PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Vertebrate Invasion of Fresh Water

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Phil. Trans. R. Soc. Lond. B 1985 **309**, 243-258
doi: 10.1098/rstb.1985.0085

Phil. Trans. R. Soc. Lond. B **309**, 243–258 (1985)   [243]
Printed in Great Britain

The vertebrate invasion of fresh water

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The origin and early evolution of the vertebrates took place in exclusively marine conditions. From the Middle Cambrian chordate *Pikaia*, through the Upper Cambrian, Ordovician and early Silurian records, there is little evidence of non-marine vertebrate faunas. With the progressive closing of the Iapetus Ocean, there developed from Wenlock times possible brackish vertebrate faunas, dominated by thelodonts, anaspids and cephalaspids, suggesting the formation of a Palaeozoic equivalent of the Tertiary Sarmatic Sea, also noted for the evolution of endemic brackish and fresh water faunas. The end of Silurian (Přídolían) times was marked by the suturing of the Old Red Sandstone continent and the establishment of the vertebrates, thelodonts, heterostracans and cephalaspids in fluvial régimes.

The amphiaspid heterostracans colonized non-marine habitats during Lochkovian or Pragian times near the northwestern margins of Angaraland. A separate invasion of fresh waters was accomplished during Wenlock or Ludlovian times by the galeaspids, a group of cephalaspidomorphs, known only from South China.

The colonization of fresh waters marked perhaps one of the most important advances in the evolution of the physiology of the vertebrates. The jawless vertebrates, microphagous detrital feeders, heralded the invasion of predators, the benthonic placoderms and nectonic acanthodian fishes.

1. INTRODUCTION

The original environment of the vertebrates has been a subject of debate over the years. The general view, long held by zoologists, was that the vertebrates arose in the sea; it was taken as axiomatic in view of all the non-vertebrate chordates being exclusively marine. The discovery of worn fragments of the bony armour from the Middle Ordovician Harding Sandstone of Colorado led Walcott (1892) to conclude that they were derived from fish that had inhabited fresh waters and on death had been transported downstream so that their disintegrated remains came to be preserved in this littoral deposit. The water-worn nature of many of the fragments was attributed to transport over considerable distances. From this moment, there was 'geological' evidence in favour of the fresh water origin of the vertebrates. There was an immediate response on the part of the zoological community which suddenly discovered that a number of basic physical features of the vertebrates could be attributed to the prevertebrates acquiring them as a means of colonizing fresh waters. The naive views of Chamberlin (1900) that the streamlined shape of fish was a direct response to the flow of running waters led to the more sophisticated views pioneered by Homer Smith (1932, 1936, 1953) that the glomerular kidney evolved as a means of combating the problem of osmosis as the vertebrates invaded fresh waters. That the glomerular kidney has this capability cannot be gainsaid and Homer Smith's advocacy was seemingly persuasive in the debate. In an attempt to resolve the issue Romer & Grove (1935) re-examined the geological evidence and came to the conclusion that, at least in North America, the localities of early vertebrates appeared to indicate fresh waters. The geological evidence and the zoological seemed to point in the same direction. Matters thus stood until Gross (1951) produced a comprehensive compilation of all known Silurian and Devonian vertebrate localities. Gross accepted the interpretation of the Harding Sandstone material as of fresh water origin but concluded that 64% of all Silurian species were marine but in the succeeding Lower Devonian only 19% were marine although in the Middle and Upper Devonian this had risen to 35.5% and 49% respectively. When the agnathan (jawless) vertebrates alone are considered, all the Ordovician material occurred in marine rocks, there were 60% marine species in the Silurian, falling to a mere 8% in the Lower Devonian. Gross only dealt with data available up to 1942, yet even so, it pointed to the major transition from marine to fresh water having occurred roughly around the Siluro-Devonian boundary. In spite of all later discoveries, the evidence has simply strengthened the thesis that emerged from Gross's compilation.

There was a clear discrepancy between the conclusions of Romer & Grove (1935) and Gross (1951) with regard to the Upper Silurian localities in North America, all of which were claimed to be non-marine by the former. This conflict of evidence was discussed by Romer (1955) who concluded 'I see no reason for serious consideration of a marine history for the early vertebrates'. In 1955 White wrote a further review of this topic, which was published in 1958, coming down firmly on the side of an original marine origin; two further reviews by Denison (1956), which was a comprehensive survey, and by Robertson (1957) which paid particular attention to the physiological aspects of the problem, further supported the marine origin. This same conclusion has been re-emphasized by Boucot & Janis' (1983) recent study.

Critical in the physiological considerations was the nature of the kidney in the myxinoids. It was demonstrated by Robertson (1954, 1957, 1963; see also Hardisty 1979) that the existence of the glomerular kidney could not be attributed to any fresh water phase in the history of this most primitive of living vertebrates. The hagfish are exclusively marine and are iso-osmotic with sea water, the body fluid ionic concentration being similar to sea water. The glomerular kidney filters by means of the hydrostatic pressure in the capillaries and is not primarily concerned with osmotic gradients. It seems that it was mainly concerned with regulation of ionic levels. This is suggested by the fact that it is capable of maintaining appropriate water balances both in fresh water fish that have to eliminate water that enters osomotically, and also serves to deal with the opposite problem of fish with lower ionic concentrations than in surrounding sea water, that experience loss of water to the surrounding medium. Apart from the hagfish, all aquatic vertebrates have a lower ionic concentration than that observed in sea water and this has been attributed to the jawed fish in particular, as well as the lampreys, having passed through a fresh water phase at sometime during their evolutionary history. The palaeontological and geological evidence suggests that this was not the case with the cartilaginous fish, the sharks and their allies, which seem to have been exclusively marine (with the exception of the Carboniferous pleuracanth sharks). Bray (this symposium) has proposed that there was a physiological advantange in reducing ionic levels *per se* and that this together with the appropriate regulatory mechanisms for ensuring the concentration of salts, such as urea, is likely to have been accomplished in the marine environment, thus obviating the need to postulate any fresh water evolutionary stage in the cartilaginous fish, it being recognized, nevertheless, that the marine teleosts have a well-documented history of a fresh water phase in their evolution. The real point, however, is that the mechanisms that deal with water balance do not insist on a fresh water environment for their initial development. Both the geological evidence and the zoological evidence point unequivocally to an original marine habitat of the vertebrates. A detailed palaeoecological study of the Harding Sandstone (Spjeldnaes 1979) has concluded that although the environment was marine, there was probably fluctuation in the salinity. The evidence is just as firm that the early vertebrates were established in fresh waters by Lower Devonian, Lochkovian and Pragian times.

