.* 1966; Forster & Goldstein 1966; Janssens & Cohen 1966, 1968) and the coelacanth (Pickford & Grant 1967; Brown & Brown 1967; Goldstein *et al.* 1973; Griffith *et al.* 1974; Lutz & Robertson 1975). Amphibians have the full complement of ornithine cycle enzymes (Brown & Cohen 1960; Cohen & Brown 1960) and can produce urea. Urea storage has been reported for some amphibians (see, for example, Gordon *et al.* 1961). Actinopterygians have been shown to possess some of the ornithine cycle enzymes (Huggins *et al.* 1969; Read 1971), although they lack the full set (Brown & Cohen 1960; Cohen & Brown 1960). This has been taken to indicate (Thomson 1980*b*) that the actinopterygians originally possessed the potential to synthesize ammonia into urea via the ornithine cycle, but, owing to the long fresh water history of the group, this capability has been lost.

High levels of urea are maintained in the body fluids of marine chondrichthyans by the selective reabsorption of urea from the glomerular ultrafiltrate in the kidney nephrons (Shaw 1960). This may also be a primitive gnathostome character. Marine chondrichthyans also combat osmotic dehydration by producing a highly concentrated urine (Shaw 1960) through substantial reabsorption of water from the glomerular ultrafiltrate. Similar water reabsorption is seen in amphibians subject to excessive dehydration (Deyrup 1964) and may also be a primitive gnathostome adaptation to the problem of maintaining a hypo-osmotic condition. The primitive gnathostome kidney therefore adapted, from its original divalent ion regulation function, to become an organic ion and body fluid volume regulator. Such an adaptation to deal with dehydration is a basic requirement of terrestrial organisms.

The presence of both purine and ornithine cycles is probably a primitive gnathostome condition and may have been present also in the extinct acanthodians and placoderms and in the extinct ancestors of the tetrapods. Actinopterygians have subsequently lost the ability to produce urea via the ornithine cycle. Upon reentry to the marine environment these fish show different adaptations to the problem of maintaining a low body fluid ionic concentration.

4*c*. *Physiology of the primitive osteichthyans*

Of the gnathostomes, it is widely agreed that the osteichthyans are most closely related to the tetrapods, although the particular subgroup most closely related is a topic of continuing debate (§2). All three osteichthyan subgroups, the actinopterygians, the dipnoans, and the crossopterygians, have members that show, or are thought to have shown, some degree of terrestrial adaptation. In one particular osteichthyan subgroup (possibly the osteolepid osteolepiforms) the degree of terrestrial adaptation led to the origin of the tetrapods.

As with the vertebrate and gnathostome groups as a whole, the osteichthyans appear to have been primitively a shallow marine group (Thomson 1969*a*, *b*, 1980*a*, *b*) (table 1). The earliest record is of possible actinopterygian material from shallow marine Upper Silurian sediments in Germany (Gross 1968).

Given that the osteichthyans were primitively hypo-osmotic with regard to sea water (Thomson 1980*b*), they would, like all gnathostomes, have experienced osmotic dehydration. They are thus likely to have had, as primitive characters: urea production via the ornithine cycle; urea retention involving active urea reabsorption in the kidney; and the production of a concentrated urine through water reabsorption in the kidney. These characters enabled them to cope with dehydration. This is an important preadaptation with respect to the invasion of the terrestrial environment.

All the osteichthyan subgroups are considered to have possessed, primitively, an air-breathing organ (Barrell 1916*b*; Romer 1966, pp. 46, 52). In the aquatic medium most fish achieve gaseous exchange through the skin and the gills, with the latter being most important (Randall 1970). The gills are specialized organs whose basic objectives are to bring oxygen-rich, carbon dioxide-poor, water into close proximity with blood in the opposite state, and to allow these gases to exchange so that carbon dioxide is removed from the blood and oxygen is replenished (Randall 1970). Without the support of water, the fine filamentous gills collapse and become useless as respiratory organs (Johansen 1970). Clearly, then, a new type of respiratory organ is required for air-breathing. The basic osteichthyan response to this problem appears to have been an inflatable sac or bladder with moist walls, across which oxygen and carbon dioxide could be exchanged (Johansen 1970). It has been suggested that air sacs or lungs might possibly be a basic gnathostome character. Denison (1941) has reported lung-like structures from the placoderm *Bothriolepis* and is supported in this interpretation by Romer (1966, p. 33). However, both Myers (1942) and Stensiö (1948) disagree with Denison's interpretation of antiarch soft-anatomy, and so there must be some doubt as to whether the presence of lungs is a gnathostome or osteichthyan character. The evidence for air-breathing in chondrichthyans (George 1953) is also in need of verification (Johansen 1970).

Air is a more efficient respiratory medium than water (Raven, this symposium). Internalization of the respiratory surfaces is an important method of reducing water loss (Raven, this symposium). Air-breathing probably evolved to supplement normal aquatic respiration in waters with low oxygen and high carbon dioxide partial pressures (Barrell 1916*b*; Johansen 1970). This is generally considered to have occurred in the fresh water environment, where the water bodies, being more superficial and part of a less stable system, have a greater chance of becoming fouled through dehydration (Westoll 1961; Romer 1966). Most of the extant air-breathing fish are associated with the tropical fresh water environment.

However, palaeontological evidence favours a marine origin of the osteichthyans, for which air-breathing is a basic character. This argues against the interpretation of lungs and air-breathing as having arisen in the fresh water environment. Air-breathing, and therefore evolution of lungs, may have evolved in the marine environment (Thomson 1980*a*). Packard (1974, 1976) has suggested that shallow, tropical marine seas are equally as liable to fouling as shallow fresh water bodies. Consideration of the Devonian atmosphere (§3*b*.i.) indicates that relatively low oxygen partial pressures existed during the early part of the Devonian. Anoxic conditions may have been relatively common in even the marine environment (usually considered to be more stable than the fluvial environment). The evolution of lungs in the osteichthyans may have been an adaptation to relatively anoxic shallow marine waters, and was a preadaptation for life on land, just as the ability to cope with dehydration (a gnathostome character) was also a preadaptation for the terrestrial environment.

4*d*. *Physiology of the actinopterygians*

The actinopterygians form the largest group of extant fish. After a marine origin much of their evolutionary history appears to have been associated with the fresh water environment, with some stocks reinvading the marine environment (Thomson 1980*b*). Extant actinopterygians include fresh water, mixed (euryhaline), and marine forms.

The main nitrogenous excretory product of the actinopterygians, freshwater or marine, is ammonia (Shaw 1960). The high solubility of ammonia leads to its elimination from the body occurring mainly across the gills (Smith 1929). For fresh water teleostean actinopterygians the elimination of ammonia across the gills appears to be linked to sodium ion uptake (Maetz & Garcia Romeu 1964). In fresh water ammonia is the ideal nitrogenous waste product, being highly soluble and exchangeable for sodium. Fresh water actinopterygians are hyperosmoregulators (Shaw 1960) (maintaining a body ionic concentration above that of the medium) and are subject to water influx by osmosis. There is no need for uraemia and the ornithine cycle has become degenerate (see §4*c*). Water influx is overcome by producing a very dilute urine (Shaw 1960). The kidneys are thus primarily body fluid volume regulators (a function they first assumed in the marine environment to retain water). The prime source of electrolytes is the diet.

Marine teleosts face the the same problem as all marine gnathostomes, that is osmotic dehydration. However, having been derived from fresh water fish that have lost the ability to develop uraemia (Thomson 1980*a*), they solve the problem in a very different manner. The kidney and its blood supply undergo structural changes (Hickman & Trump 1969) whose function is to reduce the rate of blood filtration, and thus, reduce the rate of urine production. Water loss is remedied by drinking salt water and then active secretion of the extra saline across the gills (Maetz 1971).

Some actinopterygians, however, do show a shift from ammoniotelism (ammonia production) to ureotelism (urea production), and do retain urea within the blood to quite high concentrations (Gordon *et al.* 1969; Gordon *et al.* 1970; Gordon *et al.* 1978; Ramaswamy & Reddy 1983). This shift in nitrogenous waste production occurs in some, but not all (Ramaswamy & Reddy 1983), actinopterygians that move to the terrestrial environment. Ureotelic actinopterygians do not produce urea by the ornithine cycle (Forster & Goldstein 1969). This is, therefore, not an expression of primitive gnathostome uraemia but a convergent actinopterygian specialization. Urea production and retention on land is a method of diminishing water loss. Ammonia elimination involves large volumes of water (Forster & Goldstein 1969) whereas urea elimination requires less water. Urea is also easier to store, so that excretion can be avoided until the animal returns to water.

Most actinopterygians have lost the primitive ability to use the air bladder as an accessory respiratory organ, and instead, use it as a buoyancy regulation organ, or lose it altogether (Steen 1970). Only in some primitive holostean and chondrostean actinopterygians is the air bladder used for respiration (Abdel Magid 1967; Abdel Magid *et al.* 1970; Johansen 1970; Johansen *et al.* 1970). Structurally the air bladder of these fish is considered to be primitive (Klika & Lelek 1967). Teleosts that use the terrestrial environment generally evolve new air-breathing organs, although in at least one case (*Arapaima*) the air bladder is involved (Johansen 1970). These secondary accessory air-breathing organs develop from the branchial, opercular, and pharyngeal cavities, and from the intestine.

4*e*. *Physiology of the Dipnoi*

The first records of the dipnoans are in marine sediments of Lower Devonian age (Jaeckel 1927; Denison 1968*a*, *b*). Dipnoans occur in the marine environment throughout the Devonian (Thomson 1969*b*, 1980*a*) and also occur in internal and external O.R.S. basins. The three extant genera are found in rivers and swamps in the tropical regions of South America, Africa and Australia (Thomson 1969*a*).

The lungfish are similar to the actinopterygians in that in normal fresh water conditions the main nitrogenous waste excreted is ammonia. However, the dipnoans have the full ornithine cycle and can produce urea via this pathway (Brown 1965; Brown *et al.* 1966; Janssens & Cohen 1966; Goldstein *et al.* 1967). *Protopterus* and *Lepidosiren* can both develop uraemia when water becomes scarce during the dry season. *Neoceratodus* appears to have lost this ability, probably because the rivers it inhabits rarely dry up sufficiently to warrant the retention of this adaptation (Spencer 1892). The level of ornithine cycle activity in *Neoceratodus* is only a hundredth that of *Protopterus* (Goldstein *et al.* 1967). The other dipnoans inhabit areas where anoxic conditions are more common (Carter & Beadle 1930).

