Geological Society, London, Memoirs

Chapter 8 Cambrian, Ordovician and Silurian non-stromatoporoid Porifera

Lucy A. Muir, Joseph P. Botting, Marcelo G. Carrera and Matilde Beresi

Email alerting service	click here to receive free e-mail alerts when new articles cite this article
Permission request	click here to seek permission to re-use all or part of this article
Subscribe	click here to subscribe to Geological Society, London, Memoirs or the Lyell Collection

Notes

Chapter 8

Cambrian, Ordovician and Silurian non-stromatoporoid Porifera

LUCY A. MUIR[1], JOSEPH P. BOTTING[1]*, MARCELO G. CARRERA[2] & MATILDE BERESI[3]

[1]*Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, No. 39 East Beijing Road, Nanjing 210008, China*

[2]*CICTERRA-CONICET, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 299 (5000) Córdoba, Argentina*

[3]*Departamento de Paleontologia, IANIGLA, CCT-Mendoza, CONICET, Avda. Adrian Ruiz Leal s/n, Parque General San Martin, C. C.131 (5500) Mendoza, Argentina*

Corresponding author (e-mail: acutipuerilis@yahoo.co.uk)

Abstract: The Cambrian, Ordovician and Silurian distributions of non-stromatoporoid sponges are reviewed. The earliest Cambrian faunas contain mostly hexactinellids, with protomonaxonids dominating middle Cambrian assemblages. There are no obvious palaeo-biogeographical patterns, with many genera being found widely. Vauxiids, lithistids and heteractinids are apparently confined to low latitudes, but this may be due to a poor fossil record. Most known Ordovician faunas are from low latitudes, although some high-latitude faunas are known, which contain reticulosan hexactinellids and protomonaxonids. There is some division of faunas within Laurentia, into eastern and western provinces, with the western assemblage extending across low northern latitudes during the Late Ordovician. During the Silurian Period, sponge diversity was very low during the Llandovery Epoch, probably partly owing to lack of habitat for taxa restricted to carbonate facies, and also because of sampling bias. There was a dramatic increase in diversity through the Silurian Period, mostly owing to an apparent diversification in the demosponges; however, there are many ghost lineages, indicating that their fossil record is poorly known. Non-lithistid sponges are very poorly known, with few recorded outside Euramerica. The currently available data for Early Palaeozoic sponges are too incomplete to allow any reliable palaeobiogeographical inferences.

Supplementary material: the compilation of Silurian sponge occurrences is available at: http://www.geolsoc.org.uk/SUP18666.

Large-scale studies of the palaeobiogeography of Early Palaeozoic sponges have been limited to a few major works (Webby 1980, 1992; Nestor 1990; Senowbari-Daryan 1990; Carrera & Rigby 1999; Carrera & Botting 2008). The main difficulty in reconstructing the palaeobiogeography of sponges is that their fossil record is at best intermittent. During the Palaeozoic Era they are widely represented in the Cambrian Burgess Shale-type faunas, and well known from a few regions in the Ordovician Period. With the exception of heavily calcified forms, later Palaeozoic faunas are described principally from certain productive localities or formations, and are dominated by taxa with either a fused (hexactinellid), rigid (lithistid) or secondarily calcareous (stromatoporoid, sphinctozoan) skeleton. Certain facies such as Ordovician reefs, the Devonian sandstones of New York State and the Cretaceous chalk seas of Europe, were conducive to the preservation of large numbers of sponges. However, these each represent only one community type restricted by both facies and taphonomy. Other sponge faunas living in other sedimentary regimes are virtually unknown for most time periods.

This paper represents a summary of the limited available data for Cambrian to Silurian sponge biogeography, as a review of the state of knowledge at the time of writing. We focus particularly on the Silurian record, but also reassess recent studies of Cambrian and Ordovician sponge palaeobiogeography (Carrera & Rigby 1999, 2004; Carrera & Botting 2008) in light of new data and new palaeogeographical interpretations. The Silurian sponge record is sparser than that from the Cambrian and Ordovician periods, and there are few diverse assemblages, although hexactinellids and non-lithistid demosponges are known from a range of carbonate and siliciclastic deposits. Lithistids are much rarer than in Ordovician deposits, but diverse faunas are known from Arctic Canada.

Distribution patterns of modern sponges

Interpretation of palaeobiogeographical patterns must take into account the probable life distributions of the taxa involved. This particularly applies to groups with a sparse or inconsistent fossil record, both of which are true of sponges, and some appreciation of how sponge taxa are distributed in the present day is critical to this study. Different groups and communities of living sponges exhibit very different distribution patterns, and it is likely that at least some of these patterns were already established in the Early Palaeozoic. Most of the distribution data currently available for living communities are from either the nineteenth- and early twentieth-century zoological expeditions (e.g. *Challenger*, *Terra Nova*, *Investigator*, *Albatross*), or from more recent studies of shallow-marine settings, especially tropical reefs. There has also been a recent effort to study the sponge-rich benthic assemblages of the Antarctic seas, including a significant taxonomic element (e.g. Janussen *et al.* 2004; Janussen & Tendal 2007).

Modern deep-water hexactinellids and demosponges tend to be distributed over very wide areas, although they are less well known than sponges from shallow marine environments. Where multiple records are available, hexactinellid genera covered by Hooper & Van Soest (2002) frequently show a global distribution within either the tropics, or the north or south polar regions (or, rarely, both north and south; e.g. *Anoxycalyx*). In other cases, genera are restricted to or concentrated in one ocean basin (e.g. *Asconema* in the temperate to polar North Atlantic). Some genera are distributed worldwide, but primarily in deeper water (e.g. *Chonelasma*). Given the scarcity of true deep-water sediments in the fossil record, we should expect ecologically equivalent Palaeozoic taxa to be distributed widely within a broad latitudinal band. In the Ordovician and Silurian periods, this should correspond to a very wide distribution, with perhaps some differentiation between Gondwanan and more equatorial continental areas. We might also expect to see taxa restricted to one basinal or oceanic region but across a wide range of latitude.

In shallow marine, carbonate-dominated communities, sponges are patchy in distribution (Gutt & Koltun 1995), and similar patchiness has been observed in the Mesozoic (Beresi 2003; Olóriz *et al.* 2003). Within a small area, almost entirely different assemblages of species may be present in habitats that appear very similar. The record of shallow-water sponges in the Early Palaeozoic is

very sparse, although there is rare articulated material from shallow marine siliciclastics (Botting 2005; Beresi *et al.* 2006). There are also several examples of highly distinctive communities recorded from spicule assemblages in apparently deep-water carbonates (e.g. Webby & Trotter 1993; Zhang & Pratt 1994); the diversity at these Palaeozoic sites is often high. If there was significant patchiness in Palaeozoic sponge communities, then the apparent endemism is likely to be highly misleading and based only on incomplete sampling at each site. In very few locations are there good data for shallow-water sponges across several Lower Palaeozoic sites in the same palaeogeographical complex, and this may potentially bias our results severely.

Modern demosponges are much more diverse than the other classes in their ecological habits and taxonomy. Shallow-water sponge faunas are dominated by demosponges (with some calcareans), which occupy a wide range of microhabitats. These habitat differences lead, for example, to striking population ecology differences between subtly different environments on modern rocky shores (Bell & Barnes 2003; Carballo & Nava 2007). The patchy distribution of sponges in carbonate settings (e.g. Roberts & Davies 1996) has been linked to a wide range of factors, including sediment input, human-induced eutrophication and disturbance, presence of corals and water transparency (de Voogd *et al.* 2006). This suggests that sponge distributions are in this habitat strongly constrained, but by a sufficiently complex set of parameters that the causes are unlikely to be easily discernable. It is likely that similar principles applied to at least some Palaeozoic sponges. Roberts & Davies (1996) also reported a trend towards higher diversity and lower abundance offshore, with specialist taxa that inhabited the most turbulent and stressful conditions becoming more dominant and widespread. Where environmental constraints were less obvious, in somewhat deeper or less exposed habitats, it appears that patchiness becomes even more prevalent.

Interpretation of fossil distribution patterns must take into account these observations of modern sponge faunas. In particular, the patchiness of shallow-water taxa and the constraint of sponge species distributions by multiple parameters indicate that an incomplete record will be particularly problematic for reconstructing palaeobiogeography. Even within a productive formation, different taxa will be expected to occur in different exposures. Anecdotal records of sponge fossils are likely to provide data on only the most abundant and widespread of species, and the records of the deep ocean and the shallowest water communities are likely to be more consistent than those from intermediate depths. Unfortunately, it is the intermediate depths that yield the majority of well-preserved sponge fossils, especially for taxa occurring outside reef facies. Palaeobiogeographical signals from sponges are therefore likely to be best in the more easily preservable groups living in the shallowest-water conditions. Sponge distributions in abyssal, basinal or deep shelf communities may yield coherent signals that reflect complementary palaeogeographical controls to those of shallow-water faunas, but they are limited by preservation potential. Sponges from storm-influenced shelf habitats are more likely to have been locally preserved through sudden burial, but are also most likely to show extremely incomplete, patchy distributions. Although elements of the data offer support for most of these expected patterns (discussed below), these limitations suggest that only those patterns corroborated by particularly robust data, or confirmed by other groups, should be considered to be reliable.

Taxonomic and taphonomic problems

The limited record of Palaeozoic sponges is due in large part to the fragility of spicular skeletons. Non-lithistid taxa are rarely preserved intact owing to rapid post-mortem disarticulation, and in shallow-water conditions silica is also highly soluble. This results in the inevitable loss of many spiculate shelf-dwelling taxa. Although hypercalcified and lithistid sponges are more easily preserved, these are also prone to recrystallization, which in many cases destroys diagnostic features.

The general rarity of spiculate calcareans may be partly taphonomic, as their magnesium calcite spicules would have dissolved or recrystallized easily under some conditions. This may certainly explain their absence in deep-water mudstones, but they should have been preserved reasonably commonly in limestones. The astraeospongiids have very robust skeletons, which are commonly preserved intact where they occur, and so it is surprising that they have not been more widely reported. The skeletons of polyactinellids, however, are likely to have been much less robust, and taxa of this type are normally recorded only as isolated spicules under turbulent, shallow-water conditions.

A number of taxonomic issues affect the apparent distribution of sponges. As a relatively minor, specialist group, there have been few palaeontologists specializing in their taxonomy at any time, and little continuity in their study. Where fossil sponges are discovered, they have frequently been described by non-specialists. The isolation of many previous sponge workers has led to idiosyncrasies in interpretation and taxonomic practice, and taxonomic errors have often been propagated with little discussion. For example, some well-known names such as *Protospongia* have been indiscriminately assigned to a wide range of fossils that are entirely different from each other, and in most cases these nomenclatural errors have remained unchallenged. In this paper we have found that most of the taxa erroneously assigned to *Protospongia* are either morphologically unique or too poorly described to allow a reliable generic assignment, and must be disregarded for this study. Where appropriate new genera such as *Heminectere* are available, we have used them.

Taxonomy of sponges also involves certain difficulties specific to the group in terms of reliable diagnosis and recognition. Living demosponges may adopt a variety of body forms within a single species. The flexibility of the demosponge body architecture has allowed them to become encrusting, boring or erect, in some cases with body form within a species dependent on ambient conditions (e.g. Krautter 1995; McDonald *et al.* 2002). Modern demosponge species have evolved to respond differently to different conditions, leading to complex ecological patterns in modern hard-substrate environments, especially where prone to variable sedimentation (e.g. Carballo 2006). In cases where it is not possible to tell that morphologically distinct sponges belonged to the same biological species, then this may lead to problems in interpreting biogeographical patterns in the fossil record. Sponges representing the taxonomic groups containing morphologically plastic demosponges are not yet recognized for the Silurian, but rare examples of possible Dysideidae are known from the Ordovician Period (Botting 2005). Morphological plasticity also affects lithistids to some extent, however, potentially leading to subdivision of taxa and suppression or exaggeration of biogeographical signals.