2. Old Red Continent (Laurussia)

The classic area of the Siluro-Devonian transition is in the Welsh Borderland and the nature of the sedimentary record there has been the subject of intense research, in particular by Allen (1962, 1964, 1974*a*, *b*, 1979, 1983, this symposium) and Allen & Williams (1983). It is only from a detailed analysis of the sediments that the conditions of deposition can be determined with any degree of exactitude. The problem as far as the vertebrates were concerned was that there seemed to be insufficient criteria to determine their provenance. King (1934) compared the inferred conditions in the Welsh Borderland to the partly enclosed Yellow Sea and Gulf of Pohai and he believed that the vertebrates inhabited such brackish conditions. In contrast White (1946, 1950) was of the opinion that the vertebrate faunas represented spasmodic introductions into brackish tidal waters from fresh waters. The basic data was in agreement but their interpretations were entirely divergent. The matter was resolved by the collaborative studies of Allen & Tarlo (1963) which demonstrated that during the Ludlow the vertebrates (cyathaspid heterostracans, thelodonts and acanthodians) occurred in marine sediments, in the Downtonian (Přídolían) in offshore marine sand shoals and later in intertidal sands and muds which contained a cephalaspid *Thyestes–Hemicyclaspis* fauna. Within this intertidal group there were fluviatile sediments with a different heterostracan-dominated fauna. In the succeeding Dittonian (Lochkovian, Pragian) the vertebrates, dominated by pteraspids, other heterostracans and cornuate cephalaspids, were preserved in exclusively fluviatile systems (see figure 1). Although there was evidence of transport downstream, with minor exceptions, the vertebrate remains were preserved in sediments representing the environments that the vertebrates inhabited during life (but see comments by White & Toombs (1983)). A detailed sedimentological and faunal study of a single fluvial locality was subsequently given by Allen *et al.* (1968).

The pattern that emerged was of late Silurian marine vertebrates, heterostracans and acanthodian fishes, followed by a sequence of intertidal brackish sediments dominated by cephalaspids and finally the establishment of alluvial faunas dominated by heterostracans, in particular pteraspids, but also cyathaspids, which were typically found in marine sediments in the Ludlovian and early Přídolían (Downtonian). This suggested a movement of the cyathaspids from marine to fresh water. The thelodonts that characterized the marine Silurian also seem to have become firmly established in fluvial régimes during the Lochkovian (Dittonian).

The sequence of facies with their associated vertebrates documented the transition from marine to fresh water, with particular genera being represented in marine and brackish conditions, other in brackish and fresh water and yet others in marine and fresh water but not brackish. The acanthodians and thelodonts were present in all environments but with the fluvial forms there seemed to be a significant change in the thelodont genera. Turner (1973) recognized the existence of several distinct Silurian thelodont faunas: a Scottish–Norwegian–Siberian

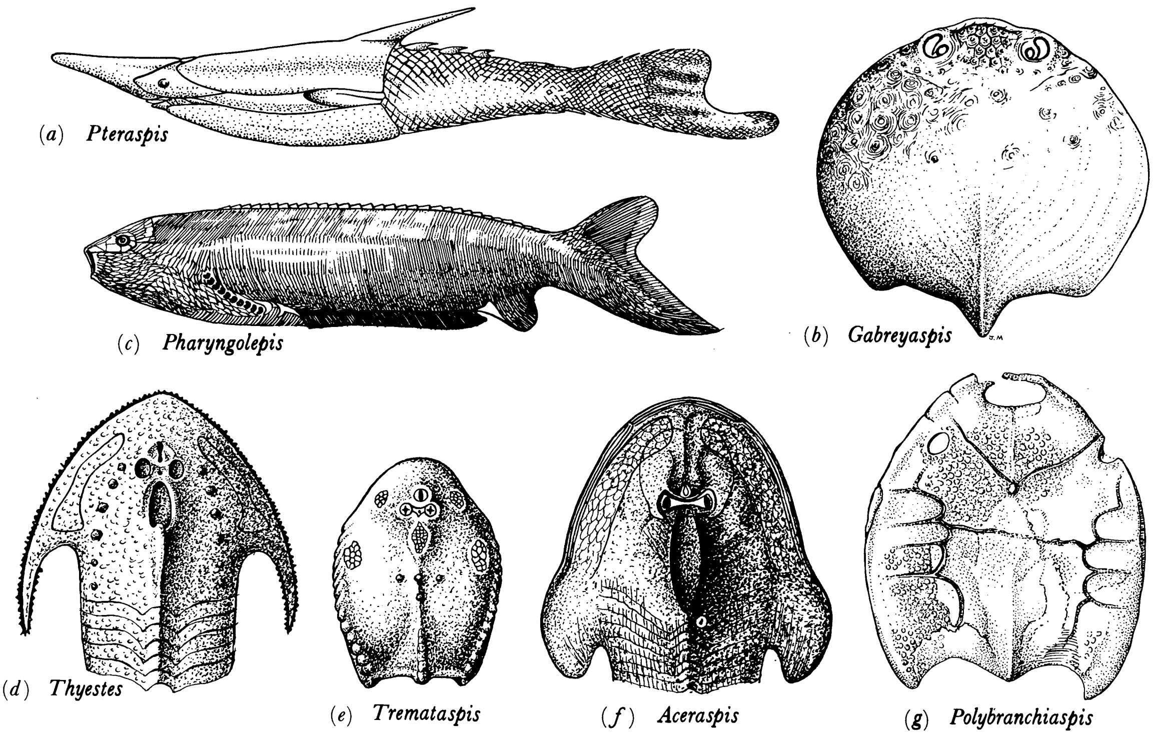

FIGURE 1. Representative agnathans. (*a*), (*b*) Heterostracans; (*a*) pteraspid; (*b*)amphiaspid; (*c*) anaspid; (*d*)–(*f*) cephalaspids; (*d*) thyestid; (*e*) trematаspid; (*f*) ateleaspid; (*g*) galeaspid.

Logania fauna, *Thelodus parvidens* of the Welsh Borderland and New Brunswick and Nova Scotia, and a *Thelodus schmidti-laevis* fauna of the Baltic and Canadian Arctic. Later Turner & Tarling (1982) recognized four distinct thelodont faunas: an Anglo-Welsh, eastern North America and Greenland, a Scottish–Norwegian, a Baltic–western Russia–Canadian Arctic and finally the Angaran or Siberian.