At the onset of the dry season *Protopterus* burrows into soft mud and builds an aestivating chamber (Johnels & Svensson 1954). *Lepidosiren* does not aestivate to the same extent (Kerr 1898; Carter & Beadle 1930) because the waters it inhabits do not dry up so completely as those inhabited by the African lungfish. Dipnoan aestivation chambers have been reported from the Upper Devonian of North America (Woodrow & Fletcher 1968), showing that the dipnoans acquired the aestivating habit as a result of adaptation to the Devonian environment. Aestivation in the primitive actinopterygian *Amia* is thought to be a convergence (Thomson 1969*a*) as no ornithine cycle activity has been demonstrated.

During aestivation the level of urea in the body fluids rises to seven times the normal level (Thomson 1969*a*). This is achieved by stopping kidney function, which requires a general decrease in the metabolic rate (Smith 1930*a*, *b*). The primitive gnathostome and osteichthyan tolerance of high levels of urea in the body has been extended in the dipnoans. This type of dehydration adaptation, involving as it does the drastic lowering of the metabolic rate, is not a viable strategy for fully terrestrial animals. Aestivation is clearly an adaptation to a particular sort of aquatic environment, that is, one that regularly undergoes drastic changes in water level.

The lungs, a primitive character of the osteichthyans, are useful in such an environment to supplement the gills as the water becomes progressively more fouled (McMahon 1969, 1970). The lungs of *Protopterus* and *Lepidosiren* are paired, like those of the tetrapods (Bischoff 1840). The dipnoan breathing mechanism is adapted from the gill irrigation mechanism and bears a close resemblance to the method used by the amphibians in breathing (Thomson 1969*a*; McMahon 1969).

4*f*. *Physiology of the coelacanthiforms*

The coelacanthiforms occur in marine and fresh water situations throughout their history (Thomson 1969*a*). The extant coelacanth *Latimeria* is a fully marine animal. The lung has been converted into a gas-filled buoyancy organ as in the actinopterygians. The full complement of ornithine cycle enzymes is present (Brown & Brown 1967) and urea is present in the body fluid in high concentration (Pickford & Grant 1967; Lutz & Robertson 1971; Griffith *et al.* 1974). Without the urea the body fluid osmolarity is well below that of sea water (Lutz & Robertson 1971; Griffith *et al.* 1974). It appears then that the coelacanth has the primitive character of uraemia, associated with a low body fluid ionic concentration with respect to sea water.

4*g*. *Physiology of the Crossopterygii*

There is no direct evidence as to the physiological character of the extinct crossopterygians. However, Andrews & Westoll (1970) infer that *Eusthenopteron* had lungs on the basis of the shape of the tail. The evolution of the fins into tetrapod-like limbs has been interpreted not just in terms of the locomotory benefits but also in terms of the respiratory benefits (Thomson 1969*a*, 1971; Rackoff 1980). It has been suggested that the fore-limbs acted as struts which raised the anterior part of the body away from the substrate. This would have lessened the pressure on the thoracic cavity and the lungs. Air-breathing could then be conducted more efficiently. The extant mudskippers exhibit the same behaviour, using their anterior fins to support the anterior part of their body. The presence of crossopterygians in marine environments indicates that they may have been uraemic.

4*h*. *Physiology of the Amphibia*

Living amphibians exhibit a range of habitat preference, varying from fully aquatic to almost fully terrestrial (Thorson & Svihla 1943). Indeed, most amphibians show a change in habitat preference during their life-cycle, metamorphosing from fully aquatic larvae to adult forms which may be at least partly terrestrial. The earliest amphibians (Upper Devonian) are associated with external and internal O.R.S. sequences, some of which show near-marine conditions (Spjeldnaes 1982; Leonardi 1983). Most of the living amphibians are fresh water and terrestrial forms. In general, water of high osmolarity is toxic to amphibians (Przylecki 1922). Some brackish water forms are known, such as *Rana cancrivora* from mangrove swamps in Thailand (Gordon *et al.* 1961). Indeed, *R. cancrivora* has been reported to tolerate fully marine conditions (Schmidt-Nielsen 1983). McBean & Goldstein (1968) indicated that when *Xenopus* is injected with a hypersaline solution that this amphibian also develops uraemia. Both of these phenomena may be an expression of the primitive gnathostome ability to become uraemic.

In fresh water the main nitrogenous waste, as with fresh water teleosts and dipnoans, is ammonia (Deyrup 1964). Furthermore, the urine is hypo-osmotic and the kidney is a net water remover (Brown & Stein 1960). Electrolytes are supplied mainly by the diet. However, sodium and chloride can also be actively taken up directly from the surrounding water by the skin (Deyrup 1964). The kidney, bladder, and cloaca also actively remove ions from the urine.

In the aquatic larvae and adult forms respiration is by means of external gills and some aquatic forms parallel the teleost fish in using the lung as a hydrostatic organ.

Amphibians that show terrestrial habits either produce urea as the main nitrogenous waste or have the ability to switch to urea production when water becomes scarce (Balinsky *et al* 1961; Cragg *et al.* 1961; McBean & Goldstein 1968; Janssens & Cohen 1968). Urea production is mainly via the ornithine cycle (Forster & Goldstein 1969). The ability to switch to ureotelism in these forms accompanies the early phases of metamorphism (Brown & Cohen 1958, 1960). Production of urea in the terrestrial environment represents a method of decreasing the amount of water loss, as urea requires less water for elimination than ammonia (Forster & Goldstein 1969; Loveridge 1970; Shoemaker *et al.* 1972).

Terrestrial amphibians suffer greatly from water loss, more so than in comparison with other tetrapods (Thorson 1955). However, they can combat this not only by producing urea but also by having a high tolerance of water loss. Up to 60% of the body water can be lost in some amphibians (Thorson & Svihla 1943). The main route of water loss is via the skin (Jorgensen 1950). Some terrestrial amphibians have lowered the permeability of their skin (Cohen 1952). Also, when severe water loss is experienced excretion of urine halts and water reabsorption through the bladder increases (Sawyer & Schisgall 1956). Glomerular filtration rate also decreases. Amphibians which have suffered dehydration can rehydrate rapidly (Smith & Jackson 1931; Thorson & Svihla 1943). During periods of severe desiccation some amphibians follow the dipnoans and aestivate (Alexander & Bellerby 1938). Behavioural responses may be important in reducing water loss (Thorson & Svihla 1943; Cohen 1952).

It has been demonstrated for the air-breathing amphibians that the lungs are important in the replenishment of oxygen while the skin is involved in carbon dioxide removal (Krogh 1904). The lungs are ventilated by means of a buccal force mechanism, similar to that observed for the dipnoans (McMahon 1969).

Amphibians, while showing terrestrial adaptations, are dependent on water, even though in some cases much of the life may be lived away from water. The ability of some amphibians to develop uraemia might be the retention of a primitive state. The close association of some of the earliest amphibians with marine conditions may indicate that these animals too could develop uraemia. In terms of terrestrial adaptations the ability to produce urea represents a major method of diminishing water loss. This is supplemented by other procedures. The lungs are used for gaseous exchange, although the skin plays an important role as well.

4*i*. *Physiology of the Reptilia*

The reptiles are the first group of vertebrates that are generally thought to have been able to live away from water bodies (Romer 1966). Their main achievement is the evolution of the cleidoic egg, which removes the necessity of returning to water to reproduce. Reptiles generally produce a hypo-osmotic urine. Water loss is reduced in a similar manner to that seen in the terrestrial amphibians. That is, the urine undergoes post-renal modification by active removal of ions and relatively insoluble nitrogenous wastes are produced which require little water for their elimination. Water loss is further impeded in these vertebrates by the presence of a dry, scaly skin. This means that all gaseous exchange must occur by way of the lungs. A more efficient method of lung ventilation involving a thoracic force pump is encountered within this group.

5. CONCLUSIONS

Both the historical development of ideas about, and the physiological information related to, the evolution of the tetrapods have contributed to the widespread acceptance of their origin in fresh water, during the Devonian, from a crossopterygian stock. These fish are thought to have been forced onto land by the evaporation of the water bodies that they inhabited.

Timing of the evolution of the tetrapods is relatively well constrained by the fossil record of the osteichthyans and the amphibians. However, the traditional view of the environment from which the tetrapods evolved may be affected by the evidence of the fossil record. The record suggests the vertebrates were primitively marine and did not pass through an early fresh water phase, and, that the osteichthyans could primitively tolerate marine conditions. The ability to produce urea via the ornithine cycle, and to breathe air, may have been primitive gnathostome characters, which are also found in the tetrapods. They are important physiological adaptations to life on land, but they may have evolved in the marine aquatic environment.

Given that the Lower Devonian land plant cover was of low density, and perhaps restricted to the vicinity of water bodies, continental drainage systems may have been characterized by water chemistry that was more electrolyte-rich than that of the present. Such a situation may have been enhanced by seasonal salinity increases in tropical areas. Originally, the osteichthyan invasion of fresh water environments may have been a seasonal event, and perhaps was linked to the sexual cycle (Thomson 1980*a*). It is tempting to suggest that the osmoregulatory effect of some hormones (vasopressin, isotocin), which also have functions related to reproduction (Holmes & Ball 1974), may have played an important part in this process.

If so, an alternative scenario for tetrapod evolution becomes feasible. The ancestors of the tetrapods seasonally invaded the continental rivers and lakes during the dry season. At the onset of the wet season the waters became rapidly diluted and 'fresh', and presumably the essentially marine osteichthyans would have experienced difficulties in such conditions. These difficulties may have been compounded by the fact that large volumes of fresh water entering the marine basin would displace marine conditions (for example, the Orinoco River (Rodriguez 1975)). In this situation it is possible that some fish attempted to escape from the fresh water influx by going out onto land.

The traditional 'drying-up pool' hypothesis suggests that fish moved onto land during the dry season. At such a time they would have experienced maximal rates of dehydration (which would have been even worse on land than in the relict pools). However, if fish moved onto land during the wet season water loss via the body surface would be less. Evolution of the tetrapods may therefore have resulted from completely the opposite environmental conditions than was previously believed.

The extant dipnoans and some primitive actinopterygians inhabit environments that undergo seasonal desiccation. These fish, far from being driven out onto land, have evolved aestivation as a method of survival. Aestivation is developed to its fullest extent in the dipnoans, which acquired this ability during the Devonian. It is questionable whether such a mechanism, which involves the drastic reduction of the metabolic rate, has any general application for tetrapod evolution.

In conclusion, some of the basic vertebrate physiological adaptations to the terrestrial environment may have been, primitively, adaptations to the marine environment. Assuming that the fish generally thought to be the ancestors of the tetrapods were primitively marine, it may be necessary to reevaluate the environmental pressures that led to the evolution of terrestrial vertebrates. It is suggested here that the dipnoans and the ancestors of the amphibians developed the ability to survive terrestrial conditions in response to different pressures. The dipnoans probably evolved aestivation in response to evaporation of water bodies during the dry season. The ancestors of the amphibians might have left the aquatic environment in response to the dilution of water experienced during the wet season.