Materials and methods

Information on Cambrian and Ordovician non-stromatoporoid sponges has been taken from Carrera & Botting (2008) and Carrera & Rigby (1999, 2004), with additional information from the recent literature. Data on Silurian non-stromatoporoid sponges were gathered from published papers and monographs. (Stromatoporoids are dealt with in a separate chapter.) A total of 173 lines of data on Silurian sponge occurrences were gathered (available online as supplementary data). We have included in the database only published occurrences with taxa identified to at least genus or species level. Thus, examples such as the spicule assemblages described by Watkins & Coorough (1997) and Beresi (2010) have not been included.

We are aware of several unpublished Silurian faunas: a hexactinellid assemblage from the Llandovery Epoch of China (Q. Liu pers. comm. 2011); an assemblage from the Welsh borders including probable dictyosponges, vauxiids and monaxonid sponges (under study by J. P. Botting); a few examples of undescribed Silurian sponges in the Natural History Museum, London; and isolated hexactinellids from graptolitic siltstones in Australia and northern England collected by the late R. B. Rickards. A major assemblage of Early Silurian lithistids (and rare examples of other groups) is under description by F. Rhebergen & J. P. Botting, and is very similar at genus level to the later Silurian faunas described from Arctic Canada. There are doubtless many other undescribed occurrences of non-stromatoporoid sponges that have previously been overlooked. These unpublished faunas are not included in the dataset, but are mentioned in the text where relevant.

This study is based on a simple tripartite division of the Silurian Period into the early (Llandovery Epoch), middle (Wenlock Epoch) and late (Ludlow and Pridoli epochs), as this can accommodate the majority of the information available. The Ludlow and Pridoli epochs are considered as one unit, because of the shortness of the Pridoli Epoch and the small number of records from that interval. Sponge occurrences for which the epoch is uncertain, for example the *Pyritonema*? illustrated by Gortani (1926), have not been included in the dataset. It has proved difficult to ascertain the exact age of sponge localities in many cases; this is particularly true of the earlier literature. Precise comparisons between faunas are therefore badly limited; if we select only those records with well constrained date information, there are too few data points to be palaeobiogeographically useful.

All maps were plotted using base maps from BugPlates (Torsvik 2009). The Cambrian map was plotted on palaeogeography for 515 Ma, the Middle Ordovician map used 466 Ma, and the Late Ordovician map used 452 Ma; these maps represent approximately the centre of their respective time intervals, rather than being focussed on the richest occurrence data. For the Silurian Period, these times are 435 Ma for the Llandovery Epoch, 425 Ma for the Wenlock Epoch and 420 Ma for the Ludlow plus Pridoli epochs. The Llandovery Epoch covers the time interval 443.7–428.2 Ma (15.5 myr duration), the Wenlock Epoch covers 428.2–422.9 Ma (5.3 myr duration) and the Ludlow–Pridoli epochs cover 422.9–416.0 Ma (6.9 myr duration; ages taken from the International Stratigraphic Chart 2009). The Llandovery Epoch thus covers a much greater time interval than either the Wenlock or the Ludlow–Pridoli epochs.

Higher taxonomy follows the current edition of the Treatise on Invertebrate Paleontology (Finks *et al.* 2004), except where it has been revised or genera are not included in the treatise, for example, *Alaskaspongiella* of Rigby *et al.* (2008). The Protomonaxonida have traditionally been regarded as demosponges, but at least some may be reticulosan hexactinellids (e.g. Debrenne & Reitner 2001), and they are treated separately for the purposes of this paper.

Cambrian sponge palaeobiogeography

The Cambrian sponge record was reviewed in outline by Carrera & Botting (2008). A summary of Cambrian sponge distribution is given in Figure 8.1. Cambrian sponge biogeography is as yet poorly known, despite the widespread occurrence of Burgess Shale-type faunas. These are concentrated in Laurentia and South China, but there are similar deposits containing sponges from Siberia, Spain and elsewhere. Sponge spicules are abundant in carbonate facies in the early and middle Cambrian, but there are few articulated remains from these environments. This excludes the hypercalcified Archaeocyatha, which occur in suitable facies worldwide, but are concentrated in low latitudes

(Debrenne 2007). The early Cambrian Period has a wide range of largely endemic hexactinellid taxa (Steiner *et al.* 1993; Wu *et al.* 2005; Xiao *et al.* 2005), whereas the late early (late C2) and middle Cambrian (C3) faunas are dominated instead by more cosmopolitan protomonaxonid genera, together with dramatic local diversification of some lineages (e.g. hazeliids; see Rigby 1986; Rigby & Collins 2004). The late Cambrian Period has very few sponge records of any groups.

The data available suggest that sponges in the Cambrian Burgess Shale-type faunas were widespread, but environmentally restricted. Although the earliest faunas (e.g. the Niutitang and Hetang biotas; Steiner *et al.* 1993; Xiao *et al.* 2005) appear to be largely endemic to South China, there are no contemporaneous faunas for comparison from elsewhere. Some faunal elements in the Hetang and Niutitang faunas, such as choiids and protospongiids, are widespread in later deposits. The apparently endemic elements (e.g. *Sanshapentella*, *Triticispongia*, *Saetaspongia*) are largely absent even from the Chinese deposits younger than the Chengjiang Biota. A single spicule of *Sanshapentella*? sp. has been collected from immediately below the Burgess Shale locality S7 (collection number S700-230, in the Royal Ontario Museum, J. P. Botting pers. obs. 2011); this occurrence is slightly older than the other Burgess Shale localities, but also represents a slightly different environment. This suggests that an evolutionary overturn or palaeoenvironmental control, rather than a biogeographical signal, are necessary to explain their absence from the later Burgess Shale and Utah assemblages. Additional problems result from a great deal of taxonomic confusion among genera in the Burgess Shale-type faunas, particularly in the application of Laurentian taxon names to Chinese material. Resolution of these issues may reduce the apparent range of some genera, and increase the range of others. A review of these taxa is in progress by J. P. Botting, but the broad palaeogeographical patterns do not appear to be affected.

There are many shared hexactinellid and protomonaxonid genera between Laurentia and South China (the best sampled regions) from the late Atdabanian Age onwards. These faunas are dominantly of C2 age in China and C3 age in Laurentia, although with some overlap around the C2–C3 boundary. The same genera are also known from both low-latitude C2 deposits (Sinsk Biota), and from high-latitude C3 sequences (Iberia, Avalonia) in the Sinsk Biota (Ivantsov *et al.* 2005). These genera are mainly protomonaxonids (*Wapkia*, *Lenica*), whereas Spain's Murero Shale (García-Bellido *et al.* 2011) yields other protomonaxonids (*Leptomitus*, *Choia* and *Crumillospongia*) and the Porth-y-Rhaw locality of South Wales is dominated by hexactinellids such as *Protospongia* (Hinde 1887). The late C2 to C3 deposits of Argentina (Beresi 2007) have yielded mostly fragmentary protomonaxonid reticulosans. This combination of faunas yields no obvious patterns, with protomonaxonid-dominated and reticulosan hexactinellid-dominated faunas seemingly unconstrained by latitude or continental mass, occurring widely in both equatorial and sub-polar regions. All these faunas occur in offshore siliciclastic facies, but there may be a constraint imposed by precise water depth; it appears that the faunas of more offshore environments are more likely to be dominated by reticulosans, with protomonaxonids primarily limited to shallower shelf habitats. This was discussed in more detail by Carrera & Botting (2008).

Other groups of sponges from Cambrian deposits have similarly uninformative records; Calcarea (Heteractinida) are known articulated from very few locations, all tropical, but similar spicules are very widespread through the C2–C3 interval. Lithistids are rare in Cambrian C3 deposits, and the few records are widely scattered in exclusively low latitudes, implying a broad tropical distribution but an incomplete record. The same is true of the Vauxiidae, which are believed to be keratosan demosponges; although widely distributed in Laurentia and China, they are not yet known from non-tropical latitudes. Spicules assigned to the Polyactinellida are apparently widespread, but the current record
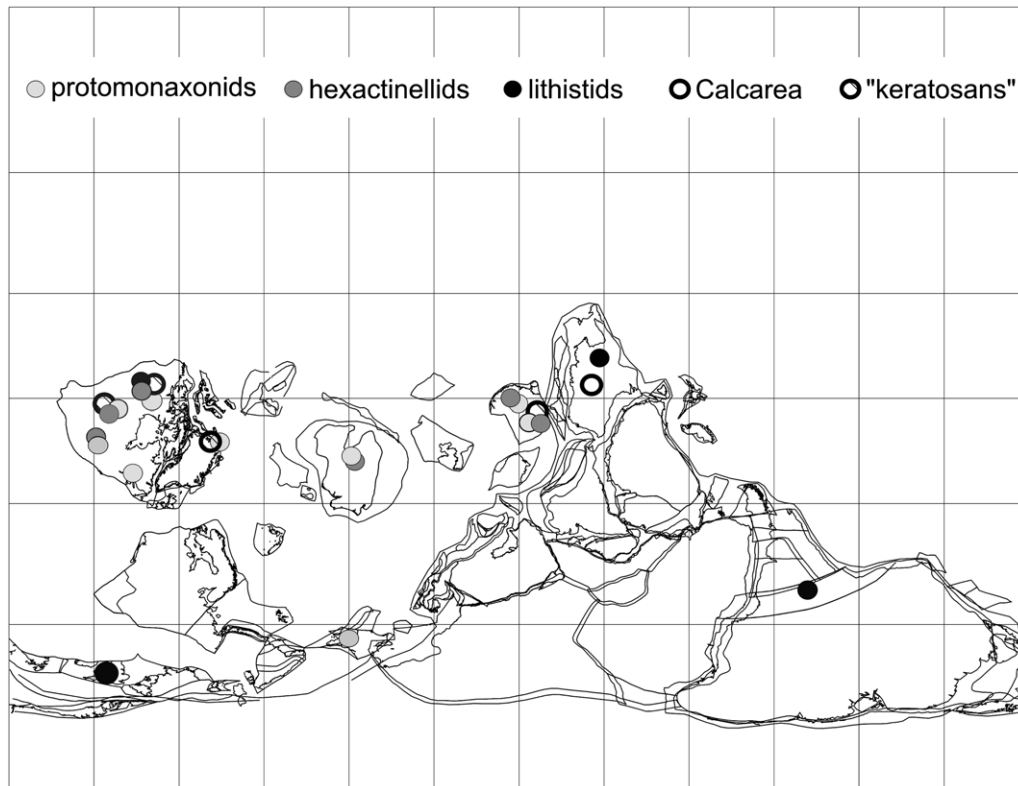
Fig. 8.1. Summary of the known distributions of major groups of Cambrian sponges, showing the largely cosmopolitan distributions (chancelloriids and archaeocyathans were very widespread and are not included). There are no consistent patterns within any group that suggest it is possible to recognize palaeobiogeographical provinces, and where endemic faunas occur, these may reflect restricted habitats rather than a limited geographical range. Many genera are shared between Laurentia, South China, and other regions. Note the apparent restriction of 'keratosans', calcareans and lithistids to low latitudes. Map plotted for the middle Cambrian Epoch (515 Ma).

consists largely of form-taxa. It is possible that many taxa were evolving in shallow water sequences where their preservation potential as complete skeletons was very low.