This pattern disappeared at the end of Přídolían (Downtonian) times with the extinction of thelodonts from Siberia but with the establishment of the cosmopolitan *Turinia–Apalolepis–Nikolivia* fauna, which extended to Iran, Thailand, Australia, China and Antarctica. Thelodonts have now been discovered in South America (Janvier, this symposium). The cosmopolitan thelodont fauna of the Lower Devonian occurs in both non-marine and marine sediments indicating a derived tolerance that did not characterize the earlier faunas. The pattern of thelodonts suggests an originally marine habitat but a degree of provincialism in the Silurian, which implies some kind of either physical or physiological barriers (see figure 2). The ubiquity of thelodonts in sediments representing differing environments suggests an ability to deal with variations of salinity. The subsequent Lower Devonian distribution of thelodonts implies that the factors controlling their previous distribution were no longer operative (see figure 2). It seems evident that the later Silurian thelodonts colonized both brackish and fresh water habitats and by Lower Devonian times there seems to have been no serious hindrances to their global spread.

In marked contrast the fusiform anaspids (see figure 1) have a highly restricted distribution being recorded from the Upper Llandovery or Lower Wenlock of the Canadian Arctic

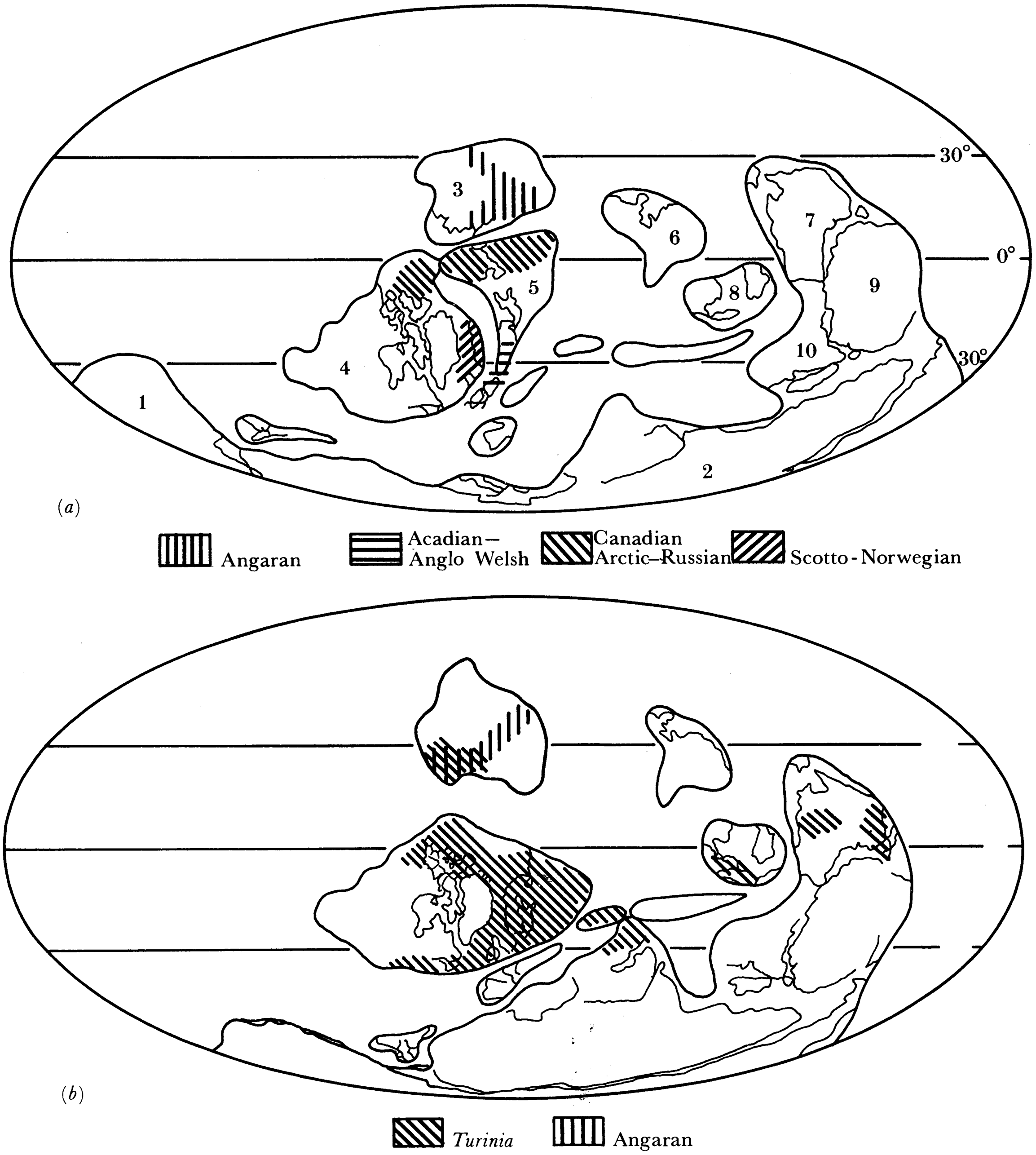

FIGURE 2. Thelodont faunal provinces and palaeogeography. (*a*) Silurian, (*b*) Lower Devonian (after Turner & Tarling 1982). 1, South America; 2, Africa; 3, Angaraland (Siberia); 4, North America; 5, Baltica; 6, North China; 7, Australia; 8, South China; 9, Antarctica; 10, India.

(Thorsteinsson 1967) and thereafter in the Wenlock of Scotland and Oesel, the Ludlovian of Norway and Přídolían of the Welsh Borderland. The supposed Dittonian of Stonehaven and Kerrera in Scotland are of Silurian age. The anaspids seem to have been restricted to a Scottish–Norwegian–Baltic province, similar to one of the thelodont provinces recognized by Turner (1973). With the exception of Canadian material as yet undescribed the anaspids seem to have been restricted to a supposedly brackish, certainly non-marine environment. There is no evidence as to their previous history but material from the Welsh Borderland suggests that they were able to inhabit fluvial regimes in the early Dittonian. In this regard, this at least hints at the ability to cope with fresh, as opposed to merely brackish, waters.

The first unequivocal evidence of cephalaspids is from the Wenlock and there seems to be a Scottish–Norwegian fauna dominated by acornuate genera, contrasting with a Baltic fauna characterized by tremataspids from Oesel and Gotland. *Thyestes* relatives of this Baltic fauna are recorded from the Downtonian of the Timan and two derived genera *Tannuaspis* and *Tuvaspis* from Tuva, the southeastern margin of the Siberian or Angaraland platform sometimes taken as a separate faunal province. By early Přídolían times, the cephalaspid fauna in the Welsh Borderland contained a mixture of representatives of the tremataspid–thyestid and acornuate forms, the former seemingly marine, the latter brackish, but by Dittonian times the typically cornuate cepalaspids were established in fluvial regimes and, moreover, with a wide distribution (see Halstead & Turner 1973).

