

The evolution, radiation and biogeography of early spiriferid brachiopods

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Abstract – Spiriferid brachiopods originated in South-East Asia during the Late Ordovician and subsequently became geographically widespread during the Silurian. This study deals with the ways this took place, the routes taken during the expansion of this group and the implications to palaeogeography. During the Silurian, two peaks of diversification are recognised. The principal evolutionary trends evident within different lineages are outlined.

INTRODUCTION

Until recently, one of the most prolific group of brachiopods, the spiriferids, was thought to have appeared in South China during the Early Silurian, but it has been now shown they originated in the Late Ordovician (Rong *et al.* 1994; Rong and Zhan 1996). This investigation probes the mode of development and geographical dispersal patterns of spiriferids during the Silurian. In order to obtain reasonable precision, a comprehensive database on Silurian spiriferid species was compiled using published literature.

In the course of the revision of the Treatise on Invertebrate Paleontology, Brachiopoda, some repeated, but incorrect, suffixes (e.g. «*idid*») created some difficulties for informal useage. All the authors endorsed the following suggestion: use «*id*» in place of «*idid*», etc., with lower case letters for informal use and, in all formal uses, uppercase first letter and termination in accordance to the ICZN code. This principle is applied herein. The families discussed below are those defined and recognised by Carter *et al.* (1994).

METHODS

The database for this investigation was compiled using recent published works (species lists published after 1980) in order to avoid nomenclatural confusion. Most works include revised lists of previously published material. Where recent papers were unavailable for certain regions, older data was used. In such cases, where necessary, original designations were re-evaluated to fit modern taxonomic concepts. The range of each species was compared to current graptolite zonation, where available, so as to obtain detailed, homogeneous age control. Silurian spiriferids consist of more than 360 species in 46 genera, 25%

of which are in open nomenclature. Space limitations preclude publication of the entire species list but requests for this information can be sent to the author.

ORIGIN OF SPIRIFERIDS

Both monophyletic and polyphyletic origins have been suggested for the spire-bearing brachiopods. Copper (in Copper and Gourvenec, 1996), in suggesting a monophyletic origin, points out that this option would require the presence of a complete jugum in the early eospiriferids. In the polyphyletic theories put forward, the spiriferids are derived either from an impunctate orthid, possibly a platyorthid (Wright 1979), or from a rhynchonellid stock (Grunt 1982). These different options are reviewed in Copper and Gourvenec (1996) who conclude that «new morphological discoveries in the oldest species from each of the three orders [respectively Atrypida, Athyrida and Spiriferida] will probably dictate the ultimate phylogenetic scenario».

In their recent work, Rong and Zhan (1996) identified a ventro-laterally directed spiridium and a small jugal process, but no jugum, in the early spiriferids, *Eospirifer* and *Strispirifer*. A re-examination of the monophyletic theory, in terms of parsimony, is therefore warranted. Focusing on the early stages of development of the brachidium, Rong and Zhan (1996) suggested possible relationships between early spiriferids and atrypoids and a common ancestor for the two groups. Although most of the early atrypoids possess a jugum, one of them, *Cyclospira*, lacks this structure and is reminiscent of *Eospirifer* but presents significative differences with other early atrypoids. Thus Rong and Zhan suggested a common ancestor for *Eospirifer* and *Cyclospira*.

