Environmental Framework of the Diversification of the Osteostraci During the Silurian and Devonian [and Discussion]

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Environmental framework of the diversification of the Osteostraci during the Silurian and Devonian

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The beginning of the Devonian is marked by the sudden occurrence of abundant vertebrate faunas, often associated with detritic facies of Old Red Sandstone type. A few groups, already represented in the Silurian and even in the Ordovician, pass through the Silurian–Devonian boundary and seem to undergo an important diversification at this particular moment of their history. The case of the Osteostraci, a group of fossil jawless vertebrates, is examined in detail to show whether or not its phylogenetic pattern displays a radiation that coincides with the extension of the Old Red Sandstone facies over the North Atlantic continent. It appears that this geological event may have triggered the radiation of the cornuate osteostracans, although this monophyletic group must have already begun to diversify in the Middle Silurian. A review of the analyses of three osteostracan-bearing localities (Welsh Borderland, Spitsbergen and Saaremaa) is presented, and it is concluded that the Osteostraci may have consisted of both fresh water and marine species. When marine, the environment of the Osteostraci may have been vast intertidal zones, hardly having any Recent equivalent. The difficulty in assigning the Old Red Sandstone (from Britain and elsewhere) to any clear-cut environment may be because the physical constants of the Earth or the amplitudes of the tide were not the same in early Devonian times as they are now.

Introduction

Vertebrates are known as early as the Lower Ordovician (Ritchie & Gilbert-Tomlinson 1977) and perhaps the Upper Cambrian (Repetski 1978), but they remain relatively rare as fossils until the Upper Silurian (Ludlow), and all the major vertebrate groups (except the tetrapods and myxinoids) are already represented in the late Lower Devonian (figure 1). The Myxinoidea, now regarded as the most primitive extant craniates, are the only major extant monophyletic group that are not known as fossils, although the peculiar Carboniferous form *Gilpichthys greeni* (Bardack & Richardson 1977) may be interpreted as a fossil myxinoid. The stratigraphical distribution of the various vertebrate monophyletic groups (figure 1) shows clearly the apparent sudden 'radiation' of the group by the Silurian–Devonian transition. Thus, certain questions arise: does this 'radiation' reflect a real biological event or simply the occurrence of particular taphonomical conditions which favoured the preservation of vertebrate remains? If the Lower Devonian 'radiation' of the vertebrates is not an illusion, did any particular global geological or climatological event trigger this intense diversification? Did, for example, the adaptation to a fresh water environment take place in that particular period?

The present attempt to answer these questions may not be satisfactory to those who expect all problems to be solved. In fact, most attempts at finding a link between palaeoenvironmental events and phylogenetic patterns have merely demonstrated the power of human imagination, even for relatively recently periods such as the Miocene or the Quaternary. Consequently, few

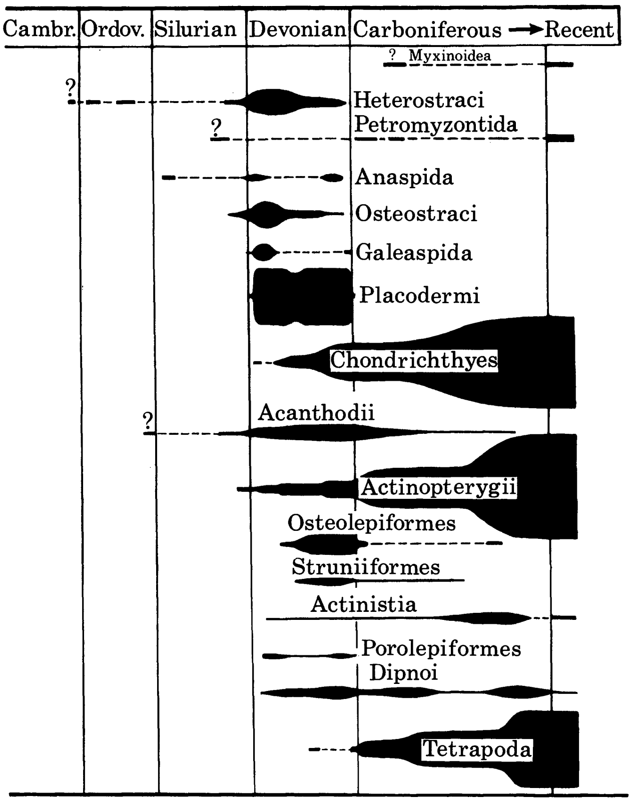

FIGURE 1. Stratigraphical distribution of the major craniate monophyletic groups. The breadth of the scrolls reflects approximately the importance of the respective groups, in terms of the number of fossil species recorded.

reliable conclusions can be expected for such remote periods as the Silurian or the Devonian. However, when this sort of research is carried out, the analysis of the phylogenetic patterns must precede the search for any change in the environment, rather than the reverse.

I have chosen the Osteostraci as an example of this type of analysis, because this group passes through the Silurian–Devonian boundary, is greatly diversified, and is directly concerned with the problem of the adaptation to fresh water. Other groups often associated with the Osteostraci in most Siluro-Devonian localities, namely, the Heterostraci, Anaspida, Acanthodii and 'Thelodonti', may also be used in the same way, but none of them (except perhaps the Heterostraci *pro parte*) has hitherto been the object of a phylogenetic analysis.