With the exception of the Siberian forms the changes in the thelodont and cephalaspid–anaspid faunas appear to be related to the closure of the proto-Atlantic or Iapetus Ocean. The mixing of marginal faunas and the subsequent invasion of fresh waters is reminiscent of the reputedly comparable situation of the closure of part of the ocean of Tethys with the movement of the African plate towards that of Eurasia during the mid Tertiary.

One of the notable consequences of the formation of the Sarmatan Sea was the evolutionary impetus that was given to marine genera which colonized brackish and fresh water regimes. Numerous new endemic genera and species evolved within a short space of time (see Crogham 1983). The formation of the Old Red Continent (Laurussia) and the presence of similar fresh water faunas around its margin, enabled them to be used for stratigraphic correlation. Although, for example, among the radiation of the cephalaspids there was a high degree of endemism in the Spitsbergen and Anglo-Welsh faunas there were, none the less, certain groups, notably among the heterostracans, in which similar if not exactly conspecific forms had a very wide geographical distribution.

When White (1950) first demonstrated the value of ostracoderms in the stratigraphy in the Welsh Borderland, he established a zonal scheme based on a succession of pteraspids, each zone being characterized by a succeeding evolutionary stage. The utility of the zonal scheme he devised was immediately recognized and was applied in western Europe (White 1956) and Nova Scotia (Dineley 1967). The practical value of the heterostracans for stratigraphic correlation purposes highlighted a major lacuna in our knowledge. There seemed to be little evidence of evolution in the sense that the connecting intermediate forms were nowhere to be found.

The discovery of such typical Dittonian fossils as *Traquairaspis* and *Corvaspis* in the Canadian Arctic by Dineley (1964, 1965) and Denison (1963) culminating in the monographic treatment by Dineley & Loeffler (1976) of many new genera led to the view that the Canadian Arctic may have been an evolutionary centre, but to date there has been little direct evidence to document this suggestion. Certain genera such as *Lepidaspis* suggest a possible connection between heterostracans and thelodonts. The recent description of the pteraspids *Anchipteraspis*, *Ulutitaspis* and *Rhachiaspis* by Elliott (1984) has resolved a long-standing controversy on the relationship of the cyathaspids and pteraspids in favour of the views of White (1935) and Denison (1964) who claimed the derivation of the latter from the former. The new material offers perfect intermediates between these two heterostracan orders.

The most significant feature of the Canadian Arctic faunas is their ages. They contain similar forms to those long-known from the Anglo-Welsh region in the Dittonian (Lochkovian); but from Cornwallis Island and Prince of Wales Island, similar faunas occur in Wenlock and Ludlovian rocks, and in Ellesmere Island in the Přídolían. There seems little doubt that the heterostracans slowly migrated from the Canadian Arctic to the Welsh Borderland, but that this arrival coincided with the final closure of the Iapetus Ocean. A coast-wise migration enabled this region to be reached without any oceanic barrier needing to be traversed. The length of time during which this migration was accomplished was between 10 and 12 Ma. The rate of evolution seems to have been somewhat tardy. During the succeeding Lochkovian and the Pragian, the rate of evolution seems to have speeded up with the origin of many new taxa. This seems to be a reflection of the radiation accompanying the colonization of a new environment, the fresh waters of alluvial plains around the margins of the Old Red Continent (Laurussia).

During Pragian and Emsian times in particular, the pteraspids and the psammosteids seem to occur in both fluvial and marine sediments, as exemplified by the pteraspids and drepanaspids of the Rineland and the Emsian psammosteids from central Poland. The latter seem to have been the basic stock of the radiation of the Middle and Upper Devonian psammosteids of the Baltic. It was from this evolutionary centre that a series of migrations to other regions took place, as documented by Tarlo (1965, 1966, 1967*b*).

The major pattern of the distribution and evolution of the faunas associated with the closure of the Iapetus Ocean and the formation of the Old Red Continent (Laurussia) is reasonably well documented, and the invasion of fresh waters seems to have been accomplished early in Přídolían times.

The invasion of fresh waters can perhaps be attributed to major environmental changes in the distribution of land and sea. If consideration were to be restricted to this geographical realm alone, a compelling and neat scenario could be constructed encompassing all the available data entirely satisfactorily; but even a cursory glance at other provinces demonstrates that the reality is more complex.

3. ANGARALAND (SIBERIA)

The knowledge of the early vertebrates from Siberia first came to light when Obruchev (1938) described a new group of heterostracans, the amphiaspids *Amphiaspis* and *Hibernaspis* from the River Kureyka in northwest Siberia. Obruchev figured a new genus, the blind *Eglonaspis* in 1959, and described seven further genera in 1964. The nature of the fused carapace as well as the unique sensory canal systems characterized this new Order, although two genera *Aphataspis* and *Putoranaspis* were included as members of the ctenaspid cyathaspids in which the dorsal and lateral parts of the carapace were fused.

The evolution of the amphiaspids was outlined by Novitskaya in 1967 and monographed in 1971. The genera *Aphataspis* and *Putoranaspis* were classed as primitive amphiaspids, although it was considered that this order probably originated from a ctenaspid-like cyathaspid ancestor. Tarlo (1962*a*, *b*, 1965) contended that the amphiaspids probably represented a separate evolutionary line of fusion of armour from an original tessellated carapace, and that the similarity to certain cyathaspids was due to convergence. The work of Novitskaya seemed to confirm the cyathaspid affinities originally postulated by Obruchev (1964), and Halstead (1973) finally accepted such a close relationship.