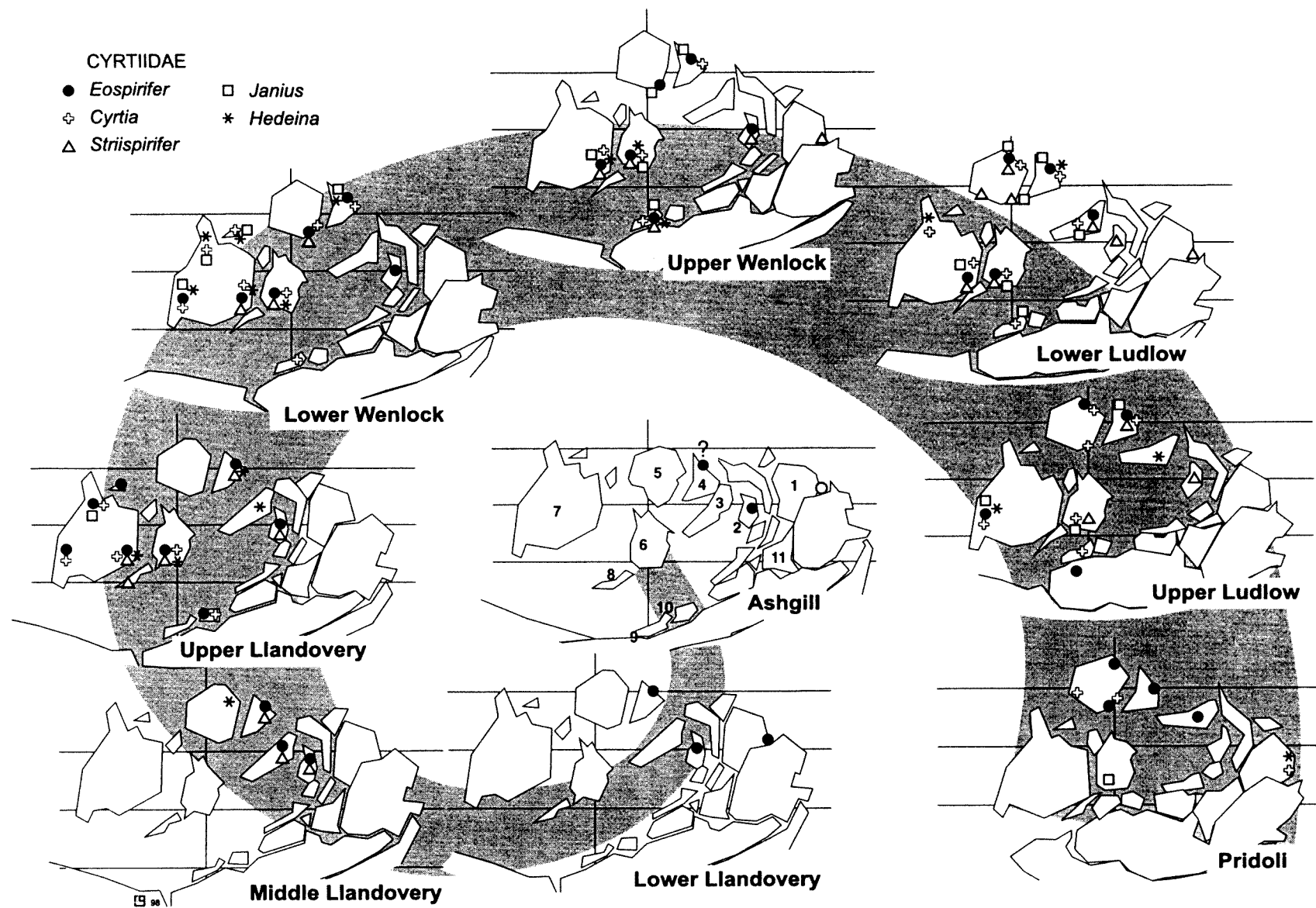


Figure 1 Palaeogeographical distribution of some Cyrtiidae during the Late Ordovician and Silurian. For the Ashgill, full circles represent middle Ashgill occurrences and open circle an upper Ashgill occurrence. 1: Australia; 2: South China; 3: North China; 4: Kazakhstania; 5: Siberia; 6: North Europe; 7: North America; 8: Avalonia; 9: Irbarmaghian Domain; 10: Bohemia; 11: India. (Base map modified from Scotese and McKerrow, 1990).

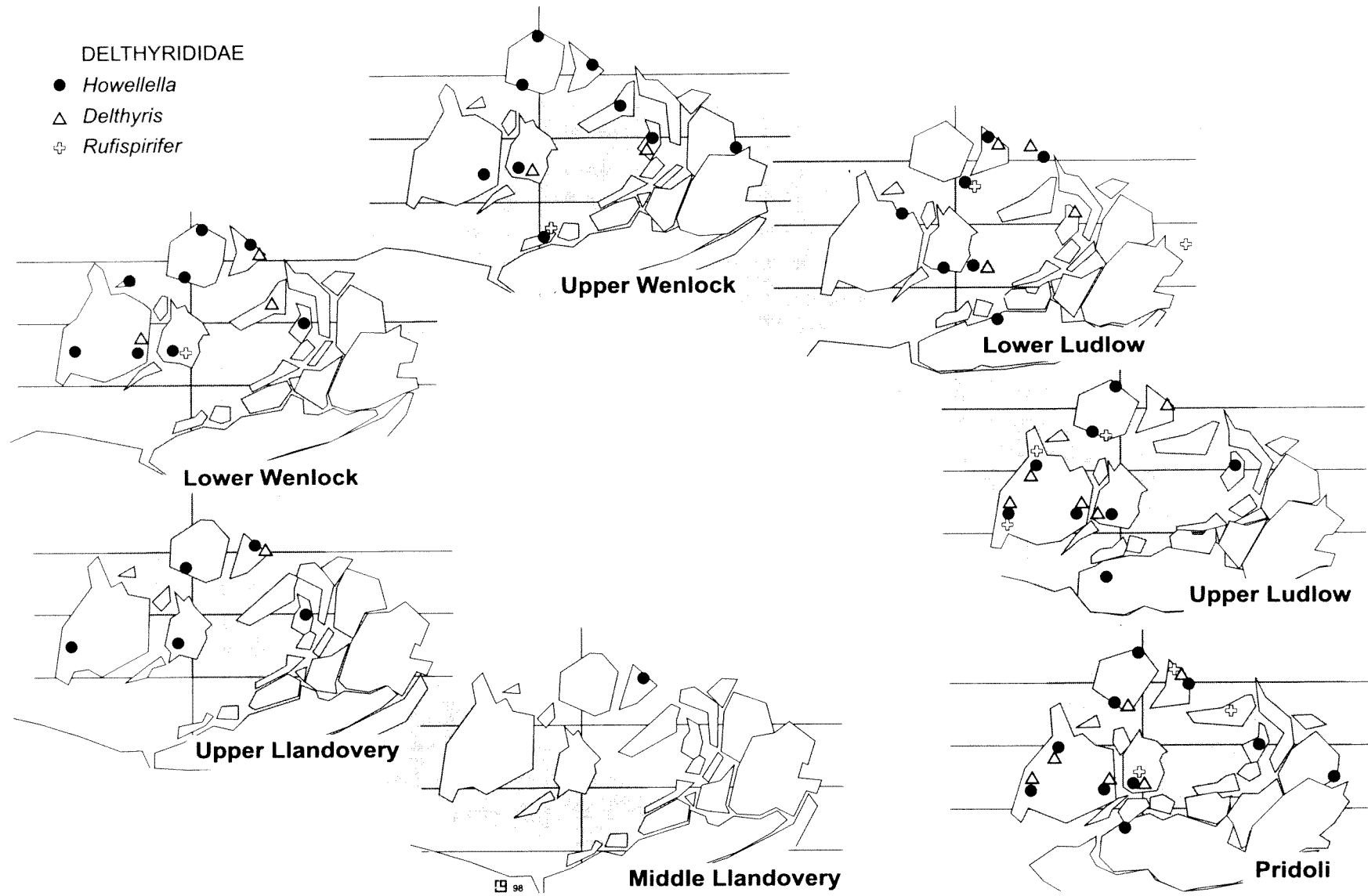


Figure 2 Palaeogeographical distribution of some Delthyrididae during the Silurian. (Base map modified from Scotese and McKerrow, 1990).

GEOGRAPHICAL DISTRIBUTION OF THE EARLY SPIRIFERIDS

The origin of the very early spiriferids in Late Ordovician sequences of South China has been documented by Rong *et al.* (1994) and Rong and Zhan (1996) who provided a detailed overview of primitive eospiriferine species and attempted to place them in an evolutionary perspective.

Eospirifer first appeared in the Ashgill Changwu Formation, Jiangshan area, SE China (Rong *et al.* 1994) and soon spread to neighbouring areas. During the lower Llandovery, *Eospirifer* reached Kazakhstan (Modzalevskaya and Popov 1995) where an Ashgillian occurrence is reported but not ascertained, and Tasmania (Sheehan and Baillie 1981) (Figure 1). From Kazakhstan *Eospirifer* dispersed to Central Asia during the Middle Llandovery and thence to Europe and North America during the Late Llandovery. During this time it also occurred in North China (Fu 1982). Significantly, *Eospirifer* is not reported from the Russian platform and is only sporadically present in the Altai Range and neighbouring areas. In South China, *Eospirifer* more or less survived the entire Silurian and is probably the centre of origin for the subsequent colonisation of Australia in the Early Lochkovian.

