



Review

Early sponge evolution: A review and phylogenetic framework

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Abstract

Sponges are one of the critical groups in understanding the early evolution of animals. Traditional views of these relationships are currently being challenged by molecular data, but the debate has so far made little use of recent palaeontological advances that provide an independent perspective on deep sponge evolution. This review summarises the available information, particularly where the fossil record reveals extinct character combinations that directly impinge on our understanding of high-level relationships and evolutionary origins. An evolutionary outline is proposed that includes the major early fossil groups, combining the fossil record with molecular phylogenetics. The key points are as follows. (1) Crown-group sponge classes are difficult to recognise in the fossil record, with the exception of demosponges, the origins of which are now becoming clear. (2) Hexactine spicules were present in the stem lineages of Hexactinellida, Demospongiae