It is currently unclear to what extent the restriction of vauxiids, lithistids and heteractinids to low latitudes is a real palaeobiogeographical signal, and what is due to preservational limitations, but the distribution of chancelloriids suggests that an incomplete record is the primary factor. Complete scleritomes of chancelloriids are known widely from Burgess Shale-type faunas in Laurentia and South China. The distinctive isolated sclerites occur in many small shelly fossil assemblages from both low and high (e.g. Beresi 2007) latitudes, and also from poorly sampled regions with no other Cambrian sponge record, such as West Africa (Culver *et al.* 1996). Despite this global distribution of their skeletal elements, no articulated chancelloriids are known from potential high-latitude deposits such as the Murero Biota, implying the limitation at least for this group is taphonomic. This constraint is less likely to apply to (at least hypercalcified) heteractinids or lithistids, which may be genuinely restricted to low latitudes, but could potentially explain the lack of high-latitude keratosans. The known late Cambrian (Furongian) sponge record is exceptionally sparse and is currently of no use for palaeobiogeographical studies.

Ordovician sponge palaeobiogeography

Ordovician non-stromatoporoid sponge palaeobiogeography was comprehensively reviewed by Carrera & Rigby (1999), with diversity changes discussed by Carrera & Rigby (2004). The described sponge record remains largely unchanged, but our understanding of palaeogeography has altered, leading to revisions to the palaeobiogeographical implications of the data. There have also been a number of additional relevant papers in recent years, including some diverse faunas (e.g. Botting 2004*a*, 2005, 2007*a*) and individual new species occurrences (e.g. Carrera 2006, 2007;

Carrera & Ortega 2009; Beresi *et al.* 2010). These new data have little effect on the patterns described by Carrera & Rigby (1999), as most records represent new genera, or additional records of widely dispersed genera. Ordovician sponge distribution is summarized in Figure 8.2.

One limitation of the known record at the time of Carrera & Rigby (1999) was the lack of assemblages from high latitudes, with most faunas being tropical. This limitation still applies, but has been mitigated slightly. The only polar sponge fauna yet known from the Ordovician Period is the Early Ordovician Fezouata Biota (Botting 2007*a*; Van Roy *et al.* 2010), of which only a few species have been described. The undescribed Fezouata Biota sponges recovered so far are largely endemic, or relict Cambrian genera (J. P. Botting pers. obs. 2012). The Fezouata sponge assemblage is dominated by protomonaxonids, an assemblage otherwise typical of middle Cambrian Burgess Shale-type deposits, which had a wide distribution at that time. Protomonaxonids are rare or absent in other Ordovician faunas, but some lineages are now recognized to have persisted into post-Cambrian communities, albeit in lower abundance. There are recent records of piraniids from the Late Ordovician Epoch of Wales (Botting 2004*a*), and choiids from the Ordovician Period of Canada (Dawson 1896) and the Ordovician (Beresi *et al.* 2010) and Silurian rocks (Botting 2007*b*) of Scotland.

Other Early Ordovician sponges are mainly associated with microbial carbonate build-ups (discussed by Carrera & Rigby 1999), and taxa are widely distributed through at least high-latitude regions. The most representative taxa are *Archaeoscyphia* and the problematic sponge-like organism *Calathium*. Isolated occurrences of reticulosan hexactinellids in offshore environments are not generally known in sufficient detail even to fully categorize individual occurrences, and are far too sparse to draw any palaeobiogeographical conclusions.

A suite of high-latitude but non-polar communities are present in the Middle Ordovician Builth Inlier of Wales (Botting 2004*a*, 2005). Additional faunas from offshore sediments of the area are under description (J. P. Botting pers. obs. 2013), and include a
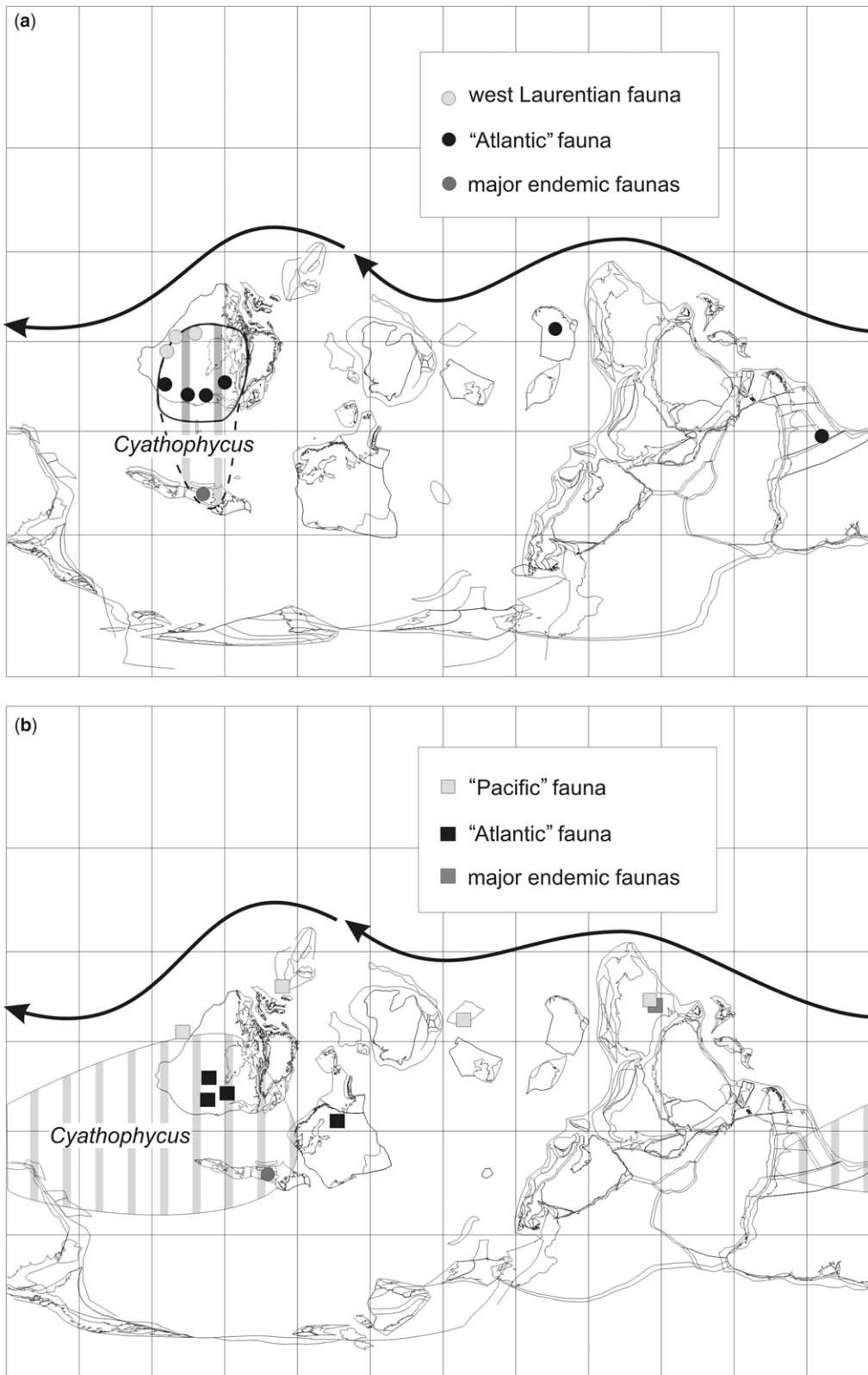
Fig. 8.2. Summary of Ordovician sponge distribution, including the previously described (Carrera & Rigby 1999) segregation into two major provinces ('Pacific' and 'Atlantic') based mainly on lithistid demosponges and sphinctozoans from shallow-water settings. The arrow represents a putative north equatorial current. The hatched region indicates the known range of the widespread offshore hexactinellid *Cyathophycus*, suggesting limitation to the surroundings of one ocean basin, with limited latitudinal constraint. (**a**) Middle Ordovician Epoch (466 Ma); (**b**) Late Ordovician Epoch (452 Ma).

range of simple reticulosan and protomonaxonid taxa. A few of the new Ordovician records have some palaeobiogeographical interest, although in general they highlight the incomplete record of spiculate sponges for the Lower Palaeozoic. Botting (2005) described *Pseudolancicula* sp. and related taxa from the Darriwilian rocks of the Builth Inlier, but the distinctive spicules of this group are otherwise known only from the Late Ordovician Period of Australia (Webby & Trotter 1993), and a recent record from the Dapingian Vinini Formation of Nevada (M. G. Carrera, pers. obs. 2012) as

part of an ongoing study of Early and Middle Ordovician spicule assemblages (Carrera & Maletz 2010). A similar signal of Laurentian taxa in the Late Ordovician Period of Australia was noted by Carrera & Rigby (1999), but the explanation for this pattern remains obscure. It implies a wide Gondwanan distribution for these taxa, but with a very limited record supporting it. It may be that the taxa in question are specialists in particular environments that were only intermittently preserved, or had localized life distributions. Patchy local distributions of widespread taxa,

as seen in recent communities, could also potentially explain this pattern.

The offshore fauna of the Llanfawr Mudstones Formation of the Builth Inlier is largely endemic at genus and species level, with only a few widely distributed and long-ranging taxa such as *Heminectere* (Botting 2004*a*). The Llanfawr Mudstones fauna also contains a species of *Asthenospongia* (Rigby *et al.* 1981), previously described only from the Floian Age of Idaho, but also probably present in the early Cambrian Hetang Biota (J. P. Botting pers. obs. 2012). Another genus shared between Avalonia and Laurentia in the Late Ordovician Epoch is *Cyathophycus*, widely distributed in North America but also reported from Bohemia (Mergl 2008) and the Argentine Precordillera (Carrera & Ortega 2009). However, *Cyathophycus* is poorly constrained taxonomically, and the sponge described by Mergl (2008) is distinct from the other examples and probably represents a separate genus; this leaves a distribution for the genus covering a relatively small part of the globe, but with a surprisingly wide range in latitude (Fig. 8.2b), as might be expected for a relatively deep-water taxon. Its first appearance is in Tremadocian rocks of Laurentia, and during the Middle Ordovician Epoch it also appears to have been restricted to that region (Fig. 8.2a) except for an undescribed, probable occurrence in the late Darriwilian Age of Wales (J. P. Botting pers. obs. 2013); it appears to have spread rapidly during late Darriwilian and Sandbian times. It is possible that this region represents the centre of a genuine deep-water province, but it is equally likely that the taxa are much more widely distributed and their absence elsewhere is due to our poor knowledge of the offshore sponge record. This is supported by the apparent presence of a sponge closely resembling *Palaeosaccus* Hinde 1893 in the Tremadocian Age of Spain (Piçarra *et al.* 2011) – a genus previously recorded only from northeastern Laurentia.

One of the major features of the Middle–Late Ordovician record is the presence of a division between eastern and western Laurentian faunas (Carrera & Rigby 1999). The faunas in the Middle Ordovician Epoch were less clearly separated than in the Late Ordovician Epoch, and largely composed of lithistids. The western Laurentian fauna has not been recognized elsewhere during the Middle Ordovician Epoch, and all of its characteristic elements appear to have been endemic to the region, with many endemic to one locality; other taxa present in the communities are cosmopolitan. This suggests that the western Laurentian fauna during the Middle Ordovician Epoch represents not so much a province, but a region with high speciation, and that the taxa that arose in the area did not, in general, subsequently disperse and colonize wider areas.