The endemic *Yingwuspirifer* also appeared in South China in the Early Llandovery, but did not survive the Llandovery-Wenlock transition. The catch-all genus «*Nikiforovaena*» also remained endemic to South China until the Llandovery-Wenlock boundary where it apparently «disappeared». However, it suddenly «reappeared» in the Lower Ludlow with a widespread distribution including South and North China, the Siberian platform and North-Western Europe. Rather than an example of the Lazarus effect, the reappearance is more likely due to the fact that earliest «*Nikiforovaena*» probably belong to another genus (see below).

South China remained a spiriferid nursery in the Middle Llandovery, since it is also the centre of origin of *Striispirifer*, a genus which becomes geographically widespread during the Upper Llandovery with occurrences recorded in North China, Europe and North America (Rong and Yang 1981; Boucot 1963; Figure 1). *Striispirifer* is also sporadically reported in Central Asia (Rong *et al.* 1985) and the Russian platform from Wenlock to Ludlow sequences (Modzalevskaja 1990). *Striispirifer* reached Australia during the Upper Wenlock (Strusz 1985) but disappeared during the Lower Ludlow. In Europe and North America, it survived until the Late Silurian.

Another early spiriferid nursery is represented by sequences in Kazakhstan with the documentation of *Eospirifer* in the early Llandovery (Modzalevskaya and Popov 1995). *Eospirifer* is also questionably reported from the Ashgill Ulkuntas

Horizon by Sapelnikov and Rukavischnikova (1975). The first occurrence of *Howellella* is also reported from this region, possibly from Middle Llandovery beds. The origin of *Howellella* is thus fairly well constrained, with the only possible ancestor present in the region at this time being *Eospirifer*. In the Upper Llandovery, *Howellella* rapidly dispersed all over the world with occurrences reported almost everywhere, Australia and North Africa excepted (Figure 2). *Hedeina* originated in Tuva approximately at the same time (Middle Llandovery). Again the only possible ancestor is *Eospirifer*. *Hedeina* became extinct at the end of the Llandovery in Tuva, but spread to the Russian platform, Europe and North America during the Upper Llandovery. In addition to the above mentioned genera, early endemic taxa appeared in Kazakhstan (the short lived *Espella*, Middle Llandovery) and on the Russian platform (*Eohowellella*, extinct in the Lower Ludlow).

In the Upper Llandovery new genera appeared for the first time outside of South-East Asia. Among them is the ubiquitous appearance of *Cyrtia*. This genus occurs synchronously in sequences from Northern Europe, Turkey, Northern and eastern America (Figure 1). With its peculiar external shape and internal morphology this genus is unmistakable in the fossil record, so that its rapid widespread distribution, like *Howellella*, is somewhat puzzling.

The appearance of endemic taxa in the Upper Llandovery slowly increased the diversity rate of spiriferids. *Mictospirifer* from central North America became extinct at the end of the Llandovery and *Myriospirifer* occurs for the first time in the Baltic area (though this identification is questionable, since it is not reported from Upper Wenlock to Lower Devonian sequences). Another significant genus is *Spirinella* which first appears in North America (Great Basin) in the Llandovery, and subsequently expands to the Canadian and Russian Arctic regions during the Wenlock, and thence to Bohemia, Mongolia, South China and Australia in the Ludlow (Figure 3).

No major evolutionary events occurred during the Lower Wenlock. Besides the stock of existing spiriferids, new taxa, most of them endemic, arose in Bohemia (*Araspirifer*), Arctic Canada (*Dicoelospirifer*, *Plicocyrtia* and *Eoplicoplasia*, another Lazarus genus), and the eastern Urals (*Eoreticularia*, *Pavdenia*). Special mention is made of the genus *Delthyris* that appeared in Central Asia in the upper Llandovery, and underwent a successful expansion first towards North China and North America (lower Wenlock), and then towards Europe and south China (upper Wenlock). The presence of *Spurispirifer* in the Lower Wenlock of the Arctic Canada (Zhang 1989) is highly questionable: all other known occurrences are from Upper Wenlock to Early Devonian sequences in Bohemia.