PHYLOGENETIC PATTERN OF THE OSTEOSTRACI

The Osteostraci are among the first fossil vertebrates encountered in the Lower Devonian sandstones of Great Britain and are, therefore, often cited in discussions about the presumably fresh water environment suggested by this geological formation. The phylogenetic position of the Osteostraci has long been uncertain. Suffice it to say that they have been related to 'siluroids', 'ganoids', chondrosteans, and even regarded as intermediates between arthropods and vertebrates, until Stensiö (1927) described in detail their internal anatomy and related them to lampreys. This view has prevailed for more than 50 years and is still accepted by most palaeontologists, although the Osteostraci share several unique characteristics with the

Gnathostomata (Janvier 1981*b*), which outnumber those shared with the lampreys. The weight of what has now become tradition hinders palaeontologists from admitting the implications of these osteostracan–gnathostome synapomorphies, which have long been neglected or regarded as mere convergences. However, this question is of little importance in the present connection.

Since Stensiö's (1927) and Wängsjö's (1952) works on the Lower Devonian Osteostraci of Spitsbergen, this group is known to display a remarkable diversity, already foreshadowed in the late 19th century monographs on the Ludlovian forms from Saaremaa (Estonia). A glance at some of the osteostracan species known by the end of the last century is enough to illuminate the difficulty that the early palaeoichthyologists had in making sense out of this kind of material (Woodward 1891, figures 18–32). The most puzzling feature was that some species had paired fins whereas others had none. Stensiö (1927) decided that the forms with no paired fins, such as *Tremataspis*, were specialized and had lost their fins. Later, Westoll (1945) gave a reverse interpretation, mainly on the basis of stratigraphical arguments: the finless forms such as *Tremataspis* or *Dartmuthia* were among the geologically oldest known Osteostraci, thus they were primitive and, consequently, paired fins appeared in later forms, independently of those of other vertebrates such as the Gnathostomata or Anaspida. This view is still held by Collins (1981) and Halstead (1982), despite several observations which refute it: (i) the Tremataspididae (*Tremataspis*, *Oeselaspis*, *Dartmuthia*, *Saaremaaspis*, *Timanaspis* and perhaps *Tyriaspis*) are not the only oldest known Osteostraci, since *Ateleaspis tessellata* Traquair is now referred to the Upper Wenlock or Middle Ludlow (Ritchie 1967) and fragments of non-tremataspid osteostracans are known from the Wenlockian Halla Beds of Gotland (Gross 1968); (ii) the tremataspid-bearing localities of Saaremaa have also yielded typical cornuate Osteostraci with well-developed paired fins, such as *Procephalaspis oeselensis* (Robertson) (figure 2), *Thyestes verrucosus* Eichwald (figure 2) and *Witaaspis schrenkii* (Pander); (iii) the distribution of the synapomorphies among the species from the Wenlock and Ludlow of Saaremaa indicates that they form a monophyletic group, the thyestidians (to which can be added the Lower Devonian genera *Auchenaspis* and *Sclerodus* from Britain, and *Timanaspis* from Timan), where the Tremataspididae represent a small and much-derived monophyletic unit (figure 2). Thus, following Stensiö (1927) and Wängsjö (1952), I consider that the Tremataspididae do not represent a stem group of the Osteostraci. In contrast, the character distribution in the so-called 'non-cornuate' Osteostraci (*Ateleaspis*, *Aceraspis*, *Hirella*, *Hemitelaspis*, *Hemicyclaspis*) points toward the hypothesis that they are the most primitive forms of the group (figure 3). The Lower Devonian Osteostraci are mainly represented by cornuate forms, that is, possessing a more or less developed process in front of the paired fins. The distribution of this character is congruent with that of the ventrally closed abdominal division of the shield, and thus indicates that the cornuate Osteostraci form a monophyletic group, the Cornuata. Within this group, five monophyletic groups have been defined (Janvier 1981*a*): cephalaspidians, benneviaspidians, thyestidians (including the Tremataspididae), kiaeraspidians and scolenaspidians. The relationships between these five groups are still virtually unresolved, and the synapomorphy scheme proposed elsewhere (Janvier 1981*a*; 1984*a*) for the interrelationships of the Cornuata is very fragile and based on characters which are preserved in only a few specimens (lack of anterior dorsal fin, etc.). The structure of the trigeminal cavity, with no medially directed posterior ventral myodome, is the only reliable synapomorphy shared by kiaeraspidians and thyestidians. Consequently, a basal polychotomy is considered here for the Cornuata, except the kiaeraspidians and thyestidians, which may be sister groups (figure 3).