Provinciality was observed to have increased markedly during Late Ordovician time (Carrera & Rigby 1999), with a broad distinction into 'Atlantic' and 'Pacific' faunas and additional largely endemic assemblages such as those of New South Wales (Australia) and, more recently, Wales (UK). The primary distinction was considered to be probably due to partial separation of the oceanic circulation patterns owing to the continental arrangement, although it is notable that the Pacific (western Laurentian) fauna was composed largely of sphinctozoans, in sharp contrast to the other diverse faunas. The new palaeocontinental reconstructions employed here reconfigures and amalgamates these provinces into a northern tropical band for the 'Pacific' fauna (Fig. 8.2b) and a southern low-latitude province ('Atlantic' fauna) focussed on eastern Laurentia and Baltica. The 'Atlantic' fauna is broadly continuous from the Middle Ordovician assemblage typical of the same area, whereas the sphinctozoan-dominated 'Pacific' fauna represents a new assemblage. Most of the major occurrences representing these faunas are constrained to between 20°S and 20°N. The two provinces, however, no longer appear distinct except in Laurentia itself. The western Laurentian ('Pacific') taxa, composed almost entirely of sphinctozoans (of which three genera are shared with New South Wales), have not been found in the Silurian Period, with the exception of *Cystothalamiella*

and *Girtyocoelia*, which both reappeared in the Ludlow Epoch of Alaska. Several new, related genera also arose in Alaska in the Silurian Period (Rigby *et al.* 2008), all of which appear to be endemic. In contrast, many of the lithistid genera present in eastern Laurentia and elsewhere survived to become major components of Silurian sponge faunas across Laurentia, Baltica and elsewhere (see below). The data are limited, but as with the Middle Ordovician faunas, it appears that Late Ordovician environments of western Laurentia produced a high diversity of endemic taxa that did not successfully colonize other regions. These interpretations are likely to change with the description of further faunas from other regions, particularly of sphinctozoans.

The clear separation of faunas on eastern and western Laurentia during the Middle Ordovician Epoch suggests that western Laurentia was the focus for diversification of the Late Ordovician sponge fauna, and particularly sphinctozoans. The only other Late Ordovician sphinctozoan faunas are from New South Wales and the Altai region (Tarim), and all these faunas are distributed in low northern latitudes. Their distribution may have been dictated by a north tropical current, and the apparent absence of sphinctozoans from south of the equator suggests that the northern and southern circulation systems may have been independent. Deeper-water faunas also appear to conform to this model, with the distribution of *Cyathophycus* covering a wide latitudinal range but not extending in Laurentia west (palaeo-north) of Nevada and Manitoba.

A possible northward progression is seen in the distribution of protomonaxonids during the Ordovician Period, from polar and high southern latitudes in the Lower Ordovician deposits of Morocco and Avalonia (Botting 2007*a* and J. P. Botting pers. obs. 2012), remaining in Avalonia during the Darriwilian and earliest Sandbian ages (Botting 2004*a*), and reaching eastern Laurentia by the Late Ordovician (Beresi *et al.* 2010). Protomonaxonids are otherwise very rare, having effectively disappeared from the fossil record in the late Cambrian Period. It is possible that choiids continued in eastern Laurentia through the Ordovician Period, based on the presence of *Choia hindei* in the (probably) Early Ordovician deep-water black mudstones of Quebec (Dawson 1896). However, the protomonaxonids are otherwise unknown in Laurentia, despite numerous studies of Ordovician offshore sponge faunas by J. K. Rigby. It is possible instead that the protomonaxonids became extinct in low latitudes during the late Cambrian, and recolonized Laurentia through the northward drift of Avalonia. A similar trend should be expected to emerge from Gondwanan sponge faunas if this is correct.

Beyond the possible north–south division around the equator, the updated palaeogeography results in little or no support for distinct oceanic provinces. Excluding the sphinctozoan community and *Cyathophycus,* Ordovician sponge genera tend to be either widespread or endemic. Northern Laurentia appears to have produced a high proportion of endemic taxa during both the Middle and Late Ordovician epochs. Other areas with diverse endemic taxa are the Late Ordovician deep-water carbonates of New South Wales and the shallow and deep-water siliciclastics of Wales. These patterns are, however, based on very few data points outside Laurentia and adjacent areas, and should be regarded as hypotheses to be evaluated when further faunas are available.

Silurian sponge diversity and palaeobiogeography

Silurian non-stromatoporoid sponges have not previously been the subject of major palaeobiogeographical studies, and this section therefore includes detailed summaries of the data as well as discussion of possible palaeobiogeographical patterns. Diversity data are given in Table 8.1, and graphically in Figure 8.3. Sponge distributions are plotted on Figures 8.4–8.6. The data show a striking overall trend from very low diversity (12 species) in the

Table 8.1. *Number of species and genera for each sponge family during the Silurian Period*

	Llandovery species	Llandovery genera	Wenlock species	Wenlock genera	Ludlow species	Ludlow genera
Hexactinellids						
Amphispongiidae	1	1				
Brachiospongiidae					1	1
Dictyospongiidae			2	2	3	3
Docodermatidae					1	1
Hintzespongiidae			2	1		
Lumectospongiidae					1	1
Malumispongiidae					2	1
Pelicaspongiidae	2	2	2	2	1	1
Protospongiidae	1	1	7	5	7	4
Stiodermatidae	1	1	1	1	1	1
Total Hexactinellids	**5**	**5**	**14**	**11**	**17**	**13**
Demosponges						
Anthaspidellidae	1	1	15	4	15	9
Aphrosalpingidae			1	1	7	4
Astylospongiidae			6	5	9	5
Auriculospongiidae					3	3
Cryptocoeliidae					1	1
Girtyocoeliidae					1	1
Haplistiidae			1	1	4	2
Hindiidae	1	1	1	1	3	1
Saccospongiidae					3	2
Streptosolenidae			2	2	4	3
Vauxiidae	1	1				
family uncertain			2	2		
Total demosponges	**3**	**3**	**26**	**14**	**50**	**31**
Heteractinids						
Astraeospongiidae	1	1	1	1	3	2
Polyactinellidae	1	1			3	3
Preperonidellidae					3	3
Total heteractinids	**2**	**2**	**1**	**1**	**9**	**8**
Protomonaxonids						
Choiidae	1	1				
Leptomiditae			1	1		
Mahalospongiidae					1	1
Total protomonaxonids	**1**	**1**	**1**	**1**	**1**	**1**
Family and order uncertain (*Nabaviella*?)	1	1				
Total non-stromatoporoid sponges	**12**	**12**	**44**	**29**	**77**	**53**

Llandovery Epoch to significant levels (77 species) in the Ludlow Epoch. There are 11 sponge families and 12 genera known from the Llandovery Epoch from seven localities. Although only seven taxa are identified to species level, there are at least 12 species present. In the Wenlock Epoch there are 15 sponge localities containing 14 families, comprising 29 genera and 44 species. In the Ludlow–Pridoli, there are 19 sponge localities, including 53 genera and 78 species from 22 families.

The Llandovery Epoch is longer than Wenlock, Ludlow and Pridoli epochs combined. However, for the whole of the Llandovery Epoch there are published data for only seven sites, and none contain a diverse community. The most species-rich locality is the Pentland Hills of Scotland (Botting 2004*b*, 2007*a*), but even here there are only four species in four families recorded (Table 8.2); an additional species is not yet formally published (Candela & Botting 2011). All the other Llandovery localities contain only one or two families (Table 8.2). In the Wenlock Epoch family diversities at most sites are low (Table 8.3), with diversities again being one or two families. The most diverse sites are the Mackenzie Mountains of Canada (seven families) and Baillie–Hamilton Island, Arctic

Canada (five families). The situation is similar for the Ludlow and Pridoli epochs, with most of the 19 sites containing one family (Table 8.4). The most diverse region for this time interval is Arctic Canada, with a total of 11 families, followed by Nevada, with five families.

The only diverse carbonate platform sponge communities currently described from the Silurian Period are from Arctic Canada (e.g. De Freitas 1987, 1989, 1991; Rigby & Chatterton 1989), although lithistids are also known from the Baltic (e.g. van Kempen 1983; Rhebergen & van Kempen 2002) and elsewhere. There are very few lithistids known from Avalonia, although some unstudied specimens from the Wenlock Limestone Formation exist in UK museum collections and one specimen from Ludlow siltstones of Shucknall Hill, Herefordshire in Hereford Museum (J. P. Botting pers. obs. 1997). Records from elsewhere are remarkably sparse. Nearshore siliciclastic sediments have yielded only a few sponge localities, most notably the Pentland Hills of southern Scotland (Botting 2007*a*). The most diverse non-lithistid Silurian assemblages are from marly shelf sediments such as those of the Roberts Mountains of Nevada (Mehl *et al.* 1993; Rigby & Maher 1995).
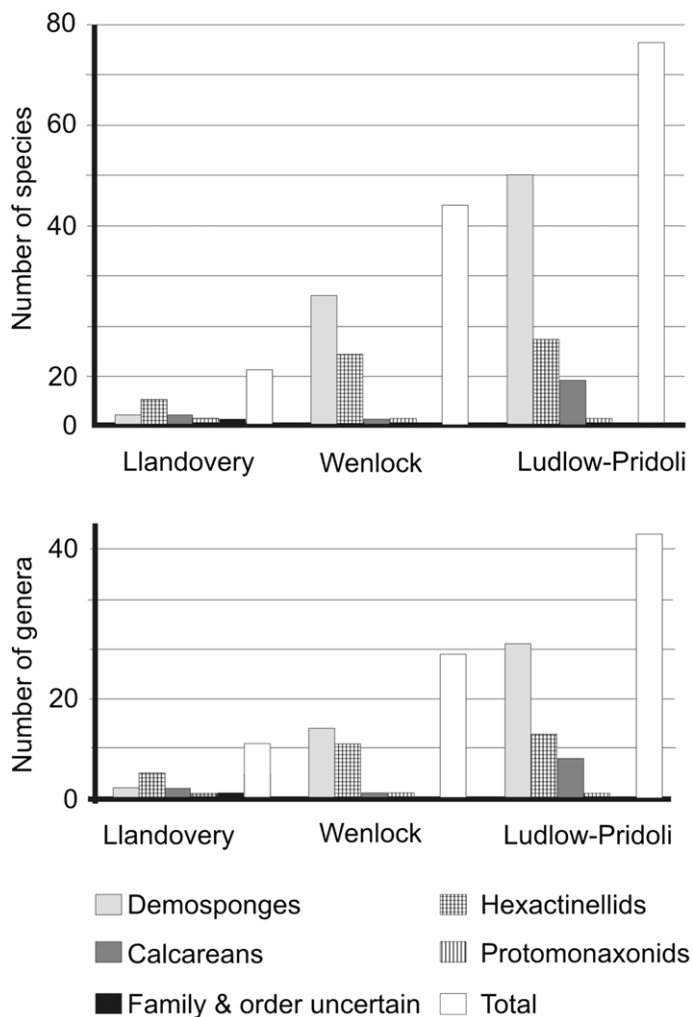
Fig. 8.3. Species- and genus-level diversity of Silurian non-stromatoporoid sponges.

Hexactinellids

Silurian hexactinellids are generally poorly represented, with a total of 45 nominal Silurian taxa, mostly from offshore or fine sediments. These appear to be largely endemic, reticulosan-grade taxa with only three species recorded from more than one site, all in Laurentia. *Heminectere conica* is recorded from the British Columbia, and also from Nevada. *Vaurealispongia minuta* occurs in the Wenlock Epoch of both Illinois and Iowa.