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References

Abdel Magid, A. M. 1967 Respiration of air by the primitive fish *Polypterus senegalus*. *Nature, Lond.* **215**, 1096–1097.

Abdel Magid, A. M., Vokac, Z. & Ahmed, N. 1970 Respiratory function of the swim-bladders of the primitive fish *Polypterus senegalus*. *J. exp. Biol.* **52**, 27–37.

Alexander, S. S. & Bellerby, C. W. 1938 Experimental studies on the sexual cycle of the South African clawed toad (*Xenopus laevis*). *J. exp. Biol.* **15**, 74–81.

Allen, J. R. L. 1962 Lower Old Red Sandstone of the southern British Isles: a facies resembling the Alpine Molasse. *Nature, Lond.* **193**, 1148–1150.

Allen, J. R. L. 1979 Old Red Sandstone facies in external basins, with reference to southern Britain. In *The Devonian System* (ed. M. R. House, C. T. Scrutton & M. G. Bassett). Special papers in palaeontology **23**, 65–80.

Allen, J. R. L. & Crowley, S. 1983 Lower Old Red Sandstone fluvial dispersal systems in the British Isles. *Trans. R. Soc. Edinb. Earth Sci.* **74**, 61–68.

Allen, J. R. L., Dineley, D. L. & Friend, P. F. 1968 Old Red Sandstone Basins of North America and northwest Europe. In *International Symposium on the Devonian System, Calgary, 1967, vol. 1* (ed. D. H. Oswald), pp. 69–98. Alberta Soc. Petrol. Geol.

Allen, J. R. L. & Friend, P. F. 1968 Deposition of the Catskill facies, Appalachian region: with notes on some other Old Red Sandstone basins. *Geol. Soc. Am. Spec. Pap.* **106**, 21–74.

Allen, J. R. K. & Williams, B. P. J. 1981 Sedimentology and stratigraphy of the Townsend Tuff Bed (Lower Old Red Sandstone) in South Wales and the Welsh Borders. *J. geol. Soc. Lond.* **138**, 15–29.

Allen, J. R. L. & Williams, B. P. J. 1982 The architecture of an alluvial suite: rocks between the Townsend Tuff and Pickard Bay Tuff Beds (early Devonian), southwest Wales. *Phil. Trans. R. Soc. Lond.* B **297**, 51–89.

Andrews, S. M. 1973 Interrelationships of crossopterygians. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), pp. 137–177. London and New York: Academic Press.

Andrews, S. M. & Westoll, T. S. 1970 The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans. R. Soc. Edinb.* **68**, 207–329.

Atz, J. W. 1952 Narial breathing in fishes and the evolution of internal nares. *Q. Rev. Biol.* **27**, 366–377.

Balinksy, J. B., Cragg, M. M. & Baldwin, E. 1961 The adaptation of amphibian waste nitrogen excretion to dehydration. *Comp. Biochem. Physiol.* **3**, 236–244.

Ball, I. 1967 The relative susceptibilities of some species of fresh-water fish to poisons. 1. Ammonia. *Water Res.* **1**, 767–775.

Banks, H. P. 1980 Floral assemblages in the Siluro-Devonian. In *Biostratigraphy of fossil plants: successional and palaeoecological analysis* (ed. D. Dilcher & T. N. Taylor). Pennsylvania: Dowden, Hutchinson, and Ross.

Barrell, J. 1913 The Upper Devonian delta of the Appalachian geosyncline: Pt. 1, The delta and its relations to the interior sea. *Am. J. Sci.* **36**, 429–472.

Barrell, J. 1914*a* The Upper Devonian delta of the Appalachian geosyncline: Pt. 2, Factors controlling the present limits of the strata. *Am. J. Sci.* **37**, 87–109.

Barrell, J. 1914*b* The Upper Devonian delta of the Appalachian geosyncline: Pt. 3, The relation of the delta to Appalachia. *Am. J. Sci.* **37**, 225–253.

Barrell, J. 1916*a* Dominantly fluviatile origin under seasonal rainfall of the Old Red Sandstone. *Bull. geol. Soc. Am.* **27**, 345–386.

Barrell, J. 1916*b* Influence of Silurian-Devonian climates on the rise of air-breathing vertebrates. *Bull. geol. Soc. Am.* **27**, 387–436.

Baur, G. 1896 The Stegocephali: a phylogenetic study. *Anat. Anz.*, **11**, 657–675.

Berkner, L. V. & Marshall, L. C. 1965 History of the major atmospheric components. *Proc. natn. Acad. Sci. U.S.A.* **53**, 1215–1226.

Bertmar, G. 1968 Lungfish phylogeny. In *Current problems of lower vertebrate phylogeny* (ed. T. Ørvig). *Proc. Nobel Symp.* **4**, 259–283. Stockholm: Almqvist and Wiksell.

Bischoff, T. L. W. von 1840 Description anatomique du *Lepidosiren paradoxa*. *Ann. Sci. nat.* **14**, 116–159.

Bjerring, H. C. 1967 Does a homology exist between the basicranial muscle and the polar cartilage? *Colloq. int. Cent. natn. Rech. Scient.* **163**, 223–267.

Bjerring, H. C. 1973 Relationships of coelacanthiforms. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles, & C. Patterson), pp. 179–205. London and New York: Academic Press.

Blieck, A., Galshani, F., Goujet, D., Hamdi, A., Janvier, P., Mark-Kurik, E. & Martin, M. 1980 A new vertebrate locality in the Eifelian of the Khush-Yeilagh Formation, Eastern Alborz, Iran. *Palaeovert.* **9**, 133–154.

Boucot, A. J. & Janis, C. 1983 Environment of the early Palaeozoic vertebrates. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **41**, 251–287.

Broom, R. 1913 On the origin of the cheiropterygium. *Bull. Am. Mus. nat. Hist.* **32**, 459–464.

Brown, F. & Stein, W. D. 1960 Balance of water, electrolytes and non-electrolytes. In *Comparative biochemistry*, vol. 2 (ed. M. Florkin & H. S. Mason), pp. 403–470. New York and London: Academic Press.

Brown, G. W., Jr 1965 Ornithine carbamyltransferase in the liver of the dipnoan *Protopterus aethiopicus*. *Science, Wash.* **149**, 1515.

Brown, G. W., Jr & Brown, S. G. 1967 Urea and its formation in the coelacanth liver. *Science, Wash.* **155**, 570–573.

Brown, G. W., Jr & Cohen, P. P. 1958 Biosynthesis of urea in metamorphosing tadpoles. In *The chemical basis of development* (ed. W. D. McElroy & B. Glass), pp. 495–513. Baltimore: John Hopkins Press.

Brown, G. W., Jr & Cohen, P. P. 1960 Activities of urea cycle enzymes in various higher and lower vertebrates. *Biochem. J.* **75**, 82–91.

Brown, G. W., Jr, James, J., Henderson, R. J., Thomas, W. N., Robinson, R. O., Thomson, A. L., Brown, E. & Brown, S. G. 1966 Uricolytic enzymes in liver of the dipnoan *Protopterus aethiopicus*. *Science, Wash.* **153**, 1653–1654.

Browne, M. A. E. 1980 The Upper Devonian and Lower Carboniferous (Dinantian) of the Firth of Tay, Scotland. *Rep. Inst. Geol. Sci.* **80**, 13.

Burton, J. D. & Wright, D. 1979 Sea-water and its evolution. In *The evolving Earth: chance, change, and challenge* (ed. P. H. Greenwood & L. Cocks). Cambridge: Cambridge University Press.

Campbell, K. S. W. & Bell, M. W. 1977 A primitive amphibian from the late Devonian of New South Wales. *Alcheringia* **1**, 369–381.

Carter, G. S. & Beadle, L. C. 1930 The fauna of the swamps of the Paraguayan Chaco in relation to its environment. 1. physico-chemical nature of the environment. *J. Linn. Soc. Lond.* (*Zool.*) **37**, 205–258.

Caster, K. E. 1938 A restudy of the tracks of *Paramphibius*. *J. Paleont.* **12**, 3–60.

Clayton, G., Graham, J. R., Higgs, K., Holland, C. H. & Naylor, D. 1979 Devonian rocks in Ireland: a review. *J. Earth Sci. R. Dubl. Soc.* **2**, 161–183.

Cloud, P. 1976 Beginnings of biospheric evolution and their biogeochemical consequences. *Palaeobiology* **2**, 351–387.

Cohen, N. W. 1952 Comparative rates of dehydration and hydration in some California salamanders. *Ecology* **33**, 462–479.

Cohen, P. P. & Brown, G. W., Jr 1960 Ammonia metabolism and urea biosynthesis. In *Comparative biochemistry*, vol. 2 (ed. M. Florkin & H. S. Mason), pp. 161–244. London and New York: Academic Press.

Cope, M. J. & Chaloner, W. G. 1980 Fossil charcoal as evidence of past atmospheric composition. *Nature, Lond.* **283**, 647–649.

Cowles, R. B. 1958 Additional notes on the origin of the tetrapods. *Evolution* **12**, 419–421.

Cox, C. B. 1967 Cutaneous respiration and the origin of the modern Amphibia. *Proc. Linn. Soc. Lond.* **138**, 37–48.

Cragg, M. M., Balinsky, J. B. & Baldwin, E. 1961 A comparative study of nitrogen excretion in some amphibians and reptiles. *Comp. Biochem. Physiol.* **3**, 227–235.

Croghan, P. C. 1983 Osmotic regulation and the evolution of brackish- and fresh-water faunas. *J. Geol. Soc. Lond.* **140**, 39–46.

Daget, J., Bauchot, R. & Arnoult, J. 1964 Développement du chondrochrane et des arcs aortiques chez *Polypterus senegalus* Cuvier. *Acta. zool., Stockh.* **46**, 201–244.

Darwin, C. 1977 *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life.* Harmondsworth: Penguin.

Dawson, W. B. 1863 *Air-breathers of the coal period.* Montreal: Dawson Bros.

Denison, R. H. 1941 The soft anatomy of *Bothriolepis*. *J. Paleont.* **15**, 553–561.

Denison, R. H. 1956 A review of the habitat of the earliest vertebrates. *Fieldiana: Geol.* **11**, 359–457.

Denison, R. H. 1968*a* The evolutionary significance of the earliest known lungfish, *Uranolophus*. In *Current problems in lower vertebrate phylogeny* (ed. T. Ørvig). *Proc. Nobel Symp.* **4**, 247–257. Stockholm: Almqvist and Wiksell.

Denison, R. H. 1968*b* Early Devonian lungfishes from Wyoming, Utah and Idaho. *Fieldiana. Geol.* **17**, 353–413.

Deyrup, I. J. 1964 Water balance and kidney. In *Physiology of the Amphibia*, vol. 1 (ed. J. A. Moore), pp. 251–328. London and New York: Academic Press.