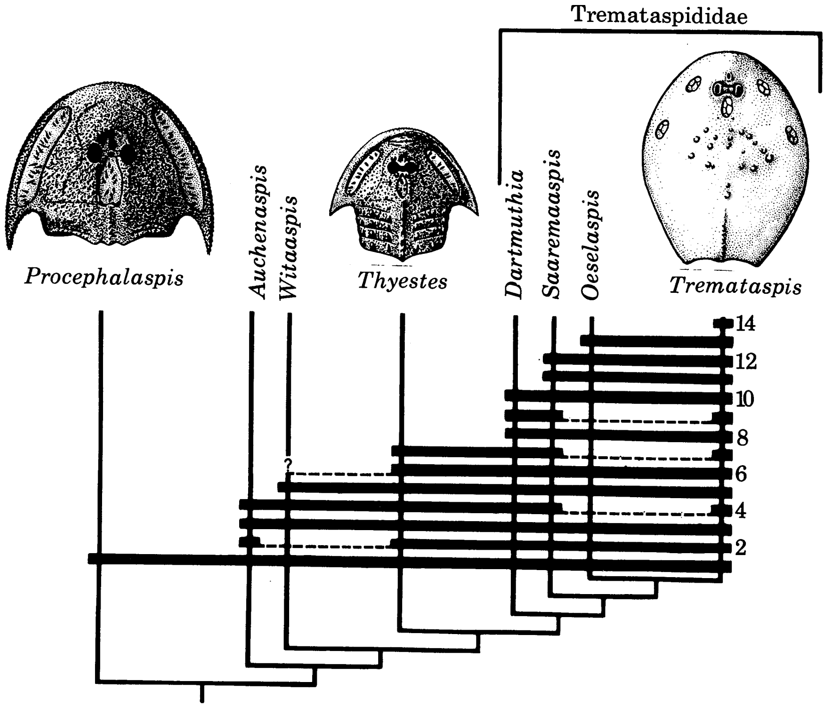

FIGURE 2. Theory of phylogenetic interrelationships of thyestidian osteostracans. Only three species are figured: *Procephalaspis oeselensis* (Robertson), *Thyestes verrucosus* Eichwald and *Tremataspis mammillata* Patten. This phylogeny intends to show that the Tremataspididae are derived from typical cornuate osteostracans and, consequently, that the latter must have existed before the rise of the former.

Key to some synapomorphies: 1, infraorbital sensory-line passing close to the naso-hypophysial region; 2, elongate abdominal division; 3, closely set orbits; 4, longitudinal rows of large tubercles on abdominal division; 5, endolymphatic duct opening outside the median dorsal field; 6, enameloid on top of tubercles; 7, triangular supraoral field covered with tubercles; 8, lack of paired fins; 9, cosmine on, at least, some parts of the shield; 10, horizontal, perforated septum (*Siebplatte*) in the porecanal system of cosmine; 11, narrow posterior opening of abdominal division; 12, shorter median dorsal field; 13, lateral fields subdivided into two parts; 14, cosmine over all the shield.

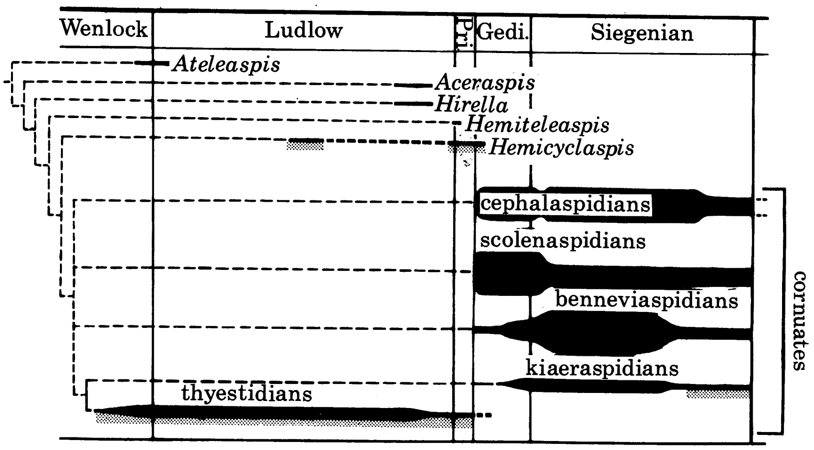

FIGURE 3. Stratigraphical distribution and interrelationships of the major osteostracan monophyletic groups. The breadth of the scrolls reflects approximately the number of recorded species. The grey band bordering some scrolls indicate the occurrence of the group in a marine environment (in Spitsbergen, only kiaeraspidians have actually been found in association with inarticulate brachiopods). Dashed lines indicate relationships, mainly according to the phylogeny proposed by Janvier (1981 *a*, *b*). Abbreviations: Gedin., Gedinnian; Prid., Přídolían (or Downtonian).

Among the Cornuata, only thyestidians are known from the Upper Silurian. Some fragments of possible cornuate osteostracans have been described by Gross (1968) from the Wenlockian of Gotland and referred to as '*Cephalaspis*' *excellens* Wängsjö by Ørvig (1969) but they cannot be assigned to any of the monophyletic groups mentioned above. The cephalaspidians, benneviaspidians, kiaeraspidians and scolenaspidians all appear in the Lower Devonian (Gedinnian) of Great Britain, Spitsbergen and Podolia (kiaeraspidians are known exclusively from Spitsbergen), but the phylogenetic pattern of the Osteostraci (figure 3) tells us that these cornuate groups must have existed long before the Lower Devonian, probably already in Wenlockian times. Their 'radiation' in the Lower Devonian of Europe appears, from the fossil record, to be very sudden. This may not be an illusion due to the occurrence of favourable conditions of fossilization, because non-cornuate osteostracans (for instance *Hemicyclaspis*) are abundant and preserved in similar conditions (red sandstone) as early as the Downtonian (Přídolí). Thus, one may suppose that this rapid diversification of the cornuate osteostracans is related to some physical change in their environment. Among the factors that can 'trigger' the diversification of a group, two have been tested by biologists on Recent examples: (i) the invasion of a new ecological niche and (ii) biogeographical events. These two aspects of the question will be examined with regard to the pattern of diversification of the Osteostraci.