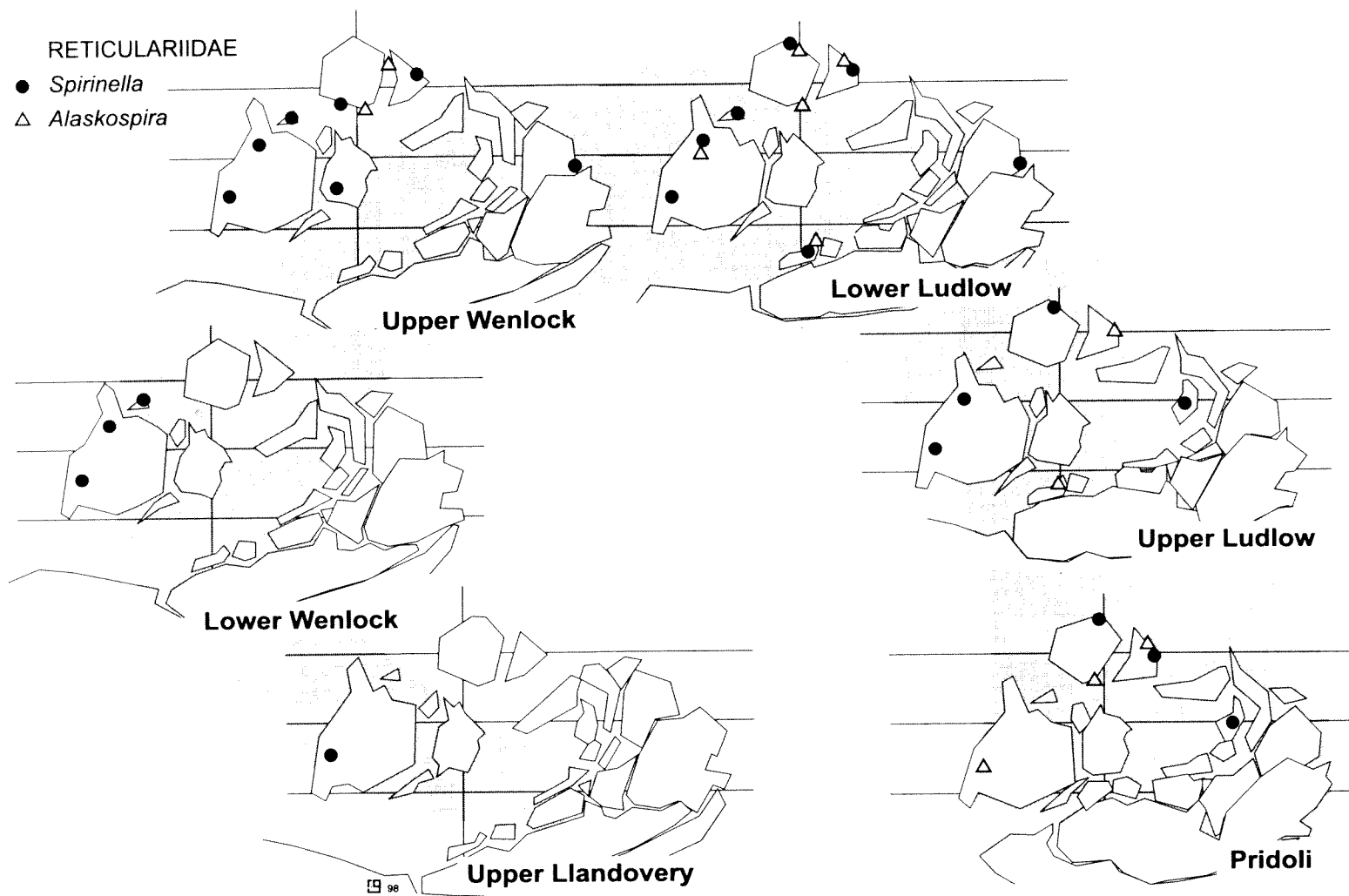


Figure 3 Palaeogeographical distribution of some Reticulariidae during the Silurian. (Base map modified from Scotese and McKerrow, 1990).

The greatest diversity of spiriferids occurred during the Upper Wenlock. Thirty one genera have been reported including twelve new taxa (Figure 4). Only one genus (*Dicoelospirifer*) became extinct. The three main centres of origin of new genera were Central Asia and the Urals (*Acanthospirifer*, *Alaskospira*, *Nurataella*, *Quadrithyris*, *Tannuspirifer*, *Havlicekia*), Europe (*Aldanospirifer* (*Holcospirifer*), *Rufispirifer*, *Spurispirifer*, *Tenellodermis*, *Hedeinopsis* and *Kozlowskiellina*, the two latter being also reported respectively in North Africa and North America) and Australia (*Endospirifer*, *Reticulariopsis* and *Vadum*). These three regions are reminiscent of the three Late Silurian (Ludlow) brachiopod provinces (*Tuvaella* fauna, *Dayia* fauna and *Retziella* fauna) discussed by Rong *et al.* (1995). With such diversity and numerical expansion, the Upper Wenlock appears to have been a turning point in the history of spiriferids. This evolutionary trend appears to be a consequence of the early-middle Homerian bioevent (Valleviken-Mulde event) that was marked by a strong decrease in relative sea-level, perhaps related to a glacial event (Kaljő *et al.* 1995). This event resulted in a mass extinction followed by a radiation during the *nassa* graptolite zone (Kaljő *et al.* 1995). It is clear that spiriferids

were not greatly affected by this extinction event, but took advantage of the ecological and/or climatic conditions following this event as indicated by their rapid radiation.

During the Lower Ludlow only three new genera are known; *Chnaurocoelia* in Nevada, *Dongbeispirifer* and *Protoreticularia* in North China. All are short lived and restricted to the Ludlow. A significant number of genera (7) do not cross the Wenlock-Ludlow boundary including *Acanthospirifer*, *Eohowellella* and *Pavdenia* in Central Asia-Urals-Russian platform. It should also be noted that *Quadrithyris* and *Tannuspirifer* have not been reported from this area at this time (but do reappear later). In Australia, *Endospirifer* and *Vadum* become extinct and *Reticulariopsis* is absent. In Bohemia, *Rufispirifer* and *Plicocyrtia* disappeared, and *Araspirifer* and *Spurispirifer* are not reported before the Upper Ludlow. Elsewhere, taxa remained stable or expand into new areas (e.g. *Alaskospira* arrived in Bohemia and North China, *Delthyris* and *Havlicekia* in North America).

The main tendencies of this relatively stable period continued during the upper Ludlow and Pridoli with, respectively for each period, only one

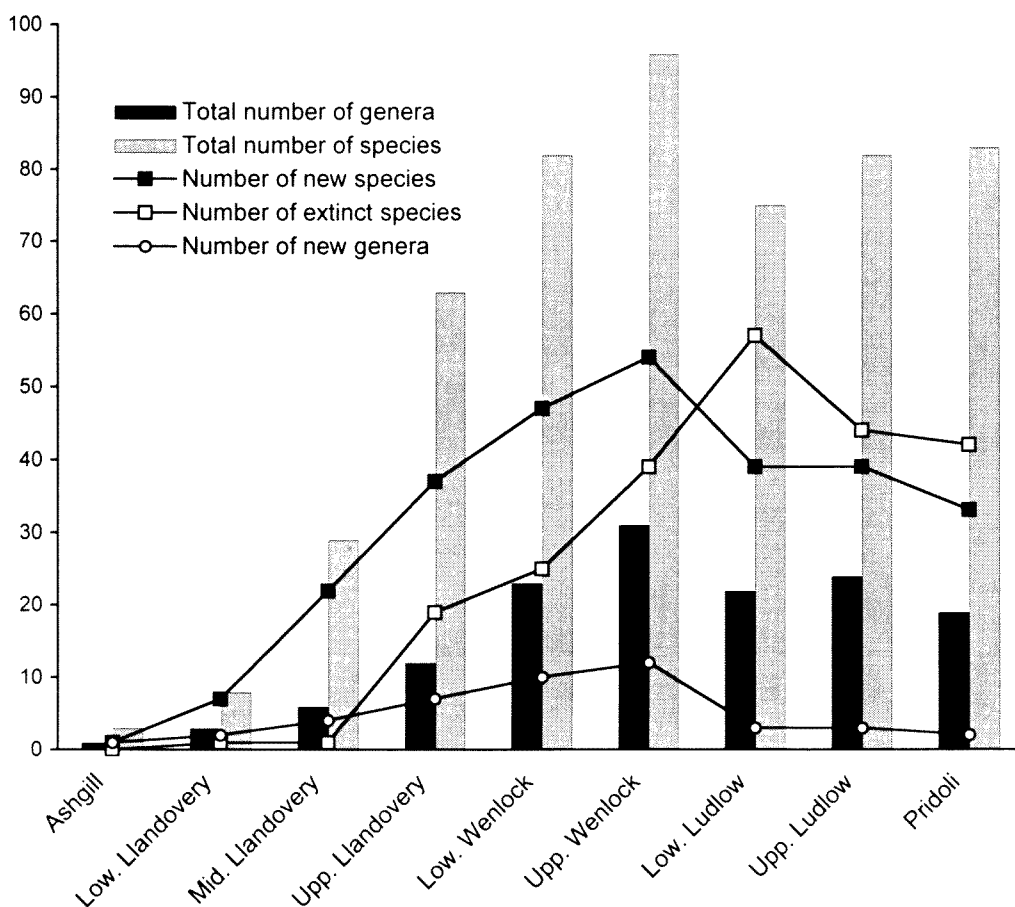


Figure 4 Evolution of the number of spiriferid genera and species during the late Ordovician-Silurian period.