Most Silurian hexactinellids have been assigned to the protospongioids. The family Protospongiidae is currently poorly defined, but had a global Cambrian–Ordovician distribution. In this dataset, the Protospongiidae is represented by the genera *Protospongia*, *Gabelia*, *Diagoniella*, *Hexatractiella*, *Plectoderma* and *Heminectere*. In Ludlow–Pridoli time, the known protospongiid diversity totals seven species. However, six of these seven are from various sites in Nevada, and the other from a single occurrence in Greenland, although there also two protospongiid-like species now assigned to the dictyospongioids from England (*Dictyophytra danbyi* and *Phormosella ovata*). Several papers (Rigby & Harris 1979; Rigby & Stuart 1988; Mehl *et al.* 1993; Rigby & Maher 1995) have been written on the Nevadan faunas, so this apparent high diversity reflects sampling and monographic bias. The most widespread hexactinellid genus is *Diagoniella*, which occurs in Laurentia, Greenland and Iberia; this also has a wide Cambrian distribution, and the Silurian distribution is not necessarily informative. Also, the genus requires revision, and some of these occurrences may not strictly be of *Diagoniella*.

There are few named records of hexactinellids from carbonate platform facies; this is almost certainly a largely taphonomic artefact, with the spicules dispersing rapidly after death in the Silurian patch-reef environments. Isolated siliceous spicules are known to rapidly dissolve in warm, shallow water (Land 1976), acting as a further taphonomic bias against this spicule type.

Hexactinellids must have occurred more widely and in greater diversity than implied by these data. Isolated spicules and semi-articulated remains are present, for example, in Llandovery-age erratics from Gotland (under study by F. Rhebergen and J. P.
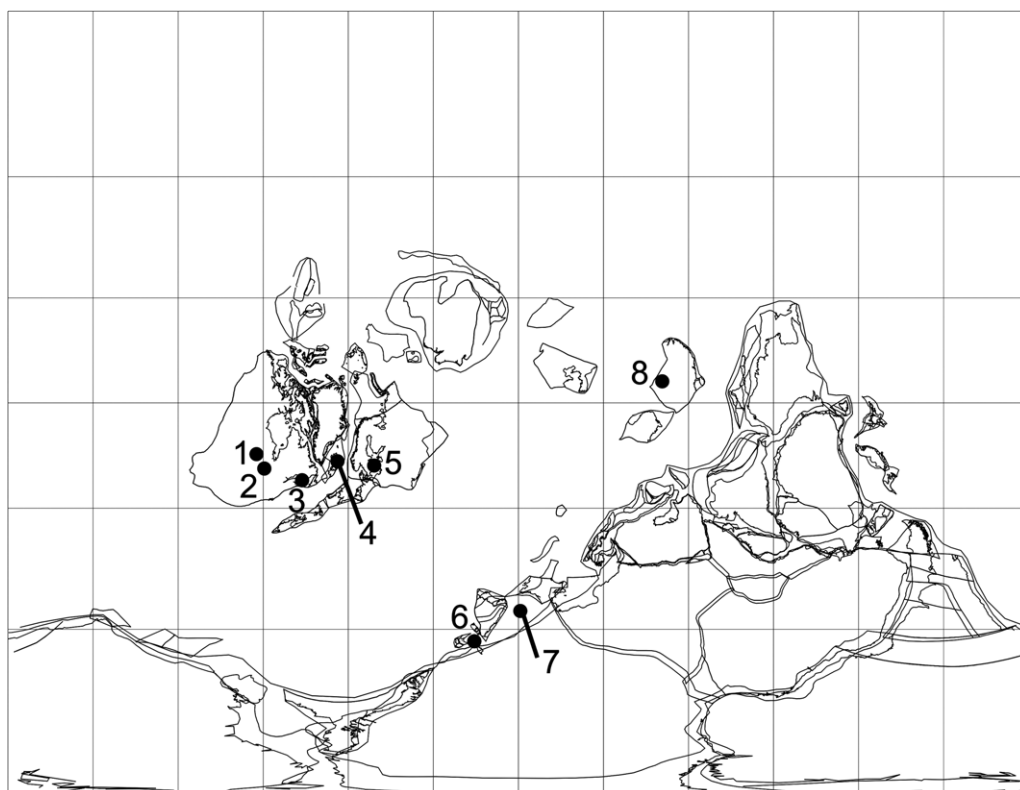

Fig. 8.4. Palaeogeographical map showing non-stromatoporoid sponge distribution for the Llandovery Epoch (435 Ma). 1, Iowa; 2, Indiana; 3, Anticosti Island, Quebec; 4, Pentlands, Scotland; 5, Gotland, Sweden; 6, Sardinia; 7, Carnic Alps; 8, Sichuan, China.
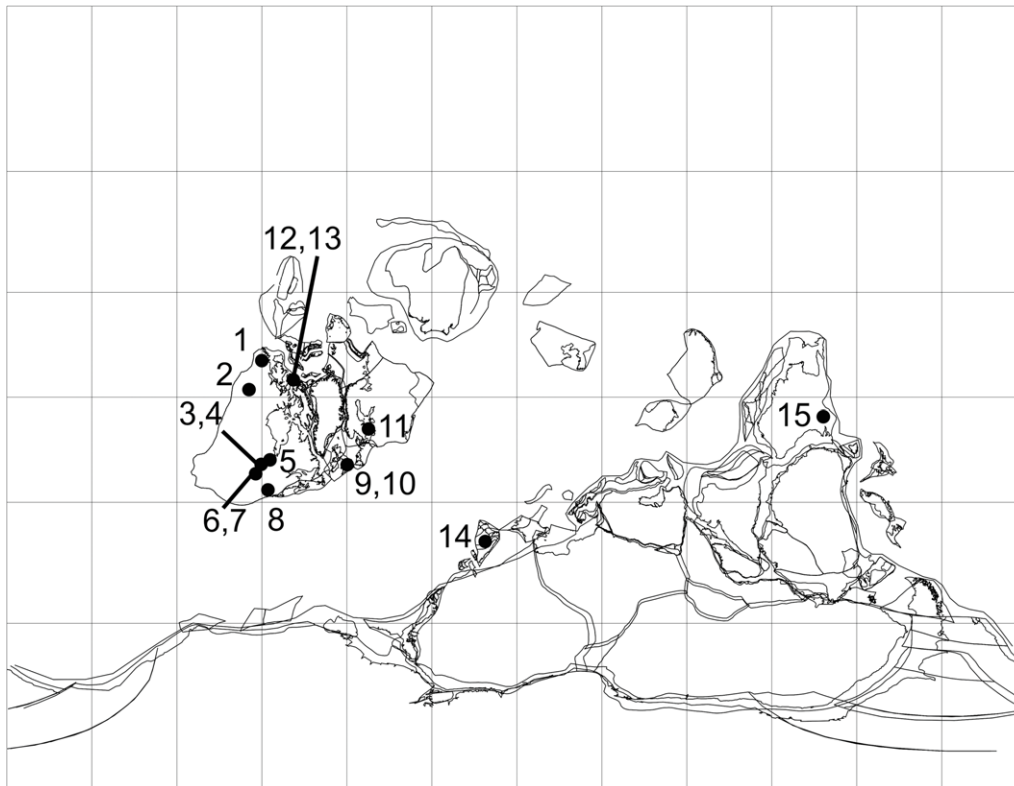
Fig. 8.5. Palaeogeographical map showing non-stromatoporoid sponge distribution for the Wenlock Epoch (425 Ma). 1, Mackenzie Mountains, NW Territories; 2, northern British Columbia; 3, Indiana; 4, Illinois; 5, Quebec; 6, Kentucky; 7, Tennessee; 8, New York State; 9, Shropshire, England; 10, Dudley, England; 11, Gotland, Sweden; 12, Baillie-Hamilton Island, Arctic Canada; 13, Cornwallis Island, Arctic Canada; 14, Baixo Alentexo, Portugal; 15, Orange, New South Wales, Australia.

Botting). We are aware of one record of Silurian hexactinellid sponges from South America (Beresi 2010), but this is of isolated spicules only and does not advance our knowledge of the palaeogeography of this group, beyond proving that they were indeed present in South America in the Silurian. Isolated hexactinellid spicules are also present rarely in the Much Wenlock Limestone Formation of England (J. P. Botting pers. obs. 1999), but no complete specimens have been recorded.

Demosponges

Demosponge diversity in the Llandovery Epoch is low (three species, three genera, three families), but increases in the Wenlock Epoch (26 species, 14 genera, six families) and Ludlow–Pridoli epochs (50 species, 20 genera, 10 families). One family, the Astylospongidae, has significant Wenlock diversity (six species), and is well known from the Ordovician Period,
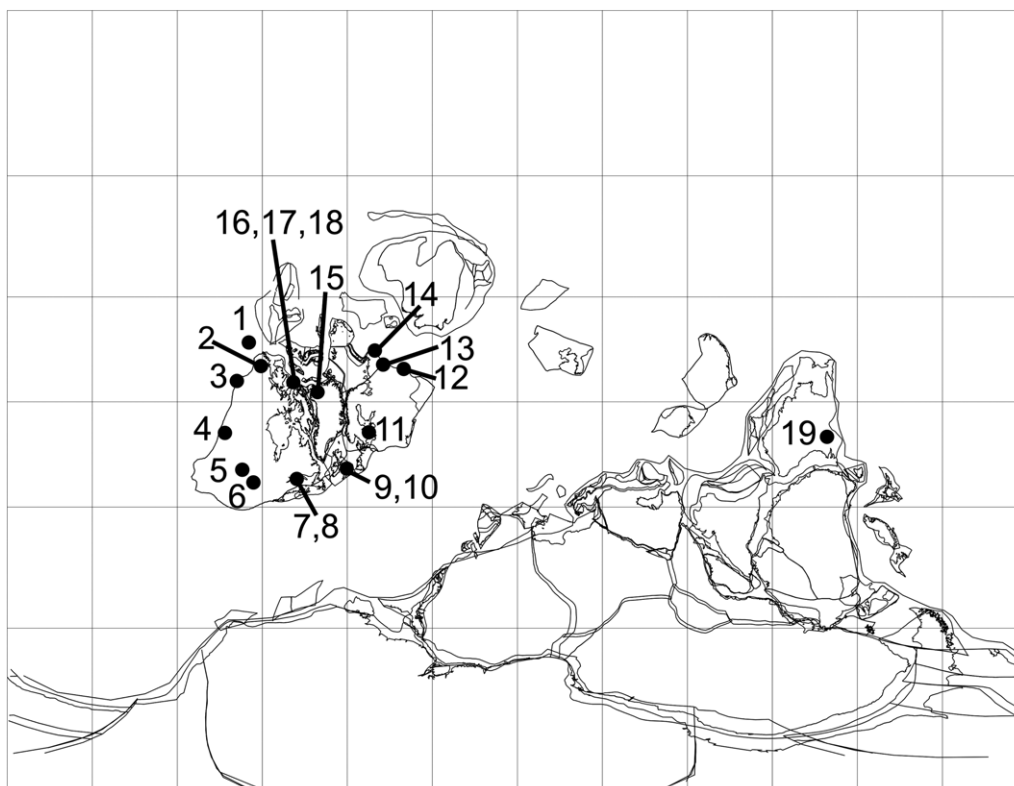
Fig. 8.6. Palaeogeographical map showing non-stromatoporoid sponge distribution for the Ludlow and Pridoli epochs (420 Ma). 1, south-central, southwestern, west-central, western Alaska; 2, Mackenzie Mountains, NW Territories; 3, Southeastern Alaska, including Prince of Wales Island; 4, Nevada; 5, Oklahoma; 6, Tennessee; 7, Gaspe Peninsula, Quebec; 8, New Brunswick; 9, Shropshire, England; 10, Cumbria, England; 11, Gotland, Sweden; 12, Eastern Urals, including Vishera River; 13, Western Urals; 14, Northern Ural Mountains, including Pai-Khoi and Vaigach Island; 15, Nyboe Land, Greenland; 16, Baillie-Hamilton Island, Arctic Canada; 17, Cornwallis Island, Arctic Canada; 18, Somerset Island, Arctic Canada; 19, Yass, New South Wales, Australia.