Osteostracan biogeography

It is extremely difficult to produce a reliable model of osteostracan biogeography for either the Ludlow or the Lower Devonian, because of many uncertainties as to the synchroneity of the localities under consideration and to the endemism of the groups (in fact, endemism is untestable in palaeobiogeography, since one cannot, and never will be able to, decide that members of a supposedly endemic fossil group did not live elsewhere). Thus, any attempt to produce a palaeogeographical model should be restricted to the analysis of relationships between *known* biotas (based on congruence of phylogenetic patterns) rather than defining 'provinces'. The data presented here are only 'fragments' of osteostracan biogeography and one must be aware that any conclusion drawn from these data should be accepted with caution.

The Osteostraci are not known outside the present northern hemisphere (figure 4). They are mainly found in regions referred to the 'North Atlantic' area, that is, in eastern North America, northern Europe and the Arctic (Mackenzie, Spitsbergen, Timan, Severnaya Zemlia). The limits of their known geographical distribution are Tuva (Tannu Ola) and

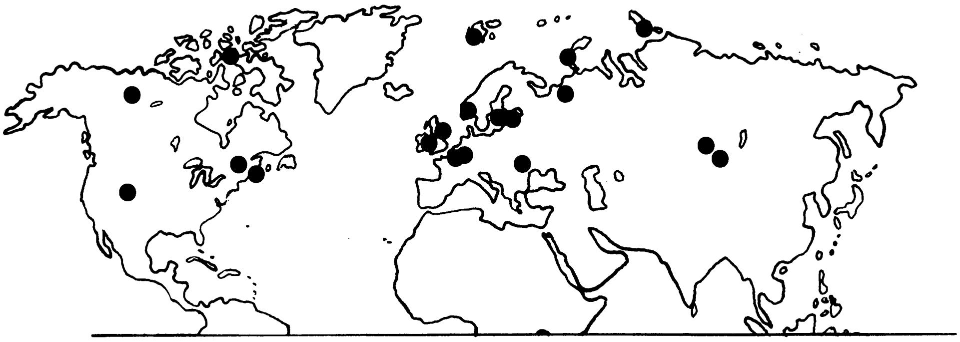

FIGURE 4. Distribution of the osteostracan-bearing localities of the world.

Severnaya Zemlia to the East, Wyoming to the West, the Arctic to the North and Podolia to the South. Their absence in other parts of the world may simply be due to the lack of proper investigations in the Lower Devonian, except in South China (Yunnan, Szechuan) where suitable facies of the Lower Devonian exist and have yielded a group of jawless craniates, the Galeaspida, which may be regarded as an ecological equivalent of the Osteostraci.

Within this apparent area of distribution of the Osteostraci, one may delimit a few possible areas of endemism. In Ludlovian times, the thyestidians are known from Saaremaa, Gotland and the Welsh Borderland, but the genus *Tremataspis* is known only from Saaremaa and Gotland. In the early Lower Devonian, the thyestidians seem to enlarge their area of distribution, since they occur in Timan (*Timanaspis*) and possibly Central Asia, with *Tannuaspis* and *Tuvaspis* from Tuva (which may be much derived Tremataspididae; Afanasieva & Janvier 1985). *Tyriaspis*, from the uppermost Ludlow or lowermost Devonian of Norway may also be a tremataspidid.

In late Gedinnian times, two groups seem to be endemic to Spitsbergen: the Boreaspididae (benneviaspidians) and kiaeraspidians (recent discoveries from the Lower Devonian of Severnaya Zemlia suggest, however, that these two groups may also occur there (E. Mark-Kurik, personal communication, 1983)). Moreover, in Gedinnian and Siegenian times, the cephalaspidian genus *Meteoraspis* (Janvier 1981 *a*) also seems to be restricted to Spitsbergen. The same applies to poorly known taxa such as *Waengsjoeaspis* ('*C.*' *excellens* and '*C.*' *vogti*) and *Ectinaspis heintzii*, both from Spitsbergen.

In contrast, scolenaspidians such as *Zenaspis*, have a wide distribution and are abundant in the Gedinnian of Great Britain, Spitsbergen and Podolia. The interrelationships of the species referred to this group are still obscure, and it would be premature to use them in drawing conclusions about area relationships. *Stensiopelta* ('*Cephalaspis*' *woodwardi*), referred to the scolenaspidians, seems to be known only from Podolia and Wales.

Cephalaspidians are known from Britain, Podolia and Spitsbergen as well as, possibly, from northern France and western Germany, but again, their interrelationships are too obscure to be used in analytical palaeobiogeography.