The general suggestion made by Tarlo (1962*c*, 1965), that the evolutionary centre of the

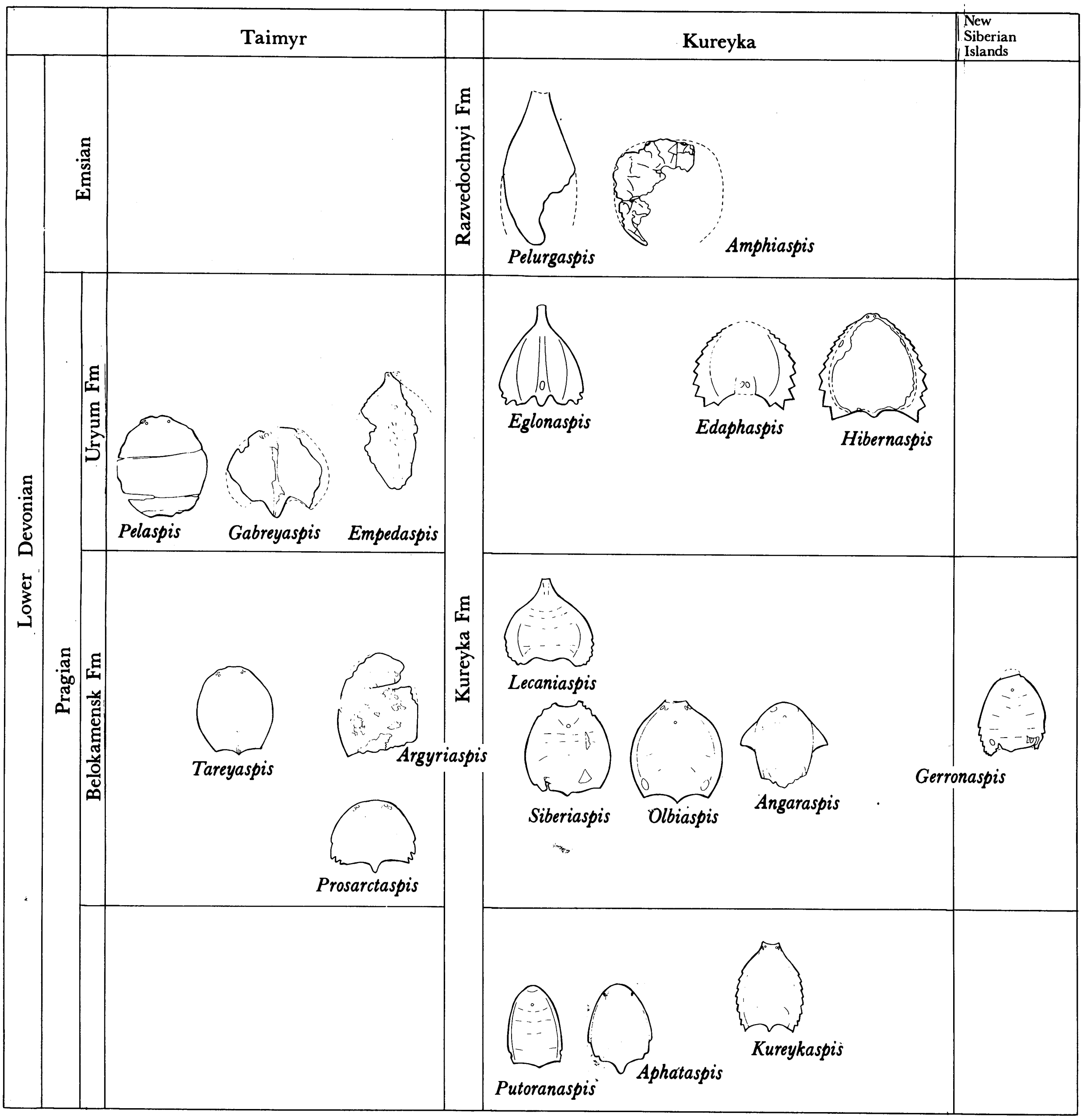

Figure 3. Stratigraphic succession and distribution of amphiaspid heterostracans of Angaraland (after Novitskaya 1971, 1976*a*).

early vertebrates may have been situated in what is now the Arctic, received support from Novitskaya (1971) and the description of *Ctenaspis* from the Canadian Arctic from Přídolían age sediments (Dineley 1976) provided a *prima facie* case that the origin of the amphiaspids could perhaps be sought from the Canadian Arctic fauna. The description from rocks of Přídolían age by Broad (1973) of several species of the new genus *Boothaspis*, which he identified as an amphiaspid belonging to the family Siberiaspididae, as well as a fragment of a lateral carina which he attributed to the family Olbiaspididae, appeared to provide striking confirmation of this thesis of their origin. Broad (1973) noted that in both the ornamentation and sensory canal system his new material differed from the amphiaspids and suggested that they may have been intermediate between the cyathaspids and the amphiaspids. The features that distinguish the amphiaspids from other heterostracan orders are absent from the Canadian fossils, and hence there is simply not sufficient evidence available to assign this material to primitive amphiaspids. The fact that Obruchev (1964) classified the two primitive amphiaspid genera in the ctenaspid cyathaspids indicates the difficulties but there seems less justification for Broad's identification in view of the absence of any distinctive amphiaspid features beyond overall geometry. To date therefore there is no unequivocal evidence of any amphiaspid occurrence in the Canadian Arctic.

Subsequent to the recognition of the major radiation of the amphiaspid heterostracans in Angaraland, and their range in time from Pragian to Emsian, it became generally recognized that Siberia was the site of a separate independent radiation of jawless vertebrates (figure 3) (Halstead 1973; Halstead & Turner 1973). Moreover, it was realized that within Siberia there were two separate provinces (Novitskaya 1976*a*, *b*). Mark-Kurik (1974) has recorded amphiaspid remains from the New Silurian Islands to the north east of Angaraland in the Soviet Arctic. The northern Taimyr region is characterized by its poor diversity of amphiaspids and it appears as if these seemingly more primitive members were adapted to the same ecological niche of benthonic detritus feeders. In the Kureyka region the amphiaspids seemed to have inhabited a brackish embayment where they underwent a major radiation, evolving a wide variety of forms implying a number of distinct ecological niches (see figure 3). Obruchev's (1967) opinion was that the amphiaspids were adapted to life in turbid waters. There is insufficient data to ascertain exactly the conditions of deposition of the sediments, from which the amphiaspids have been collected. From the available information to hand, it cannot be decided whether the amphiaspids had moved beyond the adaptation to inhabit a brackish, non-marine habitat, to invade the fresh waters of fluvial régimes. In any event the Angaran fauna represents an entirely independent attempt on the part of the vertebrates to acclimatize themselves to a non-marine habitat.

The timing of the establishment of this unique fauna is still a matter of conjecture. Taimyr is situated, and was similarly situated, at the closest point to the Canadian Arctic where, it is still believed, the stem group of the amphiaspids is to be sought. The Taimyr amphiaspids are the least diversified, but they are not the earliest nor do they include the most primitive forms. These are to be found in the Kureyka region at significantly lower stratigraphic horizons.