Table 8.2. *Distribution of sponge families for the Llandovery Epoch*

Locality number	1	2	3	4	5	6	7	8
Hexactinellids Amphispongiidae				×				
Brachiospongiidae Dictyospongiidae Docodermatidae Hintzespongiidae Lumectospongiidae Malumispongiidae								
Pelicaspongiidae		×	×					
Protospongiidae				×				
Stiodermatidae						×		
Demosponges Anthaspidellidae								×
Aphrosalpingidae Astylospongiidae Auriculospongiidae Cryptocoeliidae Girtyocoeliidae Haplistiidae								
Hindiidae					×			
Saccospongiidae Streptosolenidae								
Vauxiidae				×				
Family uncertain								
Protomonaxonids Choiidae				×				
Leptomiditae Mahalospongiidae								
Heteractinids Astraeospongiidae	×	×						
Polyactinellidae							×	
Preperonidellidae								
Family and order uncertain (*Nabaviella*?)						×		
Total number of families	**1**	**2**	**1**	**4**	**1**	**2**	**1**	**1**

Locality numbers as for Figure 8.4. Families with no recorded occurrence in the time period are greyed out.

yet is absent from the Llandovery Epoch. This indicates a higher diversity of sponges in the Llandovery Epoch than we are currently aware of, although it is possible that members of these lineages that survived the end-Ordovician interval were localized or rare. One of the Llandovery genera (*Hindia*) is widely distributed across Euramerica in the Wenlock Epoch, implying either a very rapid spread in the early Wenlock Epoch, or that it was widespread in the Llandovery Epoch but overlooked. There are currently too few records of Silurian sponges outside Euramerica to make any comments regarding their wider distribution, and it is possible that they survived through the early part of the Silurian Period on a different continent.

Sphinctozoan demosponges display strikingly different palaeobiogeographical patterns between the Ordovician and Silurian periods. Ordovician sphinctozoans exhibit a distinctive biogeographical distribution restricted to Upper Ordovician fold-belt successions (island-arc terranes) of the Palaeo-Pacific (New South Wales, Alaska, California, northwestern China and Kazakhstan). Sphinctozoans are very rare in platform associations of the Lower Palaeozoic, and the occurrence of sphinctozoans in the few preserved island arcs provides overwhelming evidence that they must have diversified and dominated in such habitats, at least during the Ordovician Period (Carrera & Rigby 2004). Sphinctozoan distribution is different in the Silurian Period.

Their distribution in North America appears to be associated with calcareous platform facies in Alaska and the Canadian Arctic, and some species are also recorded in the midcontinent area (Tables 8.3 & 8.4). The Silurian families Cryptocoeliidae, Girtyocoeliidae and Aphrosalpingidae, recorded in these areas, show considerably less diversity than the Ordovician sphinctozoans, with 33 species included in seven families. The low Silurian diversity is possibly related to a gradual decline in global temperature during the late Ordovician (Hirnantian) glaciation.

Protomonaxonids

The protomonaxonids have a global distribution in the Cambrian Period, and are coming to be recognized as still widely distributed during the Ordovician Period (Dawson 1896; Botting 2004*a*, 2007*b*; Beresi *et al.* 2010; Van Roy *et al.* 2010). In the Silurian Period, three protomonaxonid occurrences are known: the Choiidae is represented by one species from the Llandovery Epoch of Scotland, the Leptomitidae by one probable species from the Wenlock Epoch of British Columbia, and the monospecific Mahalospongiidae by *Mahalospongia floweri* from the Ludlow Epoch of Nevada. The group therefore provides no Silurian palaeobiogeographical insights at present.

Table 8.3. *Distribution of sponge families for the Wenlock Epoch*

Locality number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Hexactinellids															
Amphispongiidae															
Brachiospongiidae															
Dictyospongiidae		×										×			
Docodermatidae															
Hintzespongiidae	×	×													
Lumectospongiidae															
Malumispongiidae										×					
Pelicaspongiidae			×	×											
Protospongiidae		×												×	
Stiodermatidae									×						
Demosponges															
Anthaspidellidae	×				×										
Aphrosalpingidae	×											×	×		
Astylospongiidae	×		×				×				×	×			
Auriculospongiidae															
Cryptocoeliidae															
Girtyocoeliidae															
Haplistiidae	×											×			
Hindiidae	×		×								×		×		
Saccospongiidae															
Streptosolenidae											×	×			
Vauxiidae															
Family uncertain	×														×
Protomonaxonids															
Choiidae															
Leptomiditae		×													
Mahalospongiidae															
Heteractinids															
Astraeospongiidae			×			×	×	×		×	×				
Polyactinellidae															
Preperonidellidae															
Family and order uncertain (*Nabaviella*?)															
Total number of families	**7**	**4**	**4**	**1**	**1**	**1**	**2**	**1**	**1**	**2**	**4**	**5**	**2**	**1**	**1**

Locality numbers as for Figure 8.5. Families with no recorded occurrence in the time period are greyed out.

Calcareans

Calcarean diversity is very low during the Llandovery Epoch (two species, two genera, two families) and Wenlock Epoch (one species), but slightly higher during the Ludlow–Pridoli epochs (nine species, eight genera, three families). The calcareans are of little use for palaeobiogeography. The most widespread family, the Astraeospongiidae, are found in the present-day USA and Gotland during the Llandovery, Wenlock and Ludlow epochs, and also in England during the Wenlock Epoch. These sites were part of the same continental block during the Silurian Period.

The late Ordovician glaciation had a marked effect on the calcareans. No families are known from the Hirnantian Age, although the Astraeospongiidae and Polyactinellidae are present in both the Llandovery Epoch and the late Ordovician Katian Age. There are Silurian records for spicules of the Polyactinellidae at two sites: one in the Llandovery Epoch (Carnic Alps) and the other in the Ludlow Epoch (Gotland). The family is not recorded in the Wenlock Epoch. Both records for this family are of isolated spicules only. These two records are on opposite sides of the Rheic Ocean, but the group also had a wide distribution during the Ordovician Period and this may not be significant. The only Silurian record of the Preperonidellidae is in the Ludlow Epoch of southeastern Alaska. Three species in three genera are known from

here, which implies considerable unrecorded diversity elsewhere, unless the group was endemic and diversified only locally.

Discussion

Ghost lineages

There are many ghost lineages in the Silurian sponge record. Thirteen families of the 27 in our dataset have a pre-Silurian record (Finks *et al.* 2004; Rigby *et al.* 2008) and are absent from the Llandovery Epoch, but are known from the Wenlock and/or Ludlow epochs. These families are: Aphrosalpingidae, Astylospongiidae, Brachiospongiidae, Cryptocoeliidae, Dictyospongiidae, Girtyocoeliidae, Haplistiidae, Hintzespongiidae, Leptomiditae, Malumispongiidae, Preperonidellidae, Saccospongiidae and Streptosolenidae. This indicates a major gap in our knowledge for these groups, and also implies that many other families with few or no Silurian records may have been present.

The late Ordovician glaciation had a marked effect on sponges, especially for the calcareans and hexactinellids: in total, nine hexactinellid families disappeared during the Hirnantian Age. The extinctions may have affected demosponges less than other

Table 8.4. *Distribution of sponge families for the Ludlow–Pridoli epochs*

Locality number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Hexactinellids																			
Amphispongiidae																			
Brachiospongiidae				×															
Dictyospongiidae				×					×	×									
Docodermatidae																	×		
Hintzespongiidae																			
Lumectospongiidae																×			
Malumispongiidae				×			×										×		
Pelicaspongiidae																		×	
Protospongiidae				×											×				
Stiodermatidae				×															
Demosponges																			
Anthaspidellidae		×				×										×	×	×	
Aphrosalpingidae	×		×									×	×	×					
Astylospongiidae						×										×	×		×
Auriculospongiidae			×																
Cryptocoeliidae																	×		
Girtyocoeliidae			×																
Haplistiidae																×		×	
Hindiidae		×				×		×			×					×	×	×	
Saccospongiidae																		×	
Streptosolenidae																×			
Vauxiidae																			
Family uncertain																			
Protomonaxonids																			
Choiidae																			
Leptomiditae																			
Mahalospongiidae				×															
Heteractinids																			
Astraeospongiidae					×	×					×								
Polyactinellidae											×								
Preperonidellidae			×																
Family and order uncertain (*Nabaviella*?)																			
Total number of families	**1**	**2**	**4**	**5**	**1**	**4**	**1**	**1**	**1**	**1**	**3**	**1**	**1**	**1**	**1**	**6**	**6**	**5**	**1**

Locality numbers as for Figure 8.6. Families with no recorded occurrence in the time period are greyed out.

sponge groups: of three families known from the Hirnantian Age (Astylospongiidae, Anthaspidellidae and Hindiidae), the latter two are known from the Llandovery Epoch, and the Astylospongiidae are present in the Wenlock epoch. Thus there is less of a gap in the record, at least for these families, than for the other groups of non-stromatoporoid sponge.

Taphonomic influence on perceived sponge distributions

Environmental aspects strongly affect the few apparent patterns that are visible. In the Silurian Period, hexactinellids tend to occur in fine-grained siliciclastic rocks and demosponges in limestones, leading to significant environmental bias in sponge faunas. For example, the siltstones of the Ludlow Epoch of Nevada contain a relatively high diversity of hexactinellids. No demosponges or calcareans have been reported, despite a large number of taxonomic publications on the region (Rigby & Harris 1979; Rigby & Stuart 1988; Mehl *et al.* 1993; Rigby & Maher 1995). The reverse is true for the Ludlow Epoch of Tennessee and of southeastern Alaska (Table 8.4), where there are several species of demosponge but no hexactinellids – these are faunas from limestone facies, rather than siltstone (Rigby *et al.* 2008).

Although environmentally controlled distribution patterns have major effects on palaeobiogeographical interpretations of all groups, the taphonomic biases affecting sponges make these patterns more extreme. In the example above, there may have been heteractinid calcareans present in the Nevada siltstones, but their Mg-calcite spicules would have dissolved more easily in deep water than in shallow water. The unfused opaline skeletons of hexactinellids in carbonate platform regions would have been rapidly destroyed by water turbulence and dissolution, whereas the fused lithistid skeletons would have survived at least in part, and calcareans should be well preserved. The Silurian sponge records within a particular region generally accord with the patterns expected for these biases. Where unexpected faunas are preserved, such as the shallow-water Llandovery Pentland Hills community of protomonaxonids and hexactinellids, the genera represented are either extremely rare or unique to the deposit. This indicates that, even in the limited record of sponges that have been preserved and published, only a few very specific types of fauna are generally included. When the effects of patchy life distributions are also considered (discussed above), it is unsurprising that so few palaeobiogeographical signals have been recovered.