Finally, the genus *Benneviaspis* proper (that is, restricted to the species having a trilobate median dorsal field) is known only from Spitsbergen and Podolia (Belles-Isles & Janvier 1984), unless *B. salopiensis* (White 1961) is to be referred to this group, as it seems from White's figure. None of the osteostracan species from the Devonian of North America can be referred with certainty to any of the monophyletic groups known from Europe and Spitsbergen.

The conclusions that may be drawn from this distribution of the osteostracan groups are: (i) apparently endemic groups (Boreaspididae, kiaeraspidians) coexist with widely distributed groups (cephalaspidians, scolenaspidians); (ii) most groups known from the Devonian of Europe and Spitsbergen do not seem to occur in North America, even after the closure of the Iapetus; this implies that the possibility of dispersal of the Osteostraci was limited, contrary to what is known for most Placodermi and Heterostraci.

THE ENVIRONMENT AND MODE OF LIFE OF THE OSTEOSTRACI

Phylogenetic patterns based on character analysis and geographical distribution are basic data. Studies on the environment of the Osteostraci, however seriously they are made, are hypotheses that are one step beyond the observable reality. In fact, most plant and animal groups known from the Lower Devonian are extinct although they may have distant extant relatives. Thus, inferences based on the mode of life of the latter are often largely untestable. They are also dangerous when geologists take them for granted! The major question to be answered is: did the Osteostraci live in a marine or a fresh water environment? The problem can be tackled from two aspects: (i) what the anatomy of the osteostracans tells us; and (ii) what the other fossils found with them and the sediment tell us.

Most osteostracans were bottom-dwellers, and the loss of paired fins or pineal foramen in some forms (Tremataspididae, Acrotomaspidinae) may correspond to a burrowing habit. Any other statement on their ability to swim or migrate would be pure speculation. I can see no decisive argument for or against any particular type of environment in the anatomy of the Osteostraci, except that they were most probably aquatic animals. In the field of speculations, one can note that many osteostracans (especially scolenaspidians) have a very high spinal process, which compares to the median dorsal plates of the Groenlandaspididae (Arthrodira) and some Antiarcha (*Byssacanthus*, *Grossaspis*, some *Bothriolepis* species), a condition that may be interpreted as a response to an important and rapid sedimentary flow. In fact, a high and pointed shield is less easily covered by sand than a flat shield. This interpretation is, however, contradicted by the success of benneviaspidians which possessed a very flat shield.

The question of the environment of the Osteostraci and of groups found in the same localities, such as placoderms, heterostracans and 'thelodonts', has been dealt with in detail by Allen & Tarlo (1963) for the Downtonian and Lower Devonian of the Welsh Borderland, Märss & Einasto (1978) for the Silurian of Saaremaa, and Goujet (1984) for the Lower Devonian of Spitsbergen.

Allen & Tarlo's (1963) now classical study on the Downtonian and Dittonian fish-bearing facies of the Welsh Borderland certainly provides the most convincing data in favour of the fresh water habitat of the Osteostraci, with exception of the non-cornuate genus *Hemicyclaspis* and the cornuate genera *Didymaspis*, *Sclerodus* and *Auchenaspis*, all found in near-shore, marine facies of the Downtonian. The sequence of the Welsh Borderland clearly suggests that the sudden appearance of cephalaspidians, scolenaspidians and benneviaspidians in the fossil record is concordant with what is regarded as the beginning of fresh water sedimentation. Since I am not a sedimentologist, I rely entirely on the data present by Allen & Tarlo (1963) and Allen (1964, 1974, 1979) which suggest that osteostracans lived in a flood plain environment in Lower Devonian times. However, I must admit that I have difficulty in believing that they lived in head waters and lakes, as stated recently by White & Toombs (1983).

Goujet (1984) made a critical analysis of Denison's (1956) and Friend's (1965; Friend *et al.* 1970) conclusions that the Old Red Sandstone of Spitsbergen, as well as that of Great Britain and Podolia, were deposited in a fresh water environment. He pointed out that geologists often rely on the palaeontologist's opinion, and *vice versa*: the Old Red Sandstone is a fresh water sediment because it contains fresh water fish (and no marine invertebrates), and these fish must have lived in fresh water, because the Old Red Sandstone is a fresh water sediment! Goujet's conclusion is that the Old Red Sandstone, at least in Spitsbergen, was deposited in a near-shore marine environment because: (i) the Wood Bay Formation contains inarticulate marine brachiopods associated with vertebrate remains (*Doryaspis*, *Arctolepis*, etc.) (particularly in the Kapp Kjeldsen and Lykta divisions); (ii) most of the taxa found in Spitsbergen have a Europe-wide, if not a world-wide distribution, thus suggesting marine dispersal routes; (iii) the Red Bay group and the Wood Bay Formation yielded trace fossils *Cruziana* and *Ruzophycus*, referred to trilobites and (iv) the Stjørdalen division of the Wood Bay Formation contains several arthrodire petalichthyid and porolepiform genera (*Heterogaspis*, *Actinolepis*, *Wijdeaspis*, *Heimenia*) which pass into the overlying, undoubtedly marine, Grey Hoek Formation; thus, these forms would be fresh water dwellers when found in red sandstone, and marine when found in calcareous sediments.