Dineley, D. L. 1979 Tectonic setting of Devonian sedimentation. In *The Devonian System* (ed. M. R. House, C. T. Scrutton, & M. G. Bassett). Special papers in palaeontology **23**, 49–63. London: Palaeontological Association.

Dineley, D. L. & Williams, B. P. J. 1968 Sedimentation and palaeoecology of the Devonian Escuminac Formation and related strata, Escuminac Bay, Quebec. *Geol. Soc. Am. Spec. Pap.* **106**, 241–264.

Dollo, L. 1896 Sur la phylogenie des dipneustes. *Bull. Soc. belge. Geol. Paléont. Hydrol.* **2**, 79–128.

Donovan, R. N. 1980 Lacustrine cycles, fish ecology, and stratigraphic zonation in the Middle Devonian of Caithness. *Scott. J. Geol.* **16**, 35–50.

Eaton, T. H. 1959 The ancestory of the modern Amphibia; a review of the evidence. *Univ. Kansas Publ. Mus. nat. Hist.* **12**, 217–240.

Edwards, D. 1980*a* The early history of vascular plants based on late Silurian and Lower Devonian floras of the British Isles. In *The Caledonides of the British Isles – reviewed* (ed. B. T. Leake, A. L. Harris & C. H. Holland). London: Geol. Soc. Lond.

Edwards, D. 1980*b* Early land floras. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 55–85. London and New York: Academic Press.

Erben, H. K. 1964 Facies developments in the marine Devonian of the Old World. *Proc. Ussher Soc.* **1**, 82–118.

Fannin, N. G. T. 1970 The sedimentary environment of the Old Red Sandstone of western Orkney. Unpublished Ph.D. Thesis, University of Reading.

Florkin, M. & Duchateau, G. 1943 Les formes du systeme enzymatique de l'uricolyse et l'évolution du catabolisme purique chez les animaux. *Arch. Intern. Physiol.* **53**, 267–307.

Forey, P. 1984 L'origine des tetrapodes. *La Recherche* **15**, 476–487.

Forster, R. P. & Goldstein, L. 1966 Urea synthesis in the lungfish: relative importance of purine and ornithine cycle pathways. *Science. Wash.* **153**, 1650–1652.

Forster, R. P. & Goldstein, L. 1969 Formation of excretory products. In *Fish physiology, vol. 1* (ed. W. S. Hoar & D. J. Randall), pp. 313–350. London and New York: Academic Press.

Frakes, L. A. 1979 *Climates throughout geologic time.* Amsterdam: Elsevier.

Gans, C. & Dawson, W. R. 1976 Reptilian physiology: an overview. In *Biology of the Reptilia*, vol. 5A (ed. C. Gans & W. R. Dawson, pp. 1–17. London and New York: Academic Press.

Gardiner, B. G. 1963 Certain palaeoniscid fishes and the evolution of the snout in actinopterygians. *Bull. Br. Mus. nat. Hist.* (*Geol.*) **8**, 258–325.

Gardiner, B. G. 1967 Further notes on palaeoniscid fishes with a classification of the Chondrostei. *Bull. Br. Mus. nat. Hist.* (*Geol.*) **14**, 143–206.

Gardiner, B. G. 1973 Interrelationships of teleostomes. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), *Zool. J. Linn. Soc.* **53**, suppl. 1, pp. 105–135. London: Academic Press.

Gardiner, B. G. 1980 Tetrapod ancestry: a reappraisal. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 177–185. London and New York: Academic Press.

Gardiner, B. G. & Miles, R. S. 1975 Devonian fishes of the Gogo Formation, Western Australia. *Colloq. Int. Cent. natn. Rech. scient.* **218**, 73–79.

Gardiner, P. R. R. & MacCarthy, I. A. J. 1981 The late Palaeozoic evolution of Southern Ireland in the context of tectonic basins and their transatlantic significance. In *Geology of the North Atlantic borderlands* (ed. J. W. Kerr & J. Fergusson). *Can. Soc. Petrol. Geol. Mem.* **7**, 683–725.

Geikie, A. 1879 On the Old Red Sandstone of western Europe. *Trans. R. Soc. Edinb.* **28**, 345–452.

George, J. C. 1953 Observations on the air-breathing habit in *Chiloscyllium. J. Univ. Bombay* (n.s.) **21**, 80.

Godwin-Austin, R. 1856 On the possible extension of the Coal Measures beneath the south-eastern part of England. *Q. Jl geol. Soc. Lond.* **12**, 38–73.

Goldring, R. 1962 The bathyall lull: Upper Devonian and Lower Carboniferous sedimentation in the Variscan geosyncline. In *Some aspects of the Variscan fold belt* (ed. K. Coe), pp. 75–91. Manchester: Manchester University Press.

Goldring, R. & Langenstrassen, F. 1979 Open shelf and near-shore clastic facies in the Devonian. In *The Devonian System* (ed. M. R. House, C. T. Scrutton & M. G. Bassett). *Spec. pap. palaeont.* **23**, 81–97. London: Palaeontological Association.

Goldstein, L. & Forster, R. P. 1970 Nitrogen metabolism in fishes. In *Comparative biochemistry* (ed. J. W. Campbell), pp. 496–518. London and New York: Academic Press.

Goldstein, L., Harvey-Dewitt, S. & Forster, R. P. 1973 Activities of ornithine–urea cycle enzymes and of trimethylamine oxidase in the coelacanth, *Latimeria chalumnae. Comp. Biochem. Physiol.* **44** B, 357–362.

Goldstein, L., Janssens, P. A. & Forster, R. P. 1967 The lungfish *Neoceratodus forsteri*: activities of the ornithine-urea cycle and enzymes. *Science, Wash.* **157**, 316–317.

Goodchild, J. G. 1904 The older Deuterozoic rocks of North Britain. *Geol. Mag.* (5 December) **1**, 591–602.

Goodrich, E. S. 1908 On the scales of fish, living and extinct, and their importance in classification. *Proc. zool. Soc. Lond.* **1907**, 751–774.

Goodrich, E. S. 1928 *Polypterus* a palaeoniscid? *Palaeobiologica* **1**, 87–92.

Gordon, M. S., Boetius, I., Evans, D. H., McCarthy, R. & Oglesby, L. C. 1969 Aspects of the physiology of terrestrial life in amphibious fishes. 1. The mudskipper *Periophthalmus sobrinus. J. exp. Biol.* **50**, 141–149.

Gordon, M. S., Fischer, S. & Tarifeno, E. 1970 Aspects of the physiology of terrestrial life in amphibious fishes. 2. The Chilean clingfish *Sicyases sanguineus. J. exp. Biol.* **53**, 559–572.

Gordon, M. S., Ng, W. W. & Yip, A. Y. 1978 Aspects of the physiology of terrestrial life in amphibious fishes. 3. The Chinese mudskipper *Periphthalmus cantonensis J. exp. Biol.* **72**, 57–75.

Gordon, M. S., Schmidt-Nielsen, K. & Kelly, H. M. 1961 Osmotic regulation in the crab-eating frog (*Rana cancrivora*). *J. exp. Biol.* **38**, 659–678.

Goudie, A. & Wilkinson, J. 1977 *The warm desert environment.* Cambridge: Cambridge University Press.

Graham, J. R. 1983 Analysis of the Upper Devonian Munster Basin, an example of a fluvial distributary system. In *Modern and ancient fluvial systems* (ed. J. D. Collinson & J. Lewin). *Spec. Publ. Intern. Ass. Sedim.* **6**, 473–483.

Gregory, W. K. 1911 The limbs of *Eryops* and the origin of paired limbs from fins. *Science, Wash.* **33**, 508–509.

Gregory, W. K. 1915 Present status of the problem of the origin of the Tetrapoda, with special reference to the skull and paired limbs. *Ann. N.Y. Acad. Sci.* **26**, 317–383.

Griffith, R. W., Ummings, B. L., Grant, B. F., Pang, R. K. T. & Pickford, G. E. 1974 Serum composition of the coelacanth *Latimeria chalumnae* Smith. *J. exp. Biol.* **187**, 87–102.

Gross, W. 1968 Fragliche Actinopterygier-Schuppen aus dem Silur Gotlands. *Lethaia* **1**, 184–218.

Gunter, G. 1956 Origin of the tetrapod limb. *Science. Wash.* **123**, 495–496.

Gunther, A. C. L. G. 1872 Description of *Ceratodus*, a genus of ganoid fishes recently discovered in rivers of Queensland, Australia. *Phil. Trans. R. Soc. Lond.* **161**, 511–571.

Hall, J. 1843 *Natural history of New York*, Part 4. Geology comprising the Survey of the Fourth Geological District. New York.

Harland, W. B. 1961 An outline of the structural history of Spitzbergen. In *Geology of the Arctic*, vol. 1 (ed. G. O. Raasch), pp. 68–132. Toronto: University of Toronto Press.

Heckel, P. H. & Witzke, B. J. 1979 Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators. In *The Devonian System* (ed. M. R. House, C. T. Scrutton & M. G. Bassett). Special papers in palaeontology **23**, pp. 99–123.

Hickman, C. P. & Trump, B. I. 1969 The kidney. In *Fish physiology* (ed. W. S. Hoar & D. J. Randall), pp. 91–239. London and New York: Academic Press.

Hill, D. 1968 Devonian of eastern Australia. In *International Symposium on the Devonian System, Calgary, 1967*, vol. 1 (ed. D. H. Oswald), pp. 613–630. Alberta Soc. Petrol. Geol.

Hills, E. S. 1933 On a primitive dipnoan from the Middle Devonian rocks of New South Wales. *Ann. Mag. nat. Hist.* **11**, 634–643.

Holland, C. H. 1979 Augmentation and decay of the Old Red Sandstone continent: evidence from Ireland. *Palaeogogr. Palaeoclim. Palaeoecol.* **27**, 59–66.

Holmes, R. L. & Ball, J. N. 1974 *The pituitary gland, a comparative account.* Cambridge: Cambridge University Press.

House, M. R. 1975*a* Facies and time in Devonian tropical areas. *Proc. Yorks. geol. Soc.* **40**, 233–288.

House, M. R. 1975*b* Faunas and time in the marine Devonian. *Proc. Yorks. geol. Soc.* **40**, 459–490.

Huggins, A. K., Skutsch, G. & Baldwin, E. 1969 Ornithine-urea cycle enzymes in teleostean fish. *Comp. Biochem. Physiol.* **22** B, 587–602.

Hughes, G. M. & Shelton, G. 1962 Respiratory mechanisms and their nervous control in fish. *Adv. comp. Physiol. Biochem.* **1**, 275–364.

Inger, R. E. 1957 Ecological aspects of the origin of tetrapods. *Evolution* **11**, 373–376.