Silurian palaeobiogeography

The most obvious pattern from the maps (Figs 8.4–8.6) is that almost all the described occurrences of Silurian sponges are from Laurentia, with a few from Avalonia and Baltica. There are

very few records from palaeocontinents other than Euramerica. This cannot reflect a real pattern, but instead is correlated with the historical distribution of sponge palaeontologists. Even within Euramerica the record is extremely poor, as shown by the ghost lineages, but it is unclear how much of this reflects genuine rarity of preserved sponges, and how much is due to the rarity of specialists, and time constraints limiting formal descriptions.

Overall, the available data are too sparse to yield significant palaeobiogeographical insights. Where genera or families occur in more than one site, the geographical spread is too limited to be informative. More data on diverse sponge faunas from a large number of widely dispersed sites will be required before we can obtain any meaningful understanding of Silurian sponge distributions.

Conclusions

In Cambrian faunas, the main problem is the rarity of the relatively preservable lithistid and hypercalcified taxa (excluding archaeocyathans, which have not been included here), and the limited number of biotas with the necessary exceptional preservation to preserve recognizable taxa. In the known faunas, there is a remarkably wide distribution of many genera, although with several of the minor groups (at that time) apparently limited to low latitudes. As a result, there is insufficient information for the Cambrian to define provinces or other palaeobiogeographical units.

Our slowly increasing knowledge of Ordovician sponge faunas, combined with the revised palaeogeographical maps, undermines some previous interpretations of earlier sponge distributions (Carrera & Rigby 1999). Certain patterns appear to remain, including the limitation of Ordovician sphinctozoans to equatorial island arcs, which are further constrained to only the northern equatorial region. This may be a genuine pattern reflecting dispersal via a north tropical current. However, a longitudinal separation of faunas from separate ocean basins is not supported, with the very limited data indicating no clear segregation. We also offer some possible patterns for assessment by further research, such as the restriction of *Cyathophycus* to offshore sediments of the Iapetus region, and the possible northward spread of protomonaxonids via the drift of Avalonia. In general, however, Ordovician sponges were either distributed very widely, or appear to have been endemic.

There are currently insufficient data on Silurian non-stromatoporoid sponges to draw any firm conclusions about palaeobiogeographical patterns. The largest gaps in our knowledge are the Gondwanan sponge faunas, and faunas from the Llandovery Epoch worldwide. Many sites contain only one genus or family of sponge, and some sponge families are recorded as occurring at only one site, particularly for the hexactinellids (Tables 8.1–8.3). This paucity of data indicates either that many sponges are endemic and most sites have very few sponges, or that the sponge fossil record has been largely overlooked. We tend towards the idea that many undescribed sponge faunas exist, but they have not yet been recognized. For example, the work of Botting (2004a, 2005) in the Ordovician Builth Inlier of Wales raised the total diversity of Welsh Ordovician sponges from three species to 27, with many more under study; most of these are from well-known faunas whose sponge components had previously not been recognized. These faunas are enough to significantly alter the Ordovician sponge global diversity curve (Botting & Muir 2008). We suggest that investigations in some Silurian rocks will be equally or even more fruitful.

The rarity of sponges in the Llandovery Epoch is suprising. The Llandovery Epoch is longer than the Wenlock, Ludlow and Pridoli epochs combined, yet there are fewer sponge sites and fewer genera and families in the Llandovery Epoch. It may be that sampling effort in the Silurian Period is not biased towards the Wenlock and Ludlow epochs, but reflects the amount of material available, meaning that there really are very few Llandovery sponges. The end-Ordovician extinction probably plays a part in the depressed diversity, but the numerous ghost lineages at family level through the entire Llandovery Epoch imply that many unrecorded groups were present. Of 36 non-stromatoporoid sponge families present in the Upper Ordovician Epoch (database compiled by MGC), 15 are known to occur in the Silurian Period, but 10 of these are yet to be recognized from the Llandovery Epoch. A large part of the reason for the lack of Llandovery sponges may be the supposed rarity of reefs at that time (Stanley 1988). However reefs are widely known in the Llandovery Epoch (e.g. Nield 1982; de Freitas & Nowlan 1998; Li *et al.* 2002; Hughes & Thomas 2011) and corals had recovered substantially by late Llandovery time (Kaljo 1996). Also, the lack of carbonate facies would affect lithistids and calcareans, but not hexactinellids and demosponges, which are more characteristic of siliciclastic settings. In the Ordovician Period, hexactinellids and demosponges are found in graptolitic mudstones (e.g. Botting 2004a; Botting & Muir 2011), and so early Silurian habitats should not have been limited. We therefore have no good explanation for the apparent lack of diversity for all sponge groups in the Llandovery Epoch.

Some of the observable patterns of Silurian sponge distribution may be explained through a direct comparison with modern biotas. The sparse records of Polyactinellidae (see above), for example, and the widely separated Ordovician reports of the equally distinctive Pseudolanciculidae (Botting 2005), are likely to result from a poor record combined with ecological patchiness. These taxa must have been much more widely distributed than is currently recognized, but their spicules are rarely recovered from acid digestion residues. Despite the theoretical arguments (Carrera & Rigby 1999) that sponges should offer strong palaeobiogeographical signals, the reality is that sensitivity to a complex interplay of environmental factors has led to a sufficiently discontinuous distribution that the signals are largely obscured by a poor record. While it is tempting to over-interpret the few data available, the only rational conclusion is that the Silurian sponge fossil record is too limited in geographical coverage and too poorly known, at least at present, to offer significant palaeobiogeographical insights.

Overall, the current record of Early Palaeozoic sponge distribution is still very sparse. Owing to the grossly incomplete record, combined with taphonomic complications specific to the group, we regard all palaeobiogeographical conclusions based on the group to be suspect. We have, however, pointed out certain apparent patterns that may be supported by further research, and encourage the description of new faunas wherever possible, especially from outside Laurentia. In particular, atypical communities such as the rare faunas preserved in shallow-water siliciclastics may be palaeobiogeographically informative.

References

BELL, J. J. & BARNES, D. K. A. 2003. Effect of disturbance on assemblages: an example using Porifera. *Biological Bulletin*, **205**, 144–159.

BERESI, M. S. 2003. Oxfordian sponge association from the Neuquén basin, Mendoza, west-central Argentina. *Journal of South American Earth Sciences*, **16**, 105–112.

BERESI, M. S. 2007. Fossil sponges of Argentina: a review. *In*: CUSTODIO, M. R., LOBO-HAJDU, G., HAJDU, E. & MURICY, G. (eds) *Porifera*

Research-Biodiversity, Innovation & Sustainability. Museu Nacional, Rio de Janeiro, Brazil, 11–21.

BERESI, M. S. 2010. The first occurrence of Silurian sponge spicules of the Precordillera, San Juan Province, Argentina. *X Congreso Argentino de Paleontología y Bioestratirafía y VII Congreso Latinoamericano de Paleontología, Resumes*, 42.

BERESI, M. S., ACEÑOLAZA, G. & NIEVA, S. 2006. Cambro-Ordovician sponges and spicule assemblages from Northwest Argentina: new data from the siliciclastic platforms of western Gondwana. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, **2006**, 403–420.

BERESI, M. S., BOTTING, J. P. & CLARKSON, E. N. K. 2010. A new demosponge, *Choiaella scotica*, from the Caradoc (Ordovician) of Wallace's Cast, Southern Uplands. *Scottish Journal of Geology*, **46**, 77–83.

BOTTING, J. P. 2004*a*. An exceptional Caradoc sponge fauna from the Llanfawr Quarries, central Wales, and phylogenetic implications. *Journal of Systematic Palaeontology*, **2**, 31–63.

BOTTING, J. P. 2004*b*. A revision of the hexactinellid sponge *Amphispongia oblonga* Salter 1861: not a dasycladacean alga. *Scottish Journal of Geology*, **40**, 115–118.

BOTTING, J. P. 2005. Exceptionally-preserved Middle Ordovician sponges from the Llandegley Rocks Lagerstätte, central Wales. *Palaeontology*, **48**, 577–617.

BOTTING, J. P. 2007*a*. Algae, receptaculitids and sponges. *In*: CLARKSON, E. N. K., HARPER, D. A. T., TAYLOR, C. M. & ANDERSON, L. I. (eds) *Silurian Fossils of the Pentland Hills, Scotland*. Palaeontological Association, Field Guides to Fossils, London, **11**, 36–49.

BOTTING, J. P. 2007*b*. 'Cambrian' demosponges in the Ordovician of Morocco: insights into the early evolutionary history of sponges. *Geobios*, **40**, 737–748.

BOTTING, J. P. & MUIR, L. A. 2008. Unravelling causal components of the Ordovician Radiation: the Builth Inlier (central Wales) as a case study. *Lethaia*, **41**, 111–125.

BOTTING, J. P. & MUIR, L. A. 2011. A new Middle Ordovician (Dapingian) hexactinellid sponge from the Kirk Stile Formation (Skiddaw Group) of Cumbria, UK. *Geological Journal*, **46**, 501–506.

CANDELA, Y. & BOTTING, J. P. 2011. A unique new Silurian sponge (?Dictyospongioidea) from the Pentland Hills, Scotland. *Palaeontological Association Annual Meeting, Abstracts*, 45.

CARBALLO, J. L. 2006. Effect of natural sedimentation on the structure of tropical rocky sponge assemblages. *Ecoscience*, **13**, 119–130.

CARBALLO, J. L. & NAVA, H. 2007. A comparison of sponge assemblage patterns in two adjacent rocky habitats (tropical Pacific Ocean, Mexico). *Ecoscience*, **14**, 92–102.

CARRERA, M. G. 2006. The genus *Multispongia* (Porifera) in the Early Ordovician limetones of the Argentine Precordillera. *Ameghiniana*, **43**, 493–498.

CARRERA, M. G. 2007. The oldest Hindiid demosponge from the Darriwilian (Middle Ordovician) of the Argentine Precordillera: evolutionary implications for the Suborder Tricranocladina. *Journal of Paleontology*, **81**, 754–759.

CARRERA, M. G. & BOTTING, J. P. 2008. Evolutionary history of Cambrian spiculate sponges: implications for the Cambrian evolutionary fauna. *Palaios*, **23**, 124–138.

CARRERA, M. G. & MALETZ, J. 2010. Ordovician sponge spicules from Spitsbergen, Nevada and Newfoundland: new evidence for the Hexactinellid early differentiation. *X Congreso Argentino de Paleontología y Bioestratigrafía y VII Congreso Latinoamericano de Paleontología, Resumes*, **143**.

CARRERA, M. G. & ORTEGA, G. 2009. The hexactinellid sponge *Cyathophycus* from the Upper Ordovician of the Argentine Precordillera. *Ameghiniana*, **46**, 449–459.

CARRERA, M. G. & RIGBY, J. K. 1999. Biogeography of Ordovician sponges. *Journal of Paleontology*, **73**, 26–37.

CARRERA, M. G. & RIGBY, J. K. 2004. Chapter 12. Sponges. *In*: WEBBY, B. D., PARIS, F., DROSER, M. L. & PERCIVAL, I. G. (eds) *The Great Ordovician Biodiversification Event*. Columbia University Press, New York, 102–111.

CULVER, S. J., REPETSKI, J. E., POJETA, J., JR. & HUNT, D. 1996. Early and Middle(?) Cambrian metazoan and protistan fossils from West Africa. *Journal of Paleontology*, **70**, 1–6.

DAWSON, J. W. 1896. Additional notes on fossil sponges and other organic remains from the Quebec Group of Little Métis on the lower St. Lawrence; with notes on some of the specimens by Dr. G. J. Hinde. *Transactions of the Royal Society of Canada*, **44**, 91–121.

DEBRENNE, F. 2007. Lower Cambrian archaeocyathan bioconstructions. *Comptes Rendus Palevol*, **6**, 5–19.