A third palaeocological study has been made by Märss & Einasto (1978) on the distribution of the vertebrates in the various facies of the Upper Silurian of the Palaeobaltic basin of Estonia. This very detailed analysis shows that the Wenlockian and Ludlovian osteostracans, anaspids and 'thelodonts' occur mainly in a 'lagoonal' environment, defined by these authors as follows: calm water conditions, where dolomites are deposited (1, figure 5). This facies contains traces of limivorous invertebrates, stromatolites, eurypterids, inarticulate brachiopods and conodonts. Further toward the open sea, a second type of facies, referred to as the 'sand belt facies', consists of sandy limestone with numerous shell, coral and bryozoan remains, associated with bone beds of fragmentary osteostracan, heterostracan and acanthodian remains. The Heterostraci are predominant in this latter facies (2, figure 5). These authors, then, defined three open-sea facies: (i) the platform facies (3, figure 5), from the wave zone to the outer margin of the platform; (ii) the slope facies, from the outer margin of the platform to the bottom of the basin (4, figure 5); and (iii) the basin facies (5, figure 5), which consists of bituminous sediments with graptolites and no vertebrate remains. The Heterostraci, Acanthodii and Osteichthyes (represented there only by *Andreolepis* and *Lophosteus*, both referred to the Actinopterygii) occur mainly in or outside the sand belt facies, acanthodians being particularly abundant in the slope facies (*e*, figure 5). Moreover, thyestidians similar to those of Estonia are relatively abundant, though fragmentary,

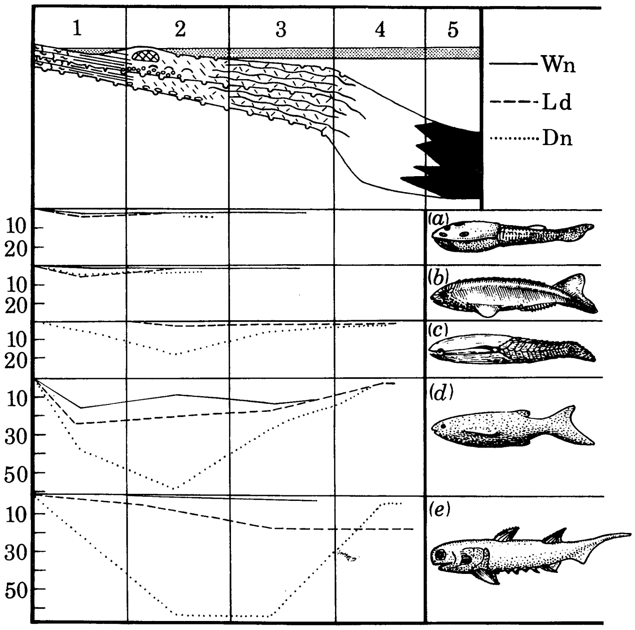

Figure 5. Distribution of the vertebrate remains in the various facies of the Upper Silurian of Estonia (adapted from Märss & Einasto 1978). Facies: 1, lagoonal; 2, sand belt; 3, open platform; 4, slope; 5, deep basin. Intertidal amplitude in grey. Taxa: (*a*) Osteostraci; (*b*) Anaspida; (*c*) Heterostraci; (*d*) 'Thelodonti'; (*e*) Acanthodii. The graphs are established for the Wenlock (Wn), Ludlow (Ld) and Downtonian (Dn). The numerical data represent the numbers of specimens referred to the respective taxa in a sample.

in the marine Ludlow of Gotland. This is concordant with the opinion expressed by Allen & Tarlo (1963) that the thyestidians known from the Downtonian of the Welsh Borderland (*Auchenaspis* and perhaps *Sclerodus*) lived in a near-shore marine environment. In the particular case of the thyestidians, we are thus concerned with a chiefly marine group, living in the intertidal or lagoonal environment, and protected from the waves by a sand belt.

This brief review of the three most reliable studies on the environment of the Osteostraci shows contradictory interpretations, particularly of the Old Red Sandstone facies of Spitsbergen. No other important osteostracan-bearing locality has been analysed from a palaeoenvironmental point of view, although sporadic remarks may be recorded here and there. Heintz (1969), for instance, mentions that in Nes (Ringerike area, Norway), marine ostracods and bryozoans are found 'quite close' to the 'Agnatha layer'.

However accurate they may be, these analyses can hardly lead to any general conclusion. The supporters of the fresh water habitat may argue that the fish remains have been washed down to the lagoons where inarticulate brachiopods lived. In contrast, the supporters of the marine habitat will rejoin by saying that the vertebrate remains are too fragile to be transported over a long distance, and that the lack of marine invertebrates in the Old Red Sandstone is because this type of sediment is not favourable to the preservation of calcareous shells (in fact, when the sandstone is slightly calcareous, such as in the *vogti* horizon of the Ben Nevis Formation of Spitsbergen, many bivalves occur). One may thus reach the unsatisfactory conclusion that the Osteostraci, like most modern fish groups, had marine and fresh water representatives, and that no generalization can be made as to the mode of life of the whole group.