Jaeckel, O. 1927 Der Kopf der Wirbelthiere. *Ergebn. Anat. EntuGesch.* **27**, 815–974.

Janssens, P. A. 1964 The metabolism of the aestivating African lungfish. *Comp. Biochem Physiol.* **11**, 105–117.

Janssens, P. A. & Cohen, P. P. 1966 Ornithine-urea cycle enzymes in the African lungfish *Protopterus aethiopicus*. *Science. Wash.* **152**, 358–359.

Janssens, P. A. & Cohen, P. P. 1968 Nitrogen metabolism in the African lungfish. *Comp. Biochem. Physiol.* **24**, 879–886.

Janvier, P. 1977 Vertébrés dévoniens de deux nouveaux gisements du Moyen-Orient. Le probleme des relations intercontinentales au Paleozoique moyen vu a la lumière de la paleobiogeographie des Rhipidistiens osteolepiformes et des premiers tetrapodes. *Ann. Soc. Geol. Nord* **97**, 373–382.

Janvier, P. 1980 Osteolepid remains from the Devonian of the Middle East, with particular reference to the endoskeletal shoulder girdle. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 223–254. London and New York: Academic Press.

Jarvik, E. 1942 On the structure of snout of crossopterygians and lower gnathostomes in general. *Zool. Biddr. Upps.* **21**, 235–675.

Jarvik, E. 1944*a* On the dermal bones, sensory canals, and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. save-soderberghi* Jarvik. *K. Svenska. VetenskAkad. Handl.* **21**, 1–48.

Jarvik, E. 1944*b* On the exoskeletal shoulder-girdle of teleostomian fishes, with special reference to *Eusthenopteron foordi* Whiteaves. *K. Svenska. VetenskAkad. Handl.* **21**, 1–37.

Jarvik, E. 1948 On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *K. Svenska. VetenskAkad. Handl.* **25**, 1–301.

Jarvik, E. 1949 On the Middle Devonian crossopterygians from the Hornelen Field in Western Norway. *Arbok Univ. Bergen* 1948 (Naturvr.), pp. 1–48.

Jarvik, E. 1950*a* Middle Devonian vertebrates from Canning Land and Wegeners Halvo (East Greenland). 2. Crossopterygii. *Medd. om Gronland* **96**, 1–132.

Jarvik, E. 1950*b* Note on the Middle Devonian crossopterygians from the eastern part of Gauss Halvo, East Greenland. With an attempt at a correlation of the Upper Old Red Sandstone of East Greenland with the marine sequence. *Medd. om Gronland* **149**, 1–20.

Jarvik, E. 1950*c* On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. *K. Svenska. VetenskAkad. Handl.* **2**, 1–35.

Jarvik, E. 1952) On the fish-like tail in the ichthyostegid stegocephalians with descriptions of a new stegocephalian and a new crossopterygian from the Upper Devonian of East Greenland. *Medd. om Gronland* **114**, 1–90.

Jarvik, E. 1954 On the visceral skeleton in *Eusthenopteron* with a discussion of the parashenoid and palatoquadrate in fishes. *K. Svenska. VetenskAkad. Handl.* **5**, 1–104.

Jarvik, E. 1955*a* The oldest tetrapods and their forerunners. *Scient. Mon., N.Y.* **80**, 141–154.

Jarvik, E. 1955*b* Ichthyostegalia. In *Traité de paléontologie*, 5 (ed. J. Piveteau), pp. 53–66. Paris: Masson.

Jarvik, E. 1961 Devonian vertebrates. In *Geology of the Arctic*, 1 (ed. G. O. Raasch), pp. 197–204. Toronto: University of Toronto Press.

Jarvik, E. 1964 Specialisations in early vertebrates. *Annls Soc. r. zool. Belg.* **94**, 1–95.

Jarvik, E. 1966 Remarks on the structure of the snout in *Megalichthys* and certain other rhipidistid crossopterygians. *Ark. Zool.* **19**, 41–98.

Jarvik, E. 1967 On the structure of the lower jaw in dipnoans: with a description of an early Devonian dipnoan from Canada, *Melanognathus canadensis* gen. et sp.nov. In *Fossil vertebrates* (ed. C. Patterson & P. H. Greenwood), *J. Linn. Soc., Zool.* **47**, 155–183.

Jarvik, E. 1968*a* The systematic position of the Dipnoi. In *Current problems of lower vertebrate phylogeny* (ed. T. Ørvig). *Proc. Nobel Symp.* **4**, pp. 223–245. Stockholm: Almqvist and Wiksell.

Jarvik, E. 1968*b* Aspects of vertebrate phylogeny. In *Current problems of lower vertebrate phylogeny* (ed. T. Ørvig). *Proc. Nobel Symp.* **4**, pp. 497–527. Stockholm: Almqvist and Wiksell.

Jarvik, E. 1972 Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n. sp. *Medd. om Gronland* **187**, 1–295.

Jarvik, E. 1975 On the saccus endolymphaticus and adjacent structures in osteolepiforms, anurans, and urodeles. *Colloq. int. Cent. natn. Rech. scient.* **218**, 191–211.

Jarvik, E. 1980 *Basic structure and evolution of vertebrates*, vol. 1, pp. 575. London and New York: Academic Press.

Jarvik, E. 1981 Lungfishes, tetrapods, paleontology, and plesiomorphy; Review. *Syst. Zool.* **30**, 378–384.

Jessen, H. 1966 Struniiformes. In *Traité de paléontologie*, vol. 4. (ed. J. Piveteau), pp. 387–398. Paris: Masson.

Jessen, H. 1967 The position of the Struniiformes (*Strunius* and *Onychodus*) among crossopterygians. *Colloq. int. Cent. natn. Rech. scient.* **163**, 173–180.

Jessen, H. 1973 Interrelationships of actinopterygians and brachiopterygians: evidence from pectoral anatomy. In *Interrelationships of fishes* (ed. P. H. Greenwood, R. S. Miles & C. Patterson), pp. 227–232. London and New York: Academic Press.

Jessen, H. 1975 A new choanate fish *Powichthys thorsteinssoni* n.g., n.sp. from the early Lower Devonian of the Canadian Arctic Archipelago. *Colloq. Cent. natn. Rech. scient.* **218**, 213–222.

Johansen, K. 1970 Air-breathing in fishes. In *Fish physiology*, 4 (ed. W. S. Hoar and D. J. Randall), pp. 361–411. London and New York: Academic Press.

Johansen, K., Hansen, D. & Lenfant, D. 1970 Respiration in a primitive air breather, *Amia calva*. *Respn. Physiol.* **9**, 162–174.

Johnels, A. G. & Svenson, G. S. O. 1954 On the biology of *Protopterus annectens* (OWEN). *Ark. Zool.* **7**, 131–164.

Johnstone, M. H., Jones, P. J., Koop, W. J., Roberts, J., Gilbert-Tomlinson, J., Veevers, J. & Wells, A. T. 1968 Devonian of western and central Australia. In *International symposium of the Devonian System, Calgary, 1967, vol. 1* (ed. D. H. Oswald), pp. 599–612. Calgary: Alberta Soc. Petrol. Geol.

Jorgensen, C. B. 1950 The amphibian water economy. *Acta Physiol. Scand.* Suppl. **78**, 1–79.

Jukes, J. B. 1866 On the subdivisions of the Carboniferous in central Ireland. *Jl. r. Geol. Soc. Ire.* (n.s.) **12**, 1–12.

Kelly, J. 1856 Researches among the Palaeozoic rocks of Ireland, with a view to determine the limits of the Old Red Sandstone, and its relation to inferior rocks. *J. geol. Soc. Dubl.* **7**, 115–146.

Kelly, J. 1857 On the subdivision of the Carboniferous of Ireland. *J. geol. Soc. Dubl.* **7**, 222–266.

Kent, D. M. 1968 Devonian of Manitoba and Sasketchewan. In *International symposium on the Devonian System, Calgary, 1967, vol. 1* (ed. D. H. Oswald), pp. 781–801. Calgary: Alberta Soc. Petrol. Geol.

Kinahan, G. H. 1880 The Old Red Sandstone (so-called) of Ireland in its relations to the underlying and overlying strata. *J. r. Geol. Soc. Ire.* (n.s.) **5**, 106–113.

Klika, E. & Lelek, A. 1967 A contribution to the study of the lungs of the *Protopterus annectens* and *Polypterus senegalensis*. *Folia Morphol.* **15**, 168–175.

Krebs, W. 1979 Devonian basinal facies. In *The Devonian System* (ed. M. R. House, C. T. Scrutton and M. G. Bassett). Special papers in Palaeontology **23**, 125–139. London: Palaeontological Association.

Krefft, J. L. G. 1870 Description of a gigantic amphibian allied to the genus *Lepidosiren*, from the Vide Bay district, Queensland (*Ceratodus forsteri*). *Proc. zool. Soc. Lond.* 1870, 221–224.

Krogh, A. 1904 Some experiments on the cutaneous respiration of vertebrate animals. *Archs Skand. Physiol.* **16**, 348–357.

Leeder, M. R. 1974 The origin of the Northumberland Basin. *Scott. J. Geol.* **10**, 283–296.

Leeder, M. R. 1976 Sedimentary facies and the origins of basin subsidence along the northern margin of the supposed Hercynian Ocean. *Tectonophysics* **36**, 167–179.

Lehman, J.-P. 1966 Actinopterygii, Dipnoi, Crossopterygii, Brachiopterygii. In *Traité de paléontologie*, 4 (ed. J. Piveteau), pp. 1–387, 398–420.

Leonardi, G. 1983 *Notopus petri* nov.gen., nov.sp.: une empreinte d'amphibien du Dévonien au Parana (Bresil). *Geobios* **16**, 233–239.

Livingstone, D. A. 1963 Chemical composition of rivers and lakes. *U.S. geol. Surv. prof. Pap.* **440** G, pp. 64.

Loveridge, J. P. 1970 Observations on nitrogenous excretion and water relations of *Chiromantis xerampelina* (Amphibia, Anura). *Arnoldia* (*natn. Mus. Rhodesia*) **5** (1), 1–6.

Lutz, P. L. & Robertson, J. D. 1975 Osmotic constituents of the coelacanth *Latimeria chalumnae* Smith. *Biol. Bull. mar. biol. Lab.*, *Woods Hole* **141**, 553–560.

Maetz, J. 1971 Fish gills: mechanisms of salt transfer in fresh-water and sea-water. *Phil. Trans. R. Soc. Lond.* B **262**, 209–249.

Maetz, J. & Garcia Romeu, F. 1964 The mechanism of sodium and chloride uptake by the gills of a fresh-water fish *Carassius auratus*. 3. Evidence for NH_4^+/Na^+ and NCO_3^-/Cl^- exchanges. *J. gen. Physiol.* **47**, 1209–1227.