The presence of *Aphataspis* and *Putoranaspis* in the Pragian suggests that the origin of the amphiaspids may not have been that much earlier, perhaps during the latter part of the Lochkovian. It seems likely that the invasion and establishment of the vertebrates in non-marine habitats of the Angaraland Realm was later in time than the invasion of comparable habitats during the Wenlock by the anaspids and cephalaspids.

4. SOUTH CHINA

A further major radiation of early vertebrates, centred on what is now South China, has only been recognized very recently and represents an important evolutionary development. Devonian vertebrates were recorded from southern China by C. C. Young during the International Geological Congress held in London in 1948 (Young 1951) but it was not until

Liu Yu-hai (1965) described *Galeaspis* (now *Eugaleaspis*), and *Nanpanaspis* as belonging to the cephalaspids and *Polybranchiaspis* as a heterostracan with separate gill openings, hence the name, that the first intimation of the uniqueness of this fauna became apparent. The identity of ornamentation and sensory canal pattern, as well as number and type of perforations in the carapace, suggested that all three genera were members of a hitherto unknown major group of jawless fish which were designated the Galeaspida, a separate cephalaspidomorph Superorder of equal rank to the anaspids and cephalaspids (Tarlo 1967*a*; Halstead & Turner 1973). It was not for some time that the assignment of the Chinese material to the Galeaspida was accepted (Halstead *et al.* 1979).

Liu (1973) described a new form *Huananaspis*, with lateral extension of the carapace, and in 1975 five further new genera: *Laxaspis*, *Dongfangaspis*, *Diadongaspis*, *Cyclodiscaspis* and the curious *Sanqiaspis* with its flattened rostral extension longer than the rest of the carapace, and as long as the trunk and tail. Also in 1975, P'an *et al.* described three new genera *Lungmenshanaspis*, *Asiaspis* and *Sinoszechuanaspis* with long rostra and lateral spines (see figure 4). P'an & Liu, Y.-P. further described a new Order represented by the genus *Hanyangaspis* which they restored as a heterostracan, albeit the shortest and widest genus even known (figure 5). An examination of the original material, all of it fragmentary, confirms Liu's (1979) note, which pointed out that the genus was a fairly typical polybranchiaspid. The plates that purported to be perforated by the orbit and branchial openings were not positioned laterally; the supposed branchial opening was in fact the central median opening. The fine details of ornamentation around the margins of this opening are identical to those of *Polybranchiaspis* (figure 5). The overall ornament is typically polybranchiaspid and, even more telling, the distance between the two perforations matches those between the orbits and central median openings of *Polybranchiaspis*. There is no justification for separating *Hanyangaspis* from the polybranchiaspids and this material cannot be used as evidence for the presence of heterostracans in the Devonian rocks of South China.

In the symposium on the Devonian of South China in 1974 (published in 1978) P'an & Wang described three new polybranchiaspid genera *Duyunolepis*, *Paraduyunaspis* and *Neoduyunaspis*. The holotype of *Duyunolepis* is to date the most remarkably preserved of any jawless vertebrate, in that much of the space within the hard tissues formerly occupied by blood vessels, nerves, brain and ear apparatus, was filled with iron compounds and the original bony material was subsequently eroded to leave behind a mineral replica of the soft anatomy. The details of the soft anatomy confirm the cephalaspidomorph nature of the galeaspids (Halstead 1979, 1982).

P'an & Wang (1978) described the new genus *Nakaolinaspis* as a member of the amphiaspid heterostracans and claimed it showed resemblances to the blind *Eglonaspis*, which had a mouth at the end of long tubular rostral process. This identification, if correct, would be the first unequivocal amphiaspid to have been found outside the Angaraland (Siberian) Realm. The specimen on which this identification was based was noted by Halstead *et al.* (1979) and seems to be the internal mould of a placoderm skull roof. Only the central part of the specimen in question was interpreted as the fossil and this does have an outline reminiscent of *Eglonaspis*. The preserved lateral and posterior margins establish that it is a natural mould of the internal surface of part of a placoderm headshield (figure 6). The recognition of the nature of this specimen removes the possible link between the Siberian amphiaspid and the South China galeaspid faunas. Both regions were dominated by their own endemic faunas.