Remarks on other Devonian vertebrate faunas found in an Old Red Sandstone facies

The problem met in the Lower Devonian as to the habitat of osteostracans occurs also in later vertebrate-bearing localities, exemplified here by the ichthyostegid-bearing *Remigolepis* Group of East Greenland (Spjeldnaes 1982) and the Upper Devonian Antalya red sandstone of southwest Turkey (Janvier & Marcoux 1976; Janvier 1984*b*).

Spjeldnaes concludes, from his palaeoecological analysis, that the ichthyostegids may have lived in 'water bodies' connected with the sea, but not typically marine (because of the lack of marine invertebrates). His main argument is the same as one of Goujet's, namely the widespread distribution of the placoderms and lungfishes associated with the ichthyostegids. He also relies on Dasch & Campbell's (1970) isotopic evidence suggesting an originally marine habitat for placoderms, lungfish and crossopterygians.

The Antalya (Armutgözlek Tepe) red sandstone, now referred to the Famennian (Janvier 1984*b*), contains antiarchs, groenlandaspids, holonematids, phyllolepids, acanthodians, lungfish, and osteolepidids, but no marine invertebrates. The association of holonematids, reputedly marine and generally found in inter-reef facies, with bothriolepidid antiarchs and phyllolepids, reputedly fresh water dwellers, throws doubt on the idea that there are clear-cut differences in the mode of life of these several groups. This particular locality is regarded as corresponding to the intertidal zone, with communications open toward the sea.

CONCLUSIONS

Evidence from geology leads to the conclusion that there were both marine and fresh water osteostracans, at least if one postulates that the animals lived in (or very near) the places where they are found as fossils (this question of the possible transportation of osteostracan shields has been dealt with by Allen & Tarlo (1963) and White & Toombs (1983); I consider that most osteostracan shields were so fragile that they cannot have been transported over a long distance). There is no evidence that any *species* was anadromous, since not one is known from both reputedly marine and fresh water deposits. The argument put forward by Westoll (1946, 1958) and Allen & Tarlo (1963), that the presence of the same taxa in remote areas such as Spitsbergen, Podolia and Great Britain shows that dispersal must have occurred through marine routes, seems unconvincing to me, although Goujet (1984) also uses it as an argument for the marine habitat of Lower Devonian placoderms. Firstly, there are virtually no species common to these three areas, except *Cephalaspis cradleyensis* in Spitsbergen and Great Britain, and perhaps *Zenaspis salweyi* in Podolia and Great Britain, although conspecificity is very doubtful in both cases. Only sister species of the same genus may occur in two widely separate areas, such as the two species of the genus *Stensiopelta* in Podolia and Wales respectively. Secondly, such a distribution can be explained either by vicariance (from a widely distributed ancestral species), or by progressive enlargement of the area of distribution, due to interconnections between fluvial basins.

The distribution of other groups, such as heterostracans, placoderms, acanthodians and osteichthyans, found in association with osteostracans complicates the problem. Again, there may be marine and fresh water species in the same genus or family. No attempt to find congruence between the distribution of the various taxa has hitherto been made, and the time is not ready for such an analysis, since most of these groups deserve phylogenetic and taxonomic revision.

Thus the question, 'is there a link between the rise of the fresh water habitat and the radiation of the Osteostraci?', can be answered at two different levels. If one trusts the palaeontological record, the sequence of the Welsh Borderland suggests that the near-shore marine osteostracan fauna was less diversified than the reputedly fresh water fauna and, consequently, that the radiation of the cornuates coincides with the Silurian–Devonian transition. Alternatively, it may be argued that the reason why cornuates are so scarce before the Gedinnian is simply that no sediment (be it marine or not) similar to the Old Red Sandstone of the Welsh Borderland is known earlier in the Silurian. I prefer the latter explanation, since the phylogeny of the Osteostraci implies that most cornuate groups existed long before the Lower Devonian.

Future studies on the environment of the Upper Silurian and Lower Devonian vertebrates should, initially, attempt to settle the question of the model to be used for the Old Red Sandstone environment. King (1934) and Allen (1974) have compared it with various Recent models (the Gulf of Pohai and the Colorado delta), but one may question if all the physical parameters were the same as they are now. How would marginal sedimentation differ if the Earth were smaller and consequently the gravity higher than now, as suggested by some geologists (Owen 1981)? Were the tides the same as now? Depending on the answers to these questions, we may consider an environment which has no Recent equivalent such as the possibility of vast flood plains invaded by considerably higher tides than now. With reference to tides in the Palaeozoic, one must note that whatever palaeogeographical reconstruction is considered, the interplay between marine and continental tides must have been different from those seen now, even with a constant Earth radius, since continents had a very different distribution.

The limits to what can be deduced from the fossils themselves, concerning the environments of Siluro-Devonian vertebrates, is very near to being reached. What is left is the search for congruent patterns in distribution, which may point toward a particular interpretation, but unfortunately, incongruent patterns of distribution still predominate. The key to less contradictory palaeoecological reconstructions may be found in palaeobiogeography (indicating to us whether these animals were sensitive to either marine or continental barriers), and perhaps also in less traditional geophysics, which would produce models of environments which no longer occur.