Marsh, O. C. 1896 Amphibian footprints from the Devonian. *Am. J. Sci.* (ser. 4) **2**, 374–375.

Marshall, E. K., Jr. & Smith, H. W. 1930 The glomerular development of the vertebrate kidney in relation to habitat. *Biol. Bull. mar. biol. Lab.*, *Woods Hole* **59**, 135–153.

Mason, B. 1958 *Principles of geochemistry*. 2nd edn. New York: John Wiley and Sons.

McBean, R. L. & Goldstein, L. 1968 Ornithine-urea cycle activity in *Xenopus laevis*: adaptation in saline. *Science*, *Wash.* **157**, 931–932.

McMahon, B. R. 1969 A functional analysis of the aquatic and aerial respiratory movements of an African lungfish *Protopterus aethiopicus*, with reference to the evolution of the lung-ventilation mechanism in vertebrates. *J. exp. Biol.* **51**, 271–285.

McMahon, B. R. 1970 The relative efficiency of gaseous exchange across the lungs and gills of an African lungfish *Protopterus aethiopicus*. *J. exp. Biol.* **52**, 1–15.

Miles, R. S. 1975 The relationships of the Dipnoi. *Colloq. int. Cent. natn. Rech. scient.* **218**, 133–148.

Miles, R. S. 1977 Dipnoan (lungfish) skulls and the relationships of the group: a study based on new species from the Devonian of Australia. *J. Linn. Soc.* (*Zool.*) **61**, 1–328.

Miller, H. 1889 *The Old Red Sandstone, or new walks in an old field*. Edinburgh: Nimmo, Hay and Mitchell.

Millot, J. & Anthony, J. 1958 Anatomie de *Latimeria chalumnae*, vol. 1. Paris: Cent. natn. Rech. scient.

Millot, J. & Anthony, J. 1965 Anatomie de *Latimeria chalumnae*, vol. 2. Paris. Cent. natn. Rech. scient.

Millot, J., Anthony, J. & Robineau, D. 1978 Anatomie de *Latimeria chalumnae*, vol. 3. Paris: Cent. natn. Rech. scient.

Miman, Z. & Xiaobo, Y. 1981 A new crossopterygian *Youngolepis praecursor*, gen.et sp.nov., from Lower Devonian of East Yunnan, China. *Sci. Sin.* **24**, 89–97.

Moy-Thomas, J. A. & Miles, R. S. 1971 *Palaeozoic fishes*, pp. 259. London: Chapman and Hall.

Murchison, R. I. & de Verneuil, E. 1841 On the stratified deposits which occupy the northern and central regions of Russia. *Rep. Brit. Ass. Advmt. Sci.* 1840 (2) Glasgow, pp. 105–110.

Myers, G. S. 1942 The 'lungs of *Bothriolepis*'. *Stanford Ichthyol. Bull.* **2**, 134–136.

Needham, J. 1938 Nitrogen excretion in relation to environment. *Biol. Rev.* **13**, 224–251.

Nelson, G. J. 1969 Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bull. Am. Mus. nat. Hist.* **141**, 475–552.

Nilsen, T. H. 1973 Devonian (Old Red Sandstone) sedimentation and tectonics of Norway. In *Arctic Geology* (ed. M. G. Pitcher), *Mem. Am. Ass. Petrol. Geol.* **19**, 471–484.

Norris, A. W. 1968 Devonian of northern Yukon territory and adjacent district of Mackenzie. In *International symposium of the Devonian System, Calgary, 1967, vol. 1* (ed. D. H. Oswald), pp. 753–780. Calgary: Alberta Soc. Petrol. Geol.

Nyebelin, O. 1976 On the so-called postspiracular bone in crossopterygians, brachiopterygians, and actinopterygians. *Acta R. Soc. Sci. Litt. Gothenburg* **10**, 5–31.

Olsen, E. C. 1961 Jaw mechanisms in rhipidistians, amphibians, and reptiles. *Am. Zool.* **1**, 205–215.

Orton, G. 1954 Original adaptive significance of the tetrapod limb. *Science*, *Wash.* **120**, 1042–1043.

Ørvig, T. 1961 New finds of acanthodians, arthrodires, crossopterygians, ganoids, and dipnoans in the upper Middle Devonian Calcareous Flags (Oberer Plattenkalk) of the Bergisch Gladbach-Paffrath Trough, Part 2. *Palaont. Z.* **35**, 10–27.

Packard, G. C. 1974 The evolution of air-breathing in Palaeozoic gnathostome fishes. *Evolution* **28**, 320–325.

Packard, G. C. 1976 Devonian amphibians: did they excrete carbon dioxide via skin, gills, or lungs? *Evolution* **30**, 270–280.

Panchen, A. L. 1967 The nostrils of choanate fishes and early tetrapods. *Biol. Rev.* **42**, 374–420.

Panchen, A. L. 1977 The origin and early evolution of tetrapod vertebrae. In *Problems in vertebrate evolution* (ed. S. M. Andrews, R. S. Miles & A. D. Walker), pp. 289–318. London and New York: Academic Press.

Paproth, E., Conil, R., Bless, M. J. M., Boonen, P., Bouckaert, J., Carpentier, N., Coen, M., Delacambre, B., Deprijk, D., Deuzon, S., Dreesen, R., Graessens, E., Hance, L., Hennebert, M., Hibo, M., Hahn, G., Hahn, R., Hislaire, O., Kasig, W., Laloux, M., Lauwers, A., Lees, A., Lys, M., Op de Beek, K., Overlau, P., Pirlet, H., Poty, H., Ramsbottom, W., Sreel, M., Swenner, R., Thorez, J., Vanguestaine, M., Vansteenwinkel, M. & Vieslet, J. L. 1983 Bio- and lithostratigraphic subdivisions of the Dinantian of Belgium, a review. *Ann. soc. Geol. Belg.* **106**, 185–239.

Parsons, T. S. & Williams, E. E. 1962 The teeth of Amphibia and their relation to amphibian phylogeny. *J. Morph.* **110**, 375–390.

Parsons, T. S. & Williams, E. E. 1963 Relationships of modern Amphibia: a re-examination. *Q. Rev. Boil.* **38**, 26–53.

Patterson, C. 1980 Origin of tetrapods: historical introduction to the problem. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 159–175. London and New York: Academic Press.

Pautard, F. G. E. 1961 Calcium, phosphorus, and the origin of backbones. *New Scient.* **12**, 364–366.

Pennington, J. J. 1975 The geology of the Argyll field. In *Petroleum and the continental shelf of north-west Europe, vol. 1, Geology* (ed. A. W. Woodland), pp. 285–291. Barking, Essex: Applied Science Publishers Ltd.

Pickford, G. E. & Grant, F. B. 1967 Serum osmolarity in the coelacanth, *Latimeria chalumnae*: urea retention and ion regulation. *Science, Wash.* **155**, 568–570.

Pollard, H. B. 1891 On the anatomy and phylogenetic position of *Polypterus*. *Anat. Anz.* **6**, 338–344.

Predtechensky, N. N. & Krasnov, I. 1968 Devonian of intermontane depressions in the Altai-Sayan region. In *International Symposium on the Devonian System, Calgary, 1967, vol. 1* (ed. D. H. Oswald), pp. 463–472. Calgary: Alberta Soc. Petrol. Geol.

Przylecki, S. J. 1922 L'echange de l'eau et des sels chez les amphibiens. *Arch. Intern. Physiol.* **19**, 148–159.

Rabein, A. 1956 Zur Stratigraphie und Facies des Ober-Devons in der Waldecker Haußtmulde. *Abh. hess. Landesamt. Bodenforsch.* **16**, 1–83.

Rackoff, J. S. 1980 The origin of the tetrapod limb and the ancestry of the tetrapods. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 1–10. London and New York: Academic Press.

Ramaswamy, M. & Reddy, T. G. 1983 Ammonia and urea excretion in three species of air-breathing fish subjected to aerial exposure. *Proc. Indian Acad. Sci.* (*Anim. Sci.*) **92**, 293–297.

Randall, D. J. 1970 Gas exchange in fish. In *Fish physiology*, vol. 4 (ed. W. S. Hoar & D. J. Randall), pp. 253–292. London and New York: Academic Press.

Read, L. J. 1971 The presence of high ornithine-cycle enzyme activity in the teleost *Ospanustau*. *Comp. Biochem. Physiol.* **39B**, 409–413.

Robertson, J. D. 1957 The habitat of the early vertebrates. *Biol. Rev.* **32**, 156–187.

Robertson, J. D. 1963 Osmoregulation and ionic regulation of cells and tissues. In *The biology of* Myxine (ed. A. Brodel & R. Fange), pp. 513–515. Oslo: Scandinavian University Press.

Rodriguez, G. 1975 Some aspects of ecology of tropical estuaries. In *Tropical ecological systems* (ed. F. B. Golley & E. Medina), *Ecol. Stud.* **11**, New York: Springer.

Romer, A. S. 1956 The early evolution of land vertebrates. *Proc. Am. phil. Soc.* **100**, 157–167.

Romer, A. S. 1958 Tetrapod limbs and early tetrapod life. *Evolution* **12**, 365–369.

Romer, A. S. 1966 *Vertebrate paleontology*. 3rd ed. Chicago: Chicago University Press.

Romer, A. S. & Grove, B. H. 1935 Environment of the early vertebrates. *Am. Mid. Nat.* **16**, 805–856.

Rudwick, M. J. S. 1979 The Devonian: a system born from conflict. In *The Devonian System*, (ed. M. R. House, C. T. Scrutton & M. G. Bassett). Special papers in palaeontology **23**, 9–21.

Save-Soderbergh, G. 1932 Preliminary note on Devonian stegocephalians from East Greenland. *Medd. om Gronland* **94**, 1–107.

Säve-Söderbergh, G. 1933 The dermal bones of the head and the lateral line system in *Osteolepis macrolepidotus* AG. With remarks on the terminology of the lateral line system and on the dermal bones of certain other crossopterygians. *Nova Acta R. Soc. Scient. upsal.* **9**, 1–129.

Säve-Söderbergh, G. 1941 Notes on the dermal bones of the head in *Osteolepis macrolepidotus* AG. and the interpretation of the lateral line system in certain primitive vertebrates. *Zool. Bidrag. Uppsala* **20**, 523–541.

Sawyer, W. H. & Schisgall, R. M 1956 Increased permeability of the frog bladder to water in response to dehydration and neurohypophyseal extracts. *Am. J. Physiol.* **187**, 312–314.

Schaeffer, B. 1965 The evolution of concepts related to the origin of the Amphibia. *Syst. Zool.* **14**, 115–118.

Schaeffer, B. 1968 The origin and basic radiation of the Osteichthyes. In *Current problems of lower vertebrate phylogeny* (ed. T. Ørvig). *Proc. Nobel Symp.* **4**, 207–222. Stockholm: Almqvist and Wiksell.