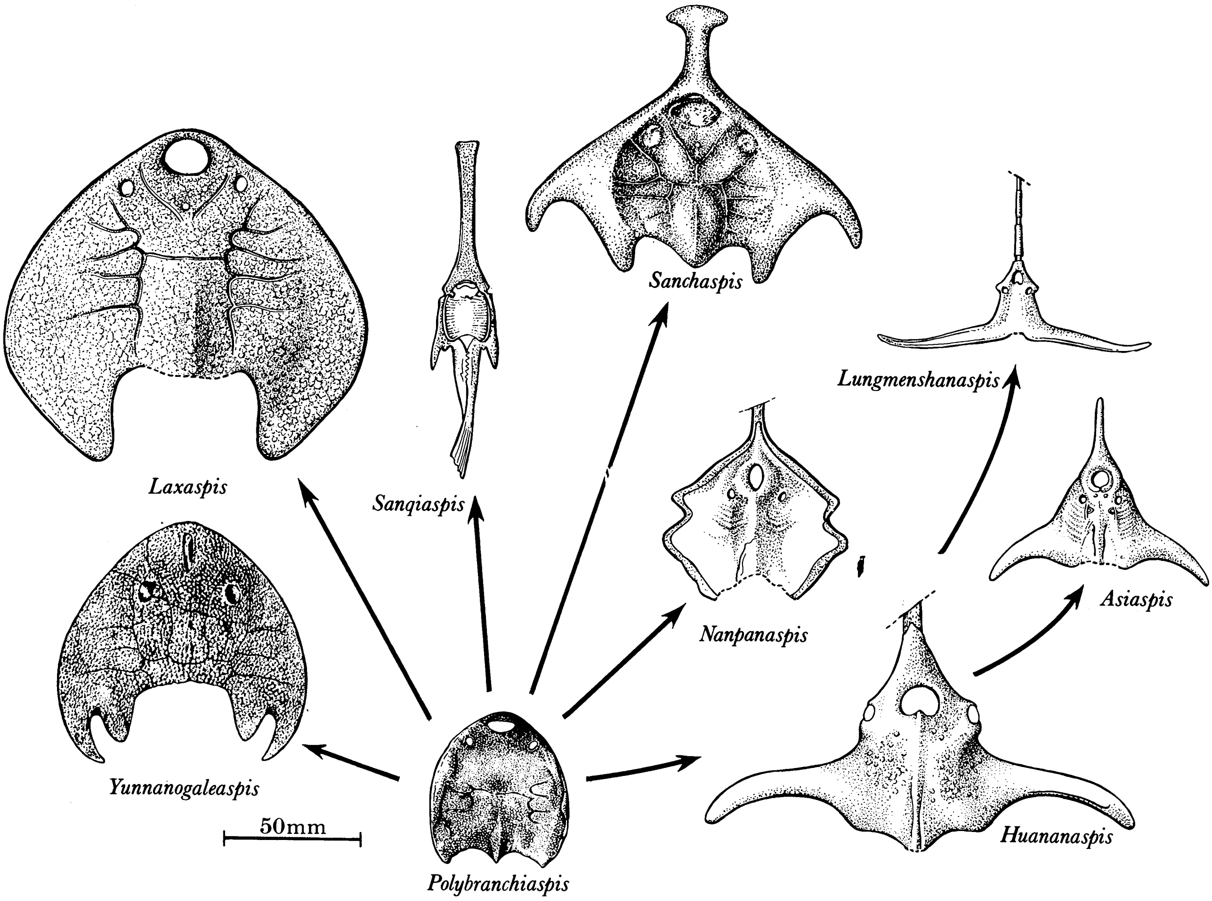

FIGURE 4. Radiation of galeaspids from South China.

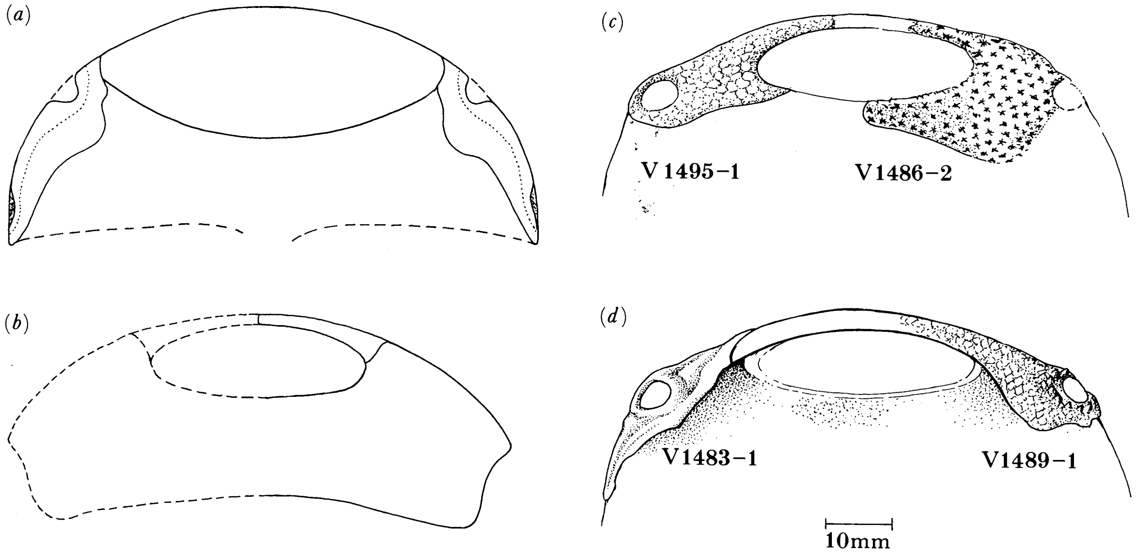

FIGURE 5. *Hanyangaspis*. (*a*), (*b*) Restoration as aberrant heterostracan; (*a*) dorsal view; (*b*) ventral view; (*c*), (*d*) restoration as normal polybranchiaspid, (*c*) dorsal fragments in dorsal view; (*d*) dorsal fragments in ventral view.

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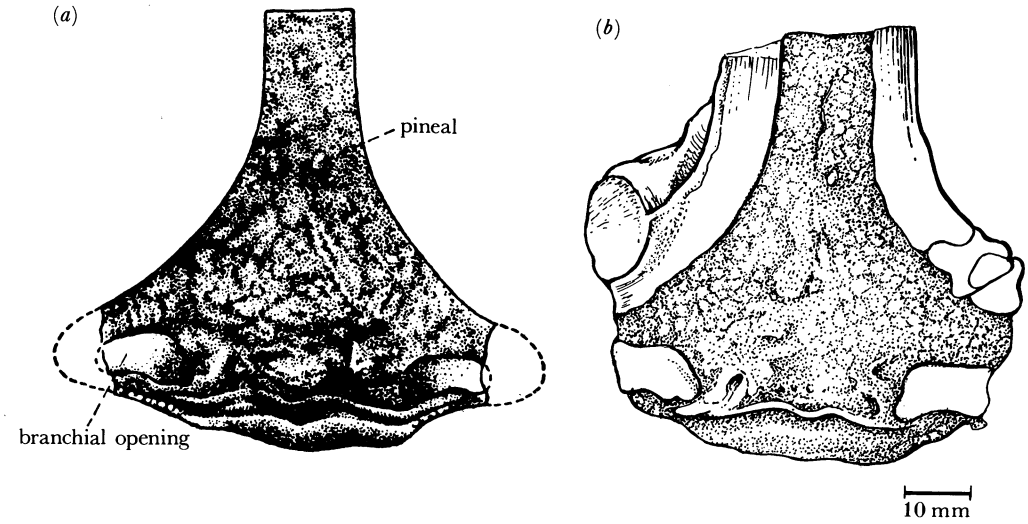

FIGURE 6. *Nakaolinaspis* (*a*) as an eglonaspid amphiaspid (P'an 1978); (*b*) complete specimen preserved as internal mould of skull roof. Pi., bro.

More recently there has been a continuing flow of descriptions of new genera: *Kwangnanaspis* (Cao 1979); *Latirostraspis* (Wang *et al.* 1980); *Yunnanogaleaspis*, *Sinogaleaspis* (Pan & Wang 1980); *Sanchaspis* with its curious spatula-like rostral projection (figure 4) and *Qingmenaspis* (Pan & Wang 1981); *Siyingia* (Wang & Wang 1982*a*); *Damaspis* (Wang & Wang 1982*b*); and *Xiushuiaspis* (Pan & Wang 1983). Several of the described genera have the general shape of *Polybranchiaspis*, some differing only in proportion. Some of the more bizarre, such as *Sanchaspis*, have now been described but there are other as yet undescribed genera which illustrate the range of form quite dramatically. One of these has the dorsal carapace perforated by five openings, the posterior pair leading either to or from the gill region. Perhaps the most enigmatic specimen, still unfortunately undescribed, shows the margin of the mouth ventrally as well as the branchial openings situated between the ventral median carapace and the lateral carina. The dorsal surface shows the dorsal medial opening and orbits, but there appears to be an elongated opening in the carapace immediately medial to the lateral carina. This is reminiscent of the lateral sensory fields of the cephalaspids and this may well represent some kind of link between cephalaspids and galeaspids.