DEBRENNE, F. & REITNER, J. 2001. Sponges, cnidarians and ctenophores. *In*: ZHURAVLEV, A. YU. & RIDING, R. (eds) *The Ecology of the Cambrian Radiation*. Columbia University Press, New York, 301–325.

DE FREITAS, T. 1987. A Silurian sphinctozoan sponge from east-central Cornwallis Island, Arctic Canada. *Canadian Journal of Earth Sciences*, **24**, 840–844.

DE FREITAS, T. A. 1989. Silurian *Archaeoscyphia* from the Canadian Arctic: a case for simplified generic taxonomy in the anthaspidellid lithistids (Porifera). *Canadian Journal of Earth Sciences*, **26**, 1861–1879.

DE FREITAS, T. A. 1991. Ludlow (Silurian) lithistid and hexactinellid sponges, Cape Phillips Formation, Canadian Arctic. *Canadian Journal of Earth Sciences*, **28**, 2042–2061.

DE FREITAS, T. A. & NOWLAN, G. S. 1998. A new, major Silurian reef tract and overview of regional Silurian reef development, Canadian Arctic and north Greenland. *Bulletin of Canadian Petroleum Geology*, **46**, 327–349.

DE VOOGD, N. J., CLEARY, D. F. R., HOEKSEMA, B. W., NOOR, A. & VAN SOEST, R. M. W. 2006. Sponge beta diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia. *Marine Ecology Progress Series*, **309**, 131–142.

FINKS, R. M., REID, R. E. H. & RIGBY, J. K. 2004. *Treatise on Invertebrate Paleontology, Part E: Porifera (revised), Volume 3: Porifera (Demospongea, Hexactinellida, Heteractinida, Calcarea)*. Geological Society of America and University of Kansas, Boulder, CO and Lawrence, KS.

GARCÍA-BELLIDO, D. C., DIES ÁLVAREZ, M. E., GÁMEZ VINTANED, J. A., LIÑÁN, E. & GOZALO, R. 2011. First report of *Crumillospongia* (Demospongea) from the Cambrian of Europe (Murero biota, Spain). *Bulletin of Geosciences*, **86**, 641–650.

GORTANI, M. 1926. Graptoliti del piano di Wenlock delle Alpi Carniche. *Giornale di Geologia Ser. 2a*, **1**, 6–19.

GUTT, J. & KOLTUN, V. M. 1995. Sponges of the Lazarev and Weddell Sea, Antarctica: explanations for their patchy occurrence. *Antarctic Science*, **7**, 227–234.

HINDE, G. J. 1887. A monograph of the British fossil sponges, Part 1, vol. 1, Sponges of Palaeozoic and Jurassic strata. *Monographs of the Palaeontographical Society, London*, **40**, 1–92.

HINDE, G. J. 1893. On *Paleosaccus dawsoni* Hinde, a new genus and species of hexactinellid sponges from the Quebec Group (Ordovician) at Little Métis, Quebec, Canada. *Geological Magazine, Series 3*, **10**, 56–58.

HOOPER, J. N. A. & VAN SOEST, R. W. M. 2002. *Systema Porifera: A Guide to the Classification of Sponges*. Kluwer Academic/Plenum Publishers, New York.

HUGHES, H. E. & THOMAS, A. T. 2011. Trilobite associations, taphonomy, lithofacies and environments of the Silurian reefs of North Greenland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **302**, 142–155.

IVANTSOV, A. YU., ZHURAVLEV, A. YU. *ET AL*. 2005. Unikal'nye sinskie mestonakhozhdeniya rannekembriiskikh organizmov, sibirskaya platforma. *Trudy Paleontologicheskogo Instituta*, **284**, 1–143 [in Russian].

JANUSSEN, D. & TENDAL, O. S. 2007. Diversity and distribution of Porifera in the bathyal and abyssal Weddell Sea and adjacent areas. *Deep-Sea Research II*, **54**, 1864–1875.

JANUSSEN, D., TABACHNICK, K. R. & TENDAL, O. S. 2004. Deep-sea Hexactinellida (Porifera) of the Weddell Sea. *Deep-Sea Research II*, **51**, 1857–1882.

KALJO, D. 1996. *Diachronous Recovery Patterns in Early Silurian Corals, Graptolites and Acritarchs*. Geological Society, London, Special Publications, **102**, 127–133.

KRAUTTER, M. 1995. Kieselschwämme als potentielle Indikatoren für Sedimentationsrate und Nährstoffangebot am Beispiel del Oxford–Schwammkalke von Spanien. *Profil*, **8**, 281–304.

LAND, S. 1976. Early dissolution of sponge spicules from reef sediments, north Jamaica. *Journal of Sedimentary Petrology*, **46**, 967–969.

LI, Y., KERSHAW, S. & CHEN, XU. 2002. Biotic structure and morphology of patch reefs from South China (Ningqiang Formation, Telychian, Llandovery, Silurian). *Facies*, **46**, 133–148.

MCDONALD, J. I., HOOPER, J. N. A. & MCGUINNESS, K. A. 2002. Environmentally influenced variability in the morphology of *Cinachyrella australiensis* (Carter 1886) (Porifera: Spirophorida: Tetillidae). *Marine and Freshwater Research*, **53**, 79–84.

MEHL, D., RIGBY, J. K. & HOLMES, S. B. 1993. Hexactinellid sponges from the Silurian–Devonian Roberts Mountains Formation in Nevada and hypotheses of hexactine–stauractine origin. *Brigham Young University Geology Studies*, **39**, 101–124.

MERGL, M. 2008. The hexactinellid sponge *Cyathophycus* from the Lower Ordovician Klabava Formation of the Prague Basin, Czech Republic. *Bulletin of Geosciences*, **83**, 233–236.

NESTOR, H. 1990. Biogeography of Silurian stromatoporoids. *In*: MCKERROW, W. S. & SCOTESE, C. R. (eds) *Palaeozoic Palaeogeography and Biogeography*. Geological Society, London, Memoirs, **12**, 215–221.

NIELD, E. W. 1982. The earliest Gotland reefs: two bioherms from the Lower Visby Beds (Upper Llandovery). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **39**, 149–164.

OLÓRIZ, F., REOLID, M. & RODRIGUEZ-TOVAR, F. J. 2003. A Late Jurassic carbonate ramp colonized by sponges and benthic microbial communities (External Prebetic, southern Spain). *Palaios*, **18**, 528–545.

PIÇARRA, J., PEREIRA, Z. & GUTIÉRREZ-MARCO, J. C. 2011. Ordovician graptolites and acritarchs from the Barrancos region (Ossa–Morena Zone, south Portugal). *In*: GUTIÉRREZ-MARCO, J. C., RÁBANO, I. & GARCÍA-BELLIDO, D. (eds) *Ordovician of the World*. Instituto Geológico y Minero de España, Madrid, 429–439.

RHEBERGEN, F. & VAN KEMPEN, T. 2002. An unusual Silurian erratic astylospongiid (Porifera) from Gotland, Sweden. *GFF*, **124**, 185–192.

RIGBY, J. K. 1986. Sponges of the Burgess Shale (Middle Cambrian) British Columbia. *Palaeontographica Canadiana Monograph*, **2**, 1–105.

RIGBY, J. K. & CHATTERTON, B. D. E. 1989. Middle Silurian Ludlovian and Wenlockian sponges from Baillie–Hamilton and Cornwallis Islands, Arctic Canada. *Geological Survey of Canada Bulletin*, **391**, 69.

RIGBY, J. K. & COLLINS, D. 2004. Sponges of the Middle Cambrian Burgess and Stephen Shale Formations, British Columbia. *Royal Ontario Museum Contributions in Science*, **1**, 1–164.

RIGBY, J. K. & HARRIS, D. R. 1979. A new Silurian sponge fauna from Northern British Columbia, Canada. *Journal of Paleontology*, **53**, 968–980.

RIGBY, J. K. & MAHER, B. J. 1995. Age of the hexactinellid beds of the Roberts Mountains Formation, Snake Mountains, Nevada, and additions to the Silurian sponge fauna. *Journal of Paleontology*, **69**, 1020–1029.

RIGBY, J. K. & STUART, R. J. 1988. Fossil sponges from the Silurian–Devonian Roberts Mountains Formation in northeastern Nevada. *New Mexico Bureau of Mines & Mineral Resources Memoir*, **44**, 129–137.

RIGBY, J. K., KING, J. E. & GUNTHER, L. F. 1981. The new Lower Ordovician protosponge, *Asthenospongia*, from the Phi Kappa Formation in central Idaho. *Journal of Paleontology*, **55**, 842–847.

RIGBY, J. K., ROHR, D. M., BLODGETT, R. B. & BRITT, B. B. 2008. Silurian sponges and some associated fossils from the Heceta Limestone, Prince of Wales Island, southeastern Alaska. *Journal of Paleontology*, **82**, 91–101.

ROBERTS, D. E. & DAVIES, A. R. 1996. Patterns in sponge (Porifera) assemblages on temperate coastal reefs off Sydney, Australia. *Marine and Freshwater Research*, **47**, 897–906.

SENOWBARI-DARYAN, B. 1990. Die systematische Stellung der thalamiden Schwammeu nd ihre bedeutungi n der Erdgeschichte. *Münchner Geowissenschaftliche Abhandlungen 2*, **1**, 326.

STANLEY, S. M. 1988. Climatic cooling and mass extinction of Paleozoic reef communities. *Palaios*, **3**, 228–232.

STEINER, M., MEHL, D., REITNER, J. & ERDTMANN, B.-D. 1993. Oldest entirely preserved sponges and other fossils from the Lowermost Cambrian and a new facies reconstruction of the Yangtze platform (China). *Berliner geowissenschaften Abhandlungen*, **9**, 293–329.

TORSVIK, T. H. 2009. *BugPlates*. http://www.geodynamics.no/bugs/SoftwareManual.pdf.

VAN KEMPEN, T. M. G. 1983. Een *Caryospongia diadema* (Klöden) Rauff (spons) van Gotland. *Grondboor en Hamer*, **37**, 100–104.

VAN ROY, P., ORR, P. J. *ET AL.* 2010. Ordovician faunas of Burgess Shale type. *Nature*, **465**, 215–218.

WATKINS, R. & COOROUGH, P. J. 1997. Silurian sponge spicules from the Racine Formation, Wisconsin. *Journal of Paleontology*, **71**, 208–214.

WEBBY, B. D. 1980. Biogeography of Ordovician stromatoporoids. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **32**, 1–19.

WEBBY, B. D. 1992. Global biogeography of Ordovician corals and stromatoporoids. *In*: WEBBY, B. D. & LAURIE, J. R. (eds) *Global Perspectives on Ordovician Geology*. A. A. Balkema, Rotterdam, 261–276.

WEBBY, B. D. & TROTTER, J. 1993. Ordovician sponge spicules from New South Wales, Australia. *Journal of Paleontology*, **67**, 28–41.

WU, WEN, YANG AI-HUA, JANUSSEN, D., STEINER, M. & ZHU MAO-YAN, 2005. Hexactinellid sponges from the Early Cambrian black shale of South Anhui, China. *Journal of Paleontology*, **79**, 1043–1051.

XIAO, S., HU, J., YUAN, X., PARSLEY, R. L. & CAO, R. 2005. Articulated sponges from the Lower Cambrian Hetang Formation in southern Anhui, South China: their age and implications for the early evolution of sponges. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **220**, 89–117.

ZHANG, X. & PRATT, B. R. 1994. New and extraordinary Early Cambrian sponge spicule assemblage from China. *Geology*, **22**, 43–46.