Schmidt, H. 1926 Schwellen- und Beckenfacies im ostrheinischen Palaozoikum. *Z. dt. geol. Ges.* **77**, 226–234.

Schmidt-Nielsen, K. 1983 *Animal physiology: adaptation and environment*, 3rd edn, pp. 619. Cambridge: Cambridge University Press.

Schooler, J. M., Goldstein, L., Hartman, S. C. & Forster, R. P., 1966 Pathways of urea synthesis in the elasmobranch *Squalus acanthias*. *Comp. Biochem. Physiol.* **18**, 271–281.

Schultze, H.-P. 1968 Palaeoniscoidea – Schuppen aus dem Unterdevon Australiens und Kanadas und aus dem Mitteldevons Spitzbergens. *Bull. Brit. Mus.* (*Nat. Hist.*) *Geol.* **16**, 341–368.

Schultze, H.-P. 1977 The origin of the tetrapod limb within the rhipidistian fishes. In *Major patterns in vertebrate evolution* (ed. M. K. Hecht, P. C. Goody & B. M. Hecht), pp. 517–540. New York: Plenum.

Shaw, J. 1960 The mechanisms of osmoregulation. In *Comparative biochemistry*, vol. 2 (ed. M. Florkin & H. S. Mason), pp. 471–518. London and New York: Academic Press.

Shoemaker, V. H., Balding, D., Ruibal, R. & McClanahan, L. L., Jr 1972 Uricotelism and low evaporative water loss in a South American frog. *Science, Wash.* **175**, 1018–1020.

Smith, H. W. 1929 The excretion of ammonia and urea by the gills of fish. *J. biol. Chem.* **81**, 727–742.

Smith, H. W. 1930*a* Metabolism of the lungfish *Protopterus aethiopicus* and on the evolution from water to land environments. *Ecology* **12**, 164–181.

Smith, H. W. 1930*b* Metabolism of the lung-fish *Protopterus aethiopicus*. *J. biol. Chem.* **88**, 97–130.

Smith, H. W. 1932 Water regulation and its evolution in the fishes. *Q. Rev. Biol.* **7**, 1–26.

Smith, H. W. 1936 The retention and physiological role of urea in the Elasmobranchii. *Biol. Rev.* **11**, 49–82.

Smith, H. W. 1953 *From fish to philosopher*. Boston: Little, Brown and Co.

Smith, J. L. B. 1939 A living fish of Mesozoic type. *Nature, Lond.* **143**, 455–456.

Smith, V. D. E. & Jackson, D. M. 1931 The changes during desiccation and rehydration in the body and organs of the leopard frog (*Rana pipiens*). *Biol. Bull. mar. biol. Lab., Woods Hole* **60**, 80–93.

Spencer, W. B. 1892 Notes on the habits of *Ceratodus forsteri*. *Proc. R. Soc. Vict.* **4**, 81–84.

Spjeldnaes, N. 1982 Palaeoecology of *Ichthyostega* and the origin of the terrestrial vertebrates. *Proc. int. Meeting 'Palaeontology, Essential of Historical Geology'* 1, Venice, 1981, 323–343.

Steen, J. B. 1970 The swim bladder as a hydrostatic organ. In *Fish physiology*, vol. 4 (ed. W. S. Hoar & D. J. Randall), pp. 413–443. London and New York: Academic Press.

Stensiö, E. A. 1948 On the Placodermi of the Upper Devonian of East Greenland. 2. Antiarchi: subfamily Bothriolepinae. With an attempt at a revision of the previously described species of that family. *Palaeozool. Gronland.* **2**, 1–622.

Szarski, H. 1963 The origin of the Amphibia. *Q. Rev. Biol.* **37**, 189–291.

Szarski, H. 1967 Sarcopterygii and the origin of the tetrapods. In *Major patterns in vertebrate evolution* (ed. M. K. Hecht, P. C. Goody & B. M. Hecht), pp. 517–540. New York: Plenum.

Thomson, J. M. & Keith, T. E. C. 1984 Chloride and fluoride in waters draining the Valley of the Ten Thousand Smokes, Alaska. *Geol. Soc. America, Abstr. with Programs* **16**, 336–337.

Thomson, K. S. 1966 The evolution of the middle ear in the rhipidistian–amphibian transition. *Am. Zool.* **6**, 379–397.

Thomson, K. S. 1968 A critical review of the diphyletic theory of rhipidistian–amphibian relationships. In *Current problems in lower vertebrate phylogeny* (ed. T. Ørvig). *Proc. Nobel Symp.* **4**, 285–305. Stockholm: Almqvist and Widsell.

Thomson, K. S. 1969*a* The biology of the lobe-finned fishes. *Biol. Rev.* **44**, 91–154.

Thomson, K. S. 1969*b* The environment and distribution of Palaeozoic sarcopterygian fishes. *Am. J. Sci.* **267**, 457–464.

Thomson, K. S. 1971 Adaptation and evolution of early fishes. *Q. Rev. Bio.* **46**, 139–166.

Thomson, K. S. 1972 New evidence on the evolution of the paired fins of Rhipidistia and the origin of the tetrapod limb, with a description of a new genus of Osteolepidae. *Postilla* **157**, 1–7.

Thomson, K. S. 1980*a* The ecology of Devonian lobe-finned fishes. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 1–10. London and New York: Academic Press.

Thomson, K. S. 1980*b* Environmental factors in the evolution of vertebrate endocrine systems. In *Evolution of vertebrate endocrine systems* (ed. P. K. T. Pang & E. Epple), *Grad. Stud. Texas Tech. Univ.* **21**, 17–32. Lubbock, Texas: Texas Tech. Press.

Thomson, K. S. & Campbell, K. S. W. 1971 The structure and relationships of the primitive Devonian lungfish *Dipnorhynchus sussmilchi* (Etheridge). *Bull. Peabody Mus. nat. Hist.* **38**, 1–109.

Thorson, T. 1955 The relationship of water economy to terrestrialism in amphibians. *Ecology* **36**, 100–116.

Thorson, T. & Svihla, A. 1943 Correlation of the habitats of amphibians with their ability to survive the loss of body water. *Ecology* **24**, 374–381.

Tunbridge, I. P. 1981 Old Red Sandstone sedimentation – an example from the Brownstones (highest Lower Old Red Sandstone) of south central Wales. *Geo. J.* **16**, 111–124.

Vorobyeva, E. I. 1975 Some peculiarities in the evolution of the rhipidistian fishes. *Colloq. intern. Cent. natn. Rech. scient.* **218**, 223–230.

Vorobyeva, E. I. 1977 Morphology and features of evolution of crossopterygian fishes. *Trudy Paleont. Inst.* **163**, 1–239. (In Russian.)

Warren, J. W. & Wakefield, N. A. 1972 Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature, Lond.* **238**, 469–470.

Watson, D. M. S. 1926 Croonian lecture – the evolution and origin of the Amphibia. *Phil. Trans. R. Soc. Lond.* B **214**, 189–257.

Watson, D. M. S. 1935 Fossil fishes of the Orcadian Old Red Sandstone. In *The geology of the Orkneys* (ed. G. V. Wilson, W. Edwards, J. Knox, R. C. B. Jones & J. V. Stephens), Mem. geol. Surv. U.K., pp. 157–169.

Westoll, T. S. 1936 On the structure of the dermal ethmoid shield of *Osteolepis*. *Geol. Mag.* **73**, 157–171.

Westoll, T. S. 1937*a* On the cheek-bones in teleostome fishes. *J. Anat.* **71**, 362–382.

Westoll, T. S. 1937*b* The Old Red Sandstone fishes of the north of Scotland, particularly of Orkney and Shetland. *Proc. Geol. Ass.* **48**, 13–45.

Westoll, T. S. 1938 Ancestory of the tetrapods. *Nature, Lond.* **141**, 127.

Westoll, T. S. 1943 The origin of the tetrapods. *Biol. Rev.* **18**, 78–98.

Westoll, T. S. 1961 A crucial stage in vertebrate evolution: fish to land animal. *Proc. R. Instn. Gt Br.* **38**, 600–618.

Westoll, T. S. 1980 Prologue: problems of tetrapod origin. In *The terrestrial environment and the origin of land vertebrates* (ed. A. L. Panchen), pp. 1–10. London and New York: Academic Press.

White, E. I. 1958 Original environment of the cranites. In *Studies on fossil vertebrates* (ed. T. S. Westoll), pp. 212–234. London: The Athlone Press.

Wiley, E. O. 1979 Ventral gill arch muscles and the interrelationships of gnathostomes, with a new classification of the Vertebrata. *Zool. J. Linn. Soc.* **67**, 149–179.

Willard, B. 1935 Chemung tracks and trails form Pennsylvania. *J. Paleont.* **9**, 43–56.

Woodrow, D. L. & Fletcher, F. W. 1968 Devonian dipnoan aestivation cylinders. *Geol. Soc. Am. Spec. Pap.* (Abstract) **121**, 383–384.

Woodrow, D. L., Fletcher, F. W. & Ahrnsbrack, W. F. 1973 Paleogeography and paleoclimate of the deposition sites of the Devonian Catskill and Old Red facies. *Bull. Geol. Soc. Am.* **84**, 3051–3064.

Woodward, A. S. 1891 *Catalogue of the Fossil Fishes in the British Museum* (*Natural History*), *Part 2*. London: British Museum (Natural History).

Ziegler, P. A. 1981 Evolution of sedimentary basins in north-west Europe. In *Petroleum geology of the continental shelf of north-west Europe* (ed. L. V. Illing & G. D. Hobson), pp. 3–39. London: Institute of Petroleum.

Ziegler, P. A. 1982 *Geological atlas of western and central Europe*. The Hague, Netherlands: Shell Internationale.

Discussion

W. T. W. Potts (*Department of Biological Sciences, University of Lancaster, Lancaster, LA*1 4*YQ*, *U.K.*). The environmental differences between sea water and air that has been discussed are so great that a direct transition must be almost impossible. Attention should be directed towards intermediate environments which might ease the transition. These include the intertidal zone, interstitial environments and fresh waters. Deoxygenated brackish and fresh waters are particularly important because the development of accessory lungs makes it possible for aquatic animals to exploit these rich environments. With the exception of the bottom of the Black Sea and a hollow in the sea bed north of Venezuela the sea is always oxygenated but eutrophic fresh waters are often deoxygenated. Both the vertebrates and the pulmonate snails developed lungs while aquatic, as the lung fishes and the basommatophoran snails such as *Lymnea* and *Planorbis* still are. If the eurypterids possessed both gill books and accessory lungs they would parallel their contemporaries the rhipidistian fish.