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Discussion

L. B. Halstead (*Department of Geology, University of Reading, RG6 2AB.*). The work on the Baltic succession by Märss & Einasto (1978) does not contradict the early synthesis on the Welsh Borderland by Allen & Tarlo (1963), but indeed provides confirmatory evidence of inherently marine faunas during Silurian times. The work of Daniel Goujet on Spitsbergen, however, although demonstrating the influence of marine conditions at certain horizons, by virtue of the presence of the brachiopod *Lingula*, in no way undermines the vast accumulation of sedimentological data, demonstrating the existence of important and dominant alluvial regimes in the Lower Devonian of Spitsbergen. To claim the Spitsbergen successsion as essentially marine would seem to be grossly mistaken.

The view that *Tremataspis*, the early cephalaspid without paired fins or cornua and with a cyathaspid-like carapace is a derived cephalaspid seems highly improbable. The shape of the carapace is such that any movement from the trunk or tail end will automatically generate lift. This geometry seems to be common to the most primitive members of different groups of jawless vertebrates. I find incomprehensible the suggestion that, in the case of the tremataspids alone, this shape is attributed to a reversion back from a more advanced and highly manoeuvrable cephalaspid.

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P. Janvier. I admit that findings of well-preserved inarticulate brachippods in the Lower Devonian Old Red Sandstone of Spitsbergen are very local, and may not indicate that the whole series of detritic sediments is marine, but one must also note that, whenever these sediments are studied by formic acid dissolution of the matrix, numerous fragments of lingulid shells occur, in association with vertebrate remains, even if complete lingulids are not preserved. Thus, marine episodes seem to be much more frequent in this series than previously believed. These data do not exclude the fact that there was an important flow of detritic sediments which was constantly brought by streams into the marginal marine environment. Whether the vertebrates were brought from streams with the detritic sediments or were killed by an excessive flow of fresh water pouring into their marine habitat is a still unanswered question. Lingulids are marine organisms, but they can stand very important variations of salinity and often indicate the proximity of deltas.

T. S. Westoll, F.R.S. (*Department of Geology, University of Newcastle upon Tyne, Newcastle upon Tyne, NE1 7RU.*). Dr Janvier considers that *Tremataspis*, a non-cornuate cephalaspidomorph with a thoroughly tadpole-like shape, is secondarily devoid of cornua and pectoral fins. *Tremataspis* is overwhelmingly the commonest fish in the Oesel (Saaremaa) beds, which are probably close to the Wenlock–Ludlow boundary. The next commonest are such genera as *Dartmuthia* and *Oeselaspis*, and cornuate genera (*Procephalaspis*, *Thyestes*) are rare.

I regard the non-cornuate form as primitive; if they are not, what adaptive advantage does Dr Janvier perceive in their loss of fins?

P. Janvier. The point raised in my communication is essentially that both the most primitive (*Ateleaspis*, *Aceraspis*) and some of the most advanced (Tremataspids) osteostracans coexisted by the end of Wenlockian times and, thus, that the rise of the Lower Devonian 'fresh water' environment did not really 'trigger' the appearance of new major groups of osteostracans but may have just favoured the increase of their diversity and number of species within pre-existing groups. The Tremataspididae share with *Thyestes* and *Procephalaspis* (two cornuate osteostracans with movable paired fins) a number of characteristics that do not occur in any other known osteostracan. These characteristics are probably not linked, since they concern the structure of the exoskeleton, the structure of the dorsal and lateral fields, the course of the cranial nerve canals and the blood vascular canals. Consequently, like Stensiö (1927), Wängsjö (1952) and Heintz (1939), I consider that these taxa form a monophyletic group, the sister group of which may be the kiaeraspids, another group of cornuate osteostracans. If the '*Cephalaspis*'-like pattern (such as that of *Procephalaspis*) is plesiomorphous, the condition in tremataspids must be regarded as derived. By contrast, if one admits that tremataspids are 'stem' osteostracans, as did, for example, Westoll (1945) and Denison (1951), with *Thyestes* and *Procephalaspis* being intermediate forms between them and the Lower Devonian cornuate osteostracans, this would lead to unparsimonious conclusions as to the position of the non-cornuate forms such as *Ateleaspis*, *Aceraspis*, *Hirella* and *Hemicyclaspis*, for which one would have to postulate a number of reversions (ventral exoskeleton, loss of the cornua, etc.) and independent appearance of characters (anterior dorsal fin, etc.).

The question of why tremataspids would have lost their paired fins is beyond the scope of character analysis and leaves the door open to any kind of speculation. It may be due to a fossorial mode of life in a muddy environment. It is noteworthy that the tail of tremataspids also undergoes a considerable reduction, the usually elongate lepidotrichia-like scales of the caudal fin of *Tremataspis* gain a tessellate pattern which suggests that it was less movable than in other osteostracans.

Finally, I cannot accept the argument that tremataspids are primitive because they have a primitive 'geometry'. With such a logic, one would be entitled to consider that snakes are not tetrapods, and that they should be closely related to eels!

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