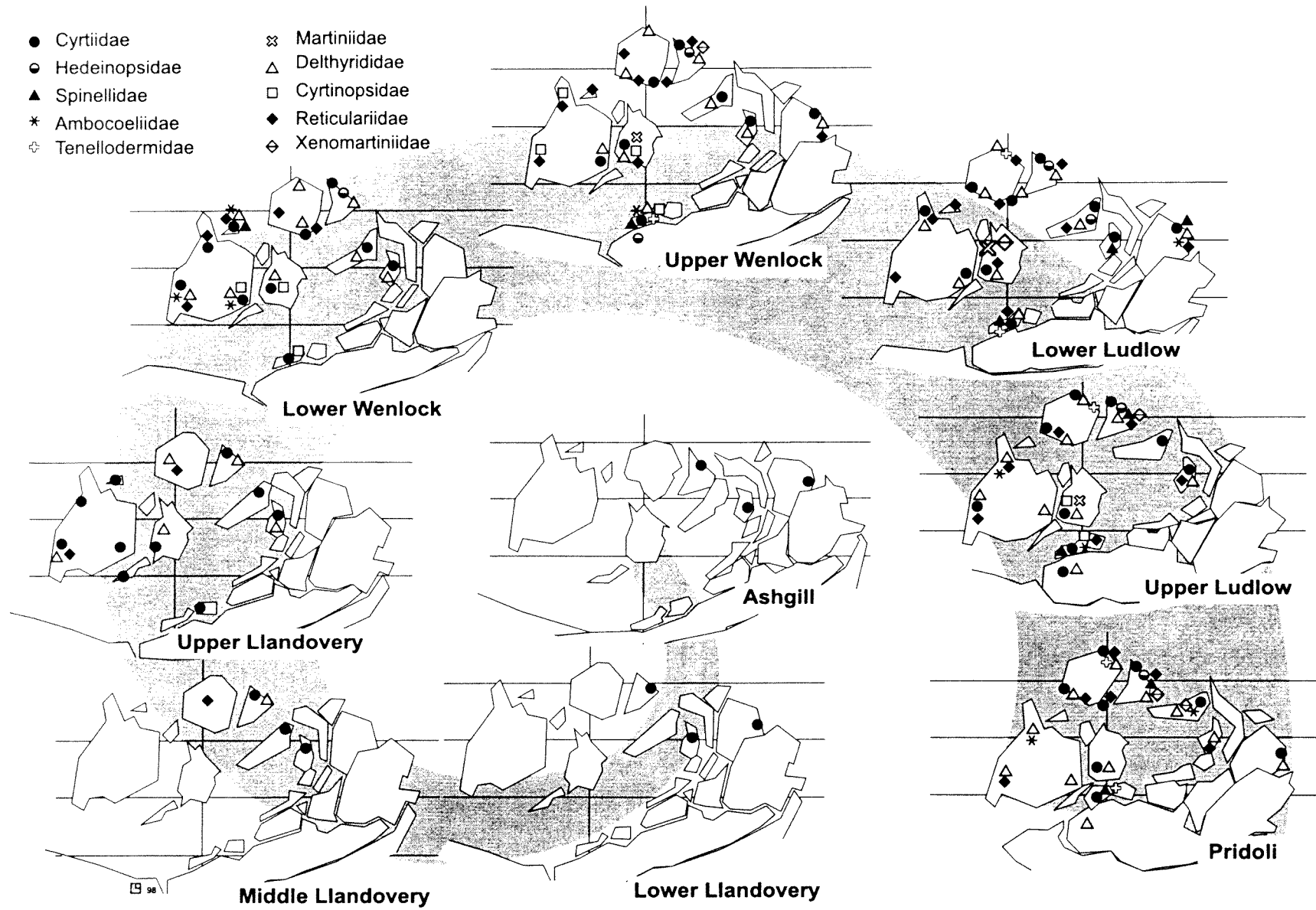


Figure 5 Palaeogeographical distribution of the late Ordovician-Silurian spiriferid families.

new taxon (*Altajella*, Ludlow, Salair; *Grebenella*, Pridoli, Russian Arctic) and three extinct taxa (*Hedeinopsis*, *Nurataella*, *Protoreticularia*, Upper Ludlow; *Araspirifer*, *Chnaurocoelia*, *Dongbeispirifer*, Pridoli). The next radiation event occurred at the Siluro-Devonian boundary.

From these observations it is possible to reconstruct a preliminary model of the distribution of the first spiriferids. The group appeared in South China and then followed a migration route via south central Asia (Kazakhstan), Europe and North America. This counterclockwise colonisation is almost completely restricted to the tropical belt. Later migrations occurred in many directions. The majority of migrations clearly occurred in the Upper Llandovery (Figure 5). Diversity increased slowly during the Ashgill and Early Silurian, became more rapid up to the upper Wenlock, and finally decreased until the Pridoli.

STRATIGRAPHIC DISTRIBUTION OF GENERA

Figure 6 shows that significant gaps occur in the stratigraphic distribution of early spiriferids. This phenomenon, known as the «Lazarus effect», may have different causes. Firstly, misidentification may occur when a taxon is poorly defined and/or difficult to identify. This may be the case for *Nikiforovaena*, for which the earliest occurrences are questionable. For some Lazarus taxa lack of sampling in poorly accessible areas may have affected the stratigraphic distribution. On the other hand, some well defined taxa are apparently missing in some strata. This is true of *Myriospirifer*, which is recorded in the Upper Llandovery of the Baltic area and Lower Wenlock of Bohemia (Havlíček 1995). However, the next occurrence of *Myriospirifer* is in Pragian sequences from Brittany (Gourvennec 1989) and possibly Moravia (Havlíček and Mergl 1990). The genus becomes more common during the Emsian in Bohemia, the Carnic Alps, Harz Mountains, and North Africa. Such a disjunct stratigraphic pattern (Upper Wenlock- Pragian) is puzzling and cannot be satisfactorily explained at present. The traditional explanation (migration) is unlikely in this case. A similar situation prevails with *Reticulariopsis* for which no occurrence are known in the Late Silurian. Nevertheless, the unique lower Ludlow occurrence in Australia has been verified (Gourvennec 1994).