The case for the fresh water origin of most fish is greatly strengthened if their evolution is compared with that of other phyla. Primitively marine animals are isoosmotic with sea water, their blood containing about 3% sodium chloride. Their tissues contain much lower concentrations of ions but high concentrations of free amino acids whose major function appears to be to make up the osmotic pressure. Many marine invertebrates, such as the crustaceans and molluscs, possess an excretory organ which produces urine by ultrafiltration followed by resorption, analogous to the vertebrate glomerulus and proximal convoluted tubule. In all these respects Myxine is primitively marine. Fresh water animals are faced with water inflow by osmosis and salt loss. To compensate most fresh water animals have reduced their blood concentration to about 1% sodium chloride or less, have lowered the concentration inside the cells by almost eliminating the free amino acids and have reduced losses of salt in the urine by adding a salt resorbing section to the kidney tubule. The fresh water fish closely resembles the fresh water crayfish or the fresh water snails and several other invertebrate groups in all these respects. The secondary convoluted tubule undoubtedly originated as an adaptation to fresh water.

Several groups of fresh water invertebrates have returned to the sea or to saline water for a second time but all have kept a blood concentration close to that of their fresh water ancestors, although this requires special adaptation to excrete salt similar to those found in all marine fish except the Myxinoids. The low blood concentration, the low concentration of free amino acids in the tissues and the presence of a secondary convoluted tubule in the kidney, all point to a fresh water origin of fish other than the myxinoids. Even the cells that excrete salt in the gills of marine fish show clear evidence of derivation from cells which originally absorbed sodium from the medium. In addition, there can be no doubt that the air bladder of the boney fish developed from a lung, not the other way around.

Nitrogen biochemistry follows the availability of water. Many terrestrial animals have independently adopted uric acid synthesis as a means of conserving water, for example the reptiles, the insects and land snails. The retention of high concentration of urea in both blood and tissues, by the frog *Rana cancrivora* when in saline conditions is clearly an adaptation to high salinity by a fresh water animal with low concentrations of ions in the blood and low concentrations of amino acids in the tissues. The presence of identical mechanisms in the selachians, the coelacanths and the holocephalans (rat fish) suggests that they too are of fresh water origin.

Finally, the blood concentrations provide a clue to the route taken onto dry land. Once on land the blood concentration is no longer subject to strong selection. Terrestrial isopods, wood lice, have blood concentrations equivalent to 60 or 70% sea water, strongly suggesting that they came through the intertidal zone. Reptiles, birds and mammals all have blood concentrations equivalent to about 1% sodium chloride like their ancestral fresh water fish. Scorpions in contrast have high blood concentrations, equivalent to about 60% sea water and have high concentrations of free amino acids in the tissues. Centipedes have blood concentrations about twice as high as millipedes suggesting that the latter were derived from fresh water ancestors.

A. R. Milner (*Department of Zoology, Birkbeck College, Malet Street, London WC1 7HX, U.K.*) A considerable reassessment of the relationship of tetrapods to choanate fish is taking place at present. One recently published hypothesis argues that the Dipnoi (lungfish) are the sister-group of tetrapods, hence more closely related to tetrapods than are the osteolepiform fish. A second hypothesis, currently being prepared for publication by Dr A. L. Panchen and Dr T. R. Smithson at the University of Newcastle upon Tyne, argues that the osteolepidid fish are the sister-group, not the ancestors, of tetrapods but are more closely related to tetrapods than the lungfish. Both dipnoans and osteolepidids are present in the Lower Devonian so that a common consequence of these otherwise conflicting hypotheses is that the earliest distinct stem-tetrapods must also have been present in the Lower Devonian (400 Ma), although they may still have been more fish-like than tetrapod-like. Given this perspective, the life-style of one genus of tetrapod (*Ichthyostega*) on the Devonian–Carboniferous boundary (360 Ma) is not necessarily very relevant to the origin of tetrapods. Consider the historical precedents. In the first half of the 19th century when the earliest tetrapods known were Mesozoic marine reptiles and crocodiles, these were invoked by some early evolutionists as representing the pathway from water to land. After the discovery of Carboniferous amphibian fossils in the Coal Measures in the 1860s, it was believed that the vertebrates had moved onto land via a tropical coal-swamp environment. After the discovery of the ichthyostegids in the uppermost Devonian of Greenland in the early 1930s, it was first believed that the redbeds in which they were preserved indicated a periodically arid environment and the origin of tetrapods was thereafter believed to have occurred in such an environment. Now it is believed that the red beds merely represent a fluctuating water table which may have had some proximity to sea water, and it is suggested that the origin of tetrapods may have been coastal. It seems to me that, at any given time, the fossils that appear to represent the earliest tetrapods have carried or are carrying a greater ecological and physiological burden than they should be expected to bear, considering the evident poverty of the fossil record of early tetrapods.

A. A. Bray. As Professor Potts points out, most extant fish have (probably as primitive features) physiological adaptations which might be expected in fresh water fish (for example, low body fluid ionic concentrations). However, the most primitive living fish, the hagfish, are clearly a marine group. The elasmobranchs also appear to be principally a marine group, although some members of this group have invaded the fresh water environment.

Furthermore, the earliest known osteichthyans occur in marine deposits, and this group as a whole shows connections with the marine environment throughout its history, although, again, some members have also invaded the fresh water environment. Neither the vertebrates as whole, nor the gnathostomes or osteichthyans in particular, has a fossil record consonant with an early fresh water phase. Indeed, vertebrate palaeontologists (Gross 1951; Denison 1956; White 1958; Halstead, this symposium) have long argued that the vertebrates evolved in marine conditions, and that they invaded non-marine environments only during the latter part of the Silurian.

Potts suggests that we should turn our attention to the intermediate environments. However, it is not always an easy matter to distinguish fully marine and brackish environments. Environmental analysis for the Siluro-Devonian is dependent largely upon sedimentological interpretations of sequences of strata. However, as John Allen pointed out in his presentation at this meeting: 'sedimentology cannot offer an unequivocal interpretation of the environments'.

As I have stated in the paper, there is a noticeable absence of delta models for sedimentary sequences within the Devonian, precisely the sort of setting that involves transitional environments. Whether this absence is a true reflection of the types of environments present during the Siluro-Devonian is a matter that should be pursued.

Furthermore, postulating an early fresh water phase in the evolutionary history of the vertebrates relies on an *a priori* assumption that non-marine water chemistry at this time was comparable to that of the present. For several reasons outlined in the paper this assumption may be incorrect. Lower Palaeozoic and early Devonian non-marine drainage systems may only have been, at best, seasonally 'fresh' water.

Andrew Milner has highlighted the current debate on the topic of fish–tetrapod interrelationships. The work of Smithson and Panchen may provide a sounder basis for the assumption of a close relationship between the osteolepiforms and the tetrapods. In this, the true value of their work will be in denying a close relationship between the dipnoans and the tetrapods, and also, in refuting the possibility that the tetrapods were derived polyphyletically.

The possibility that the osteolepidids are the osteolepiforms most closely related to the tetrapods has already been advanced, on the basis of the paired fin morphology, by Thomson (1972) and Rackoff (1980). Their conclusions are based on studies of *Sterropterygion* and *Rhizodopsis*. The former is placed with the osteolepidids mainly on the basis of the scale morphology and presence of an external layer of cosmine. *Rhizodopsis* has undergone a somewhat chequered systematic history, but current opinions favour this fish being an osteolepidid (Andrews & Westoll 1970; Rackoff 1980). Both of these fish have pectoral fins with 'screw-like' humeri, similar to those of tetrapods. Is this type of humerus like that of the Lower and Middle Devonian osteolepidids (for example, *Osteolepis*). If not it is possible that the osteolepidids, as currently recognized, are a paraphyletic group. The tetrapods were the closest relatives (sister group) of *Sterropterygion*-like osteolepidids. *Sterropterygion* is known from the Famennian, while the oldest *Rhizodopsis* has been reported from very uppermost Devonian sediments.

Vorobyeva (1975, 1977) has indicated that it is the panderichthyids that are the closest osteolepiform relatives of the tetrapods. This family includes *Elpistostege*, which Westoll (1938, 1943) has long believed to be a prototetrapod. Work currently in preparation by H.-P. Schultze and M. Arsenault supports the suggestion of Vorobyeva and Westoll. *Elpistostege* is a Frasnian aged form.

Clearly then, both of these hypotheses support a 'late' origin of the tetrapods (upper Middle or Upper Devonian). The ecology of Upper Devonian amphibians is therefore particularly pertinent.

With regard to the historical aspects of tetrapod evolution, these are dealt with at greater length in the paper. The arid environment hypothesis of tetrapod origin did not result from the discovery of ichthyostegids (of which two genera are recognized) in O.R.S. type sediments. This idea pre-dates the discovery of the ichthyostegids and has its roots in the history of the discovery of Devonian fish faunas, and the interpretation of the environment that O.R.S. sediments represented. Presence of Upper Devonian amphibians in these sediments lent support to the 'arid' hypothesis.

Postulation of a marine origin for the tetrapods is not dependent upon analysis of the few, rather poor records of the very earliest amphibians, but rather, the more extensive and much better known fossil fish record.

References

Andrews, S. M. & Westoll, T. S. 1970 The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Trans. R. Soc. Edinb.* **68**, 207–329.

Denison, R. H. 1956 A review of the habitat of the earliest vertebrates. *Fieldiana*: *Geology* **11**, 359–457.

Gross, W. 1951 Die paläontologische und stratigraphische Bedeutung der Wirbeltierfaunen des Old Reds und der marinen altpaläozoichshen Schichten. *Abh. dtsch. Akad. Wiss. Berl., Math.-Nat. Kl.* 1949 (**1**), 1–130.

Rackoff, J. S. 1980 The origin of the tetrapod limb and the ancestry of the tetrapods. In *The terrestrial environment and the origin of land vertebrate* (ed. A. L. Panchen), pp. 1–10. London and New York: Academic Press.

Thomson 1972 New evidence on the evolution of the paired fins of Rhipdistia and the origin of the tetrapod limb, with a description of a new genus of Osteolepidae. *Postilla* **157**, 1–7.

Vorobyeva, E. I. 1975 Some peculiarities in the evolution of the rhipidistian fishes. *Colloq. intern. Cent. natn. Rech. scient.* **218**, 223–230.

Vorobyeva, E. I. 1977 Morphology and features of evolution of crossopterygian fishes. *Trudy Paleont. Inst.* **163**, 1–239. (In Russian.)

Westoll, T. S. 1938 Ancestory of the tetrapods. *Nature, Lond.* **141**, 127.

Westoll, T. S. 1943 The origin of the tetrapods. *Biol. Rev.* **18**, 78–98.

White, E. I. 1958 Original environment of the cranites. In *Studies on fossil vertebrates* (ed. T. S. Westoll), pp. 212–234. London: The Athlone Press.