The galeaspids are best known from the Cuifenshan Formation and the overlying Xuijiachong Formation, which seem to span most of the Lower Devonian and are considered to be non-marine or continental facies.

The first description of vertebrate remains from the underlying Silurian, the Fentou Formation, was made by P'an (1962) when he identified part of the ventral shield of *Kiangsuaspis* as a cyathaspid heterostracan. Examination of the original material makes such as identification not unreasonable, but it cannot be stated with complete confidence that the cyathaspids were present in the Silurian of South China. From the invertebrate remains the Fentou Formation is of probable Wenlock age.

Wang *et al.* (1980) described fragments of a typical polybranchiaspid from the Silurian Fentou Formation hence extending the range of the galeaspids from the Devonian down into the Silurian. This material was placed in the new genus *Latirostraspis*, an allusion to the broad nature of the carapace as reconstructed. This material was compared with the fragments named *Hanyangaspis* by P'an (P'an & Wang 1978). The proportions as restored do not seem to be entirely convincing on the basis of the evidence presented and seem to owe much to the earlier mistaken restoration of *Hanyangaspis*. Further material from the Silurian, as yet undescribed, and which is preserved complete, even to having the trunk squamation preserved, reveals the typical polybranchiaspid proportions.

It begins to appear that the South China Realm was colonized from an unknown source by some polybranchiaspid during Silurian times and that this group underwent a major adaptive radiation throughout Lower Devonian times. Although the detailed sedimentological evidence is not yet available it seems more than likely that the galeaspid faunas of South China represent an independent invasion of fresh waters by the early vertebrates. Since new genera are being continually described, the full extent of this radiation is yet to be documented but there can be little doubt as to the remarkable degree of endemism of this fauna.

5. Conclusions

The invasion of fresh waters seems not to have presented any major problems to the early marine vertebrates. The physiological adaptations necessary for the successful colonization of non-marine and even terrestrial habitats seem to have been evolved in response to life in a salt water medium and can be taken as examples of preadaptation, in that the organisms concerned were fortuitously adapted to conditions they were yet to meet.

The colonization of fresh waters in Laurussia, possibly Angaraland and South China do not seem to be correlated with any particular geographical event, involving either the closing or opening of oceans. The formation of the Old Red Continent as a consequence of the closure of the Iapetus Ocean could be interpreted as the one physical factor that determined the nature of the distribution of the early vertebrate faunas (figure 7). However, although intellectually satisfying, there are no such events that could serve to explain the amphiaspid endemic non-marine radiation nor the radiation of the Chinese galeaspids. One of the most striking features of the three independent radiations is the repeated, yet entirely independent, evolution of forms with similar geometry even to the extent of having long, narrow, lateral projections of the carapace in conjunction with elongated rostral processes.

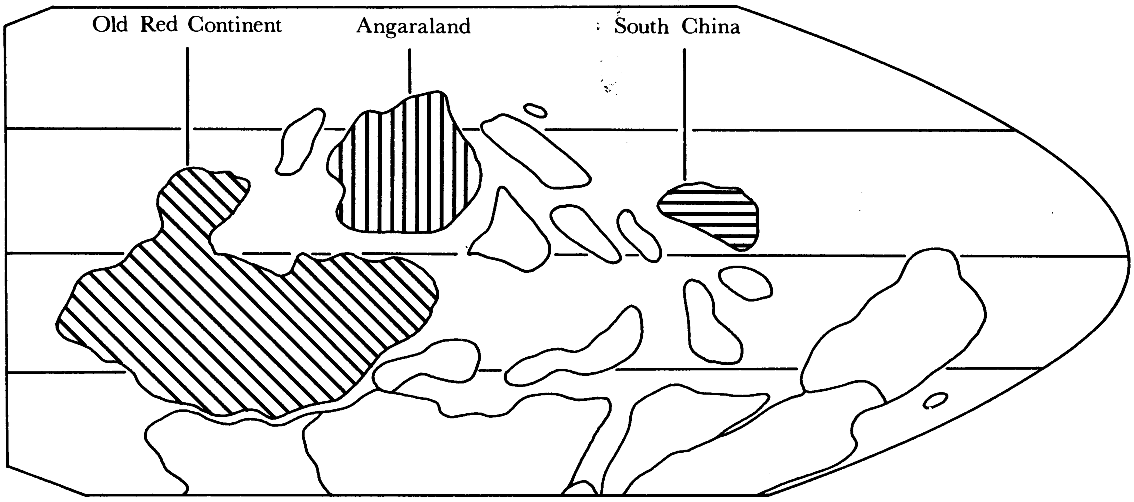

Figure 7. Major faunal provinces during the Lower Devonian (after Young 1981).

The overall pattern of many groups is that a successful invasion of fresh waters took place from a marine origin, with a concomitant provincialism or endemism, followed still later in some instances by a wider distribution both geographically and in terms of salinity tolerances, implying that many species were in fact euryhaline. Many questions relating to the exact environments of deposition as well as the likely timing of the movements from marine to non-marine habitats still remain to be answered. The impression, with the evidence currently to hand, is that with the three major invasions there is no evidence of any degree of synchroneity. There is no sound basis for suggesting that the invasion of fresh waters was due to factors of geography or of the internal physiology of the vertebrates. Fluvial regimes were in existence long before the vertebrates travelled upstream; the physiology of the vertebrates would have allowed them to ascend fresh waters, yet they did not do so.

The invasion of fresh waters could have been part of a reproductive strategy, laying eggs in an uninhabited environment and hence safe from predators. However, for microphagous detritivores, mud grubbers, there could have been no alimentary incentive to enter fresh waters before the establishment of fresh water or terrestrial plants as the primary producers, on which both the invertebrate and vertebrate components of a food web could be supported. With the establishment of non-marine plant life, the opportunity for the vertebrates to follow was presented. The real question that remains to be answered relates to the timing of the invasion of fresh waters and the land by the plants. It would appear that the physical and physiological conditions must have existed long before the Wenlock–Siegenian period, yet there is no unequivocal evidence of any significant movement previous to that time.

I am grateful for help and discussion to Pan Kiang and Liu Yuhai (Beijing), Philippe Janvier (Paris), Tony Bray and John Collins (Reading). Alan Cross drew figures 2, 3 and 7, and Jennifer Halstead figures 1, 4, 5 and 6.

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