In terms of evolutionary relationships, this situation potentially results in serious problems if the «missing taxa» are not properly identified. The family Cyrtinopsidae, for instance, has no known representative during the Lower Ludlow despite the cosmopolitan distribution of *Kozłowskiellina* in the upper Wenlock, so that the origin of the younger genera belonging to this family remains problematic. At this stage, the family

Ambocoeliidae similarly has no known representative during the Upper Wenlock. It could be that future studies, both on new collections and the re-study of old collections, might fill the gaps. Otherwise it is unlikely that genera separated by wide geographic and/or time gaps may have been genetically closely related. For example the supposed links between *Kozłowskiellina* and *Megakozłowskiella* need to be revisited. The last known *Kozłowskiellina* is reported from the lower Ludlow of Gotland (Bassett and Cocks 1974) and the first *Megakozłowskiella* appears in North America (and perhaps Salair) in the lower Lochkovian. This disjunct pattern in both time and space precludes a direct link between the two taxa. A potential link could be represented by *Araspirifer*, but this genus is neither close to *Kozłowskiellina* nor to *Megakozłowskiella* but rather recalls *Howellella* in external morphology.

PROVINCIALISM AND COSMOPOLITANISM

Some of the cosmopolitan genera require more detailed inquiry. Examination of the distribution of genera for each geological period, indicates that some taxa may temporarily become endemic e.g. *Nikiforovaena*, *Kozłowskiellina* or *Alaskospira* (Figure 6). This may be due to either biological or palaeogeographical reasons: the migration or disappearance of a taxon in several areas may be the result of unsuitable environmental conditions and this may affect the distribution of benthic communities. It is well known that periods of provincialism alternate with periods of cosmopolitanism (e.g. Boucot *et al* 1967, 1969; Talent 1972; Boucot 1983) and these fluctuations are related to major geological events. Only a few genera are not affected by global changes and the term «cosmopolitan» should be restricted to genera that remain widespread both in time and space, i.e. during their entire lifetime, except the period immediately following their origination. In terms of Silurian spiriferids, this represents about one third of the total number of genera for each period (Figure 6). This number is subject to revision since several endemic genera might represent minor variations of more widely distributed genera and/or be identified as synonyms when further investigations are undertaken.

For example, if the distribution of *Eospirifer* is considered, it is obvious that its geographical expansion is constant from middle Ashgill to upper Wenlock. But, from the lower Ludlow, the genus declined until its range was almost reduced to its original area of distribution in the Lower Silurian (South-eastern and Central Asia). *Eospirifer* finally became extinct in the Lower Devonian. However, there may be a gap in our present knowledge of this genus. *Eospirifer* is

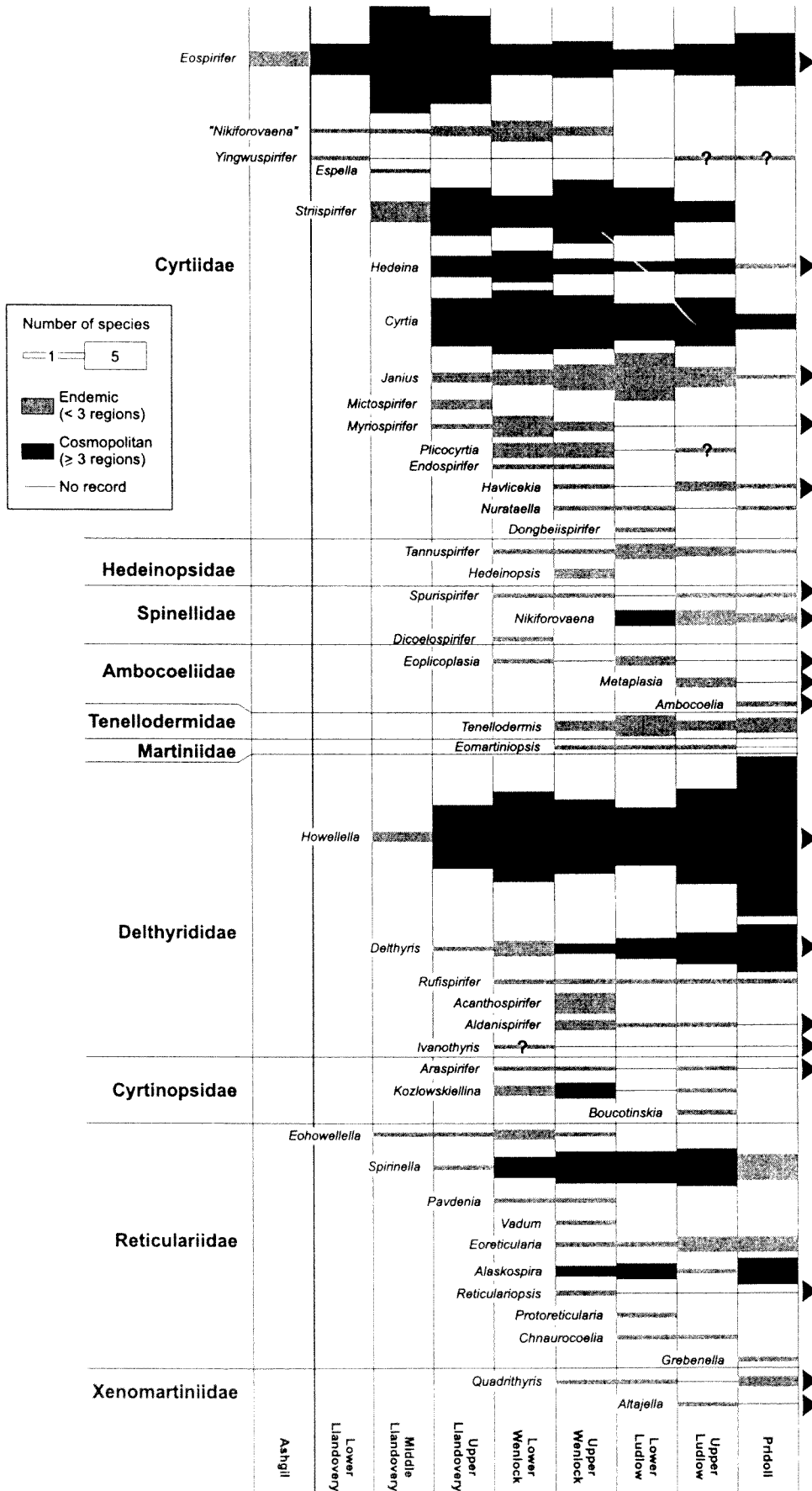


Figure 6 Diagram showing the stratigraphical distribution, number of species and level of endemism of the Silurian spiriferid genera.

recorded in the upper Wenlock and upper Ludlow of North-western America but is apparently absent during the lower Ludlow in this area. This is either a sampling artefact or represents the real decline of the genus. The same pattern is apparent for the occurrences in Turkey (upper Llandovery), Bohemia (upper Wenlock) and the Iarmaghian domain (upper Ludlow). In Bohemia and the Iarmaghian domain sampling bias cannot be suspected, but little is known concerning the Turkish domain. On the other hand, this situation may reflect difficulty for *Eospirifer* to migrate along the North Gondwanan margin. According to most reconstructions based on different groups of invertebrates or micro-organisms (e.g. Bergström 1990; Rickards *et al.* 1990), the palaeocurrents along the northern margin of Gondwana circulated in a counterclockwise direction, preventing migration of larvae from east to west. Furthermore, during the greater part of the Silurian, this region was located beyond the tropical belt (30° S) and thus did not represent a suitable climatic environment for the development of spiriferids.

EVOLUTIONARY TRENDS

The relationships between the very early spiriferids have been discussed by Rong and Zhan (1996). The first descendants of *Eospirifer*, namely *Yingwuspirifer orientalis* Rong and Xu 1974 and "*Nikiforovaena*" *primordialis* Rong and Yang 1981 are very closely related and are also close to *Eospirifer praecursor* Rong *et al.* 1994. All these species display a "primitive" morphology: reduced width (longitudinally extended to subcircular shells), fold sharply delimited by deep "sulci", resulting in a parasulcate commissure and indicating a tendency to plication of flanks (e.g. Rong and Yang 1978, pl. 1, fig. 8; Rong and Yang 1981, pl. 22, fig. 10 and 12; Rong *et al.* 1994, fig. 9–12). I follow here these authors designation of the species *primordialis* to "*Nikiforovaena*" with quotation marks. Carter *et al.* (1994) only considered upper Silurian (Pridoli) and Devonian species and thus recognised the presence of a ctenophoridium in *Nikiforovaena*. However, this structure is not present in "*N*". *primordialis* (cf. Rong and Yang 1981, fig. 59) and it seems that all Silurian species assigned to "*Nikiforovaena*" lack a ctenophoridium. Moreover, *Nikiforovaena sensu stricto* possess plicae on the flanks. So it seems likely that the Silurian "*Nikiforovaena*" belongs to another (probably new) genus. As far as is known, the type species of *Nikiforovaena*, *N. ferganensis* (see Nikiforova 1937) has not been revised and the inner structure of the dorsal valve is not known.

Spurispirifer (Pinguispiriferinae) and *Tenellodermis*

(*Tenellodermidae*) are very close both in external aspect and internal structure. They differ only in micro-ornament. Havlíček (1971) suggested the existence of a common ancestor for these two genera. If only the external morphology is considered, *Howellella* may have been a possible ancestor, but the "advanced" aspect of its micro-ornament precludes such a relationship. A common ancestor among the Cyrtiidae is more likely and *Striispirifer* with its "howellelliform" morphology and lack of a ctenophoridium, may be a possible candidate.

Another evolutionary tendency in early spiriferids is the gradual loss of the fold/sulcus (*Espella*) accompanied by the emergence of complex internal structures (cruralium). This stock is probably by neotenic development, at the origin of the Ambocoeliidae, characterised by aberrant or complex structures, uncommon among other spiriferids (e.g. reduction of interareas, bisulcate commissures, often accompanied by the strong or total loss of crural or dental plates, etc.). Concurrently, the acquisition of a rudimentary delthyrial plate in *Nurataella* is accompanied by a nearly flat dorsal valve reminiscent of the ambocoeliids. A common ancestor with *Espella* may have been, by neotenic development, at the origin of *Eoplicoplasia* and its descendants. Differential development of the dorsal and ventral valves also exists in the lineage that leads from *Hedeina* to the Araspiriferinae, with a marked elevation of the ventral interarea. This development reaches a peak in the *Cyrtia-Plicocyrtia* lineage. Nevertheless in the latter case, the dorsal valve does not become flat or concave as observed in the ambocoeliids.

Finally, *Nurataella* and *Dongbeispirifer* are close to the ambocoeliids and further study, particularly of the poorly known genus *Dongbeispirifer*, will perhaps result in referral to the Ambocoeliidae. As mentioned above, *Striispirifer* is the probable ancestor of *Tenellodermis* and *Spurispirifer*. It is also the ancestor of the plicate cyrtiids, by the acquisition of a well delimited, elevated interarea (*Hedeina*), then a rudimentary (*Mictospirifer*) or more developed ctenophoridium (*Havlicekia*). In this lineage there is a tendency to reduce the lateral plications (Havlíček 1980).

The *Cyrtia* branch is characterised by a very high, hemipyramidal ventral valve. Such a morphology appears sporadically and independently in diverse families during the evolution of the spiriferids. It is commonly associated with a peculiar mode of life: shell freely reposing on the substrate by its ventral interarea, suggesting a quiet environment. The presence of lateral plicae, that give rise to *Plicocyrtia*, is also repeated many times in spiriferid evolution. The relationship between *Eospirifer* and *Cyrtia* reinforces the "enigma" of the first appearance of *Cyrtia*. *Cyrtia* appears in the upper Llandovery of

the North American-North European domain when *Eospirifer* was formerly absent in this area. *Eospirifer* must have arrived in the region at this time and immediately diversified to give *Cyrtia*. It is worth noting that at the same time, and in the same domains, *Myriospirifer* and *Janius* appeared. It is clear that the environmental conditions in the North American-North European domain were very favourable for diversification at this time. Strong competition was prevalent resulting in a significant increase in species disappearance on a global scale (Figures 4 and 5).

As noted previously by Havlíček (1980), the presence of a particular micro-ornament in the genus *Myriospirifer* is not of critical importance in the systematics and evolution of the spiriferids since it has only been identified in unrelated genus *Havlicekia*. Apart from ornament, the genus *Myriospirifer* does not represent notable evolutionary progress compared to *Eospirifer*. Despite its long duration, *Myriospirifer* (still present in the Devonian) has no known descendants. *Janius* is characterised by the existence of secondary costae and by the presence of ribs on the fold/sulcus in some species. Here again the genus (known in the Emsian) is long ranging but did not apparently give rise to a new phyletic branch during the Silurian.

Araspirifer and related genera (e.g. *Kozlowskiellina*) evolved an external morphology close to *Hedeina*, including an elevated interarea (the type species of *Araspirifer* was first assigned to *Hedeina*). But *Araspirifer* possesses a frilly ornament suggesting a relationship with the delthyridids, particularly *Howellella*. Following the observations of Ivanova (1973), the appearance of free rhythmic growth lamellae corresponds to a fundamental change in the evolution of the spiriferids. The *Araspiriferinae* are related to the Delthyrididae despite their morphologic resemblance to the Cyrtiidae. Except for *Araspirifer*, all Silurian *araspiriferines* possessed a ctenophoridium, a feature common to the delthyridids. The "temporary" loss of the ctenophoridium in *Araspirifer* is somewhat puzzling, but may simply reflect imperfect preservation.

The Hedeinopsidae form a small group characterised by the presence of a delthyrial plate, an important, but not unique, innovation since it is also found in numerous spiriferid groups. This family includes two genera (*Tannuspirifer* and *Hedeinopsis*) and is also characterised by the loss of crural plates.

It is possible to consider the hypothesis that a common ancestor of *Howellella* and *Tannuspirifer*, would have been characterised by plicate flanks, the presence of a ctenophoridium and probably crural plates shorter than in *Eospirifer*. However, no such has been described at present.

As mentioned above, the presence of regularly

spaced (rhythmic) growth lamellae, often terminating in spines, constitutes a major feature in the spiriferid evolution. The first genus bearing such an ornament is *Howellella*. This evolutionary stage coincides with the appearance of the ctenophoridium and lateral plications also occurs during this early Llandovery period simultaneously in *Howellella* and some cyrtiids (*Striispirifer*). The genus *Howellella* thus bears many innovations and constitutes a potential source for innovation in later descendants. The origin of *Delthyris* is characterised by the development of a ventral median septum. It is also the ancestor of the *Rufispirifer*-*Ivanothyris* lineage by the loss of crural plates and apical thickening in *Ivanothyris* *chanxiensis* (see Xian and Jiang 1978). It is worth noting that the assignment of this species to *Ivanothyris* is doubtful. It is probably a homeomorph of *Ivanothyris* *s. s.* because all species of this genus are known only from Devonian series. Another lineage that developed from *Howellella* is distinguished by an incipient sinal plication (*Acanthospirifer*) and the loss of crural plates (*Aldanispirifer*).

The last important group of spiriferids is the reticulariids. The oldest genus of this group is *Eohowellella* which is very similar to *Howellella* but differs in its internal features, with the presence of a rudimentary spondylium. This makes any direct relation with *Howellella* highly improbable. The remaining characters of the genus are poorly known and its relationship with other genera is difficult to establish. *Eohowellella* could be the ancestor of the family Xenomartiniidae which includes genera with relatively complex internal structures. Two Silurian representatives are known; *Quadrithyris* (with a ventral septum) and *Altajella* (in which the septum and dental plates join to form a supported spondylium).

Another group originating with *Spirinella* is characterised by the loss of lateral plications and the fold and sulcus. *Vadum* is characterised by the loss of the ctenophoridium. This is followed by the development of a delthyrial plate and/or a strong apical thickening in conjunction with a septalium (*Eoreticularia*) or, on the other hand, with the loss of apical plates (*Protoreticularia*, *Chnaurocoelia*). Although *Alaskospira* belongs to another subfamily (Obesariinae), for which it is the single Silurian representative, it is morphologically very similar.

Concurrently, the conservation of the fold/sulcus, sometimes exaggerated (*Pavdenia*), may be accompanied by the neotenic development of lateral plications, first discrete (*Reticulariopsis*), then well developed (*Grebenella*) in the late Silurian. This group of the Reticulariidae originated with *Spirinella* or from an unidentified common ancestor that could have been at the origin of the Reticularioidea. Many Reticularioidea are endemic with short stratigraphic ranges: *Vadum* (Australia),

Protoreticularia (N. China; not to be confused with *Proreticularia*), *Chnaurocoelia* (Nevada).

CONCLUSIONS

Migration pathways of genera, if they can be deciphered, can provide better understanding of evolutionary history. *Howellella* for example, clearly originated in Kazakhstan during the early Llandovery, derived seemingly from *Eospirifer* in the same region. Two different «strategies» of expansion are observed: 1) slow geographic migration, not necessarily linked with the number of species (e.g. *Eospirifer*), and 2) wide and rapid expansion following emergence (e.g. *Howellella*). The most spectacular example of the latter is *Cyrtia*, becoming swiftly ubiquitous in the late Llandovery, a very favourable period for spiriferids. Significant evolutionary events occurred in the tropical belt. It appears that the spiriferids migrated in a counterclockwise direction, following palaeocurrents of that time.

During Ashgill and Early Silurian, the diversity increased at a moderate rate until the late Llandovery when a peak of diversification occurred (Figure 4). No major evolutionary event occurred during the early Wenlock, but a new radiation event occurred in the late Wenlock. This event probably represents the turning point in the history of spiriferids. It appears to have resulted from the early-middle Homeric bioevent. The Ludlow was a relatively stable period, though a significant number of genera did not cross the Wenlock-Ludlow boundary. Similar conditions prevailed during the Pridoli. The next crisis and radiation events occurred at the Siluro-Devonian boundary.

Some genera are weakly affected by global events, remaining widespread both in time and space during their entire life-span (e.g. *Howellella*). Such genera represent about one third of the total number of genera for each specified interval during the Silurian. Considering the wide distances between their areas of distribution, and bearing in mind the length of larval life of present-day brachiopods, the supposed links between some genera are thought to be unlikely.

A relatively common problem is the «Lazarus effect» apparent in many genera. It cannot be explained as merely a reflection of inadequate sampling or misidentification; but is probably the result of ambiguities in systematics when a family has no representatives for a significant time-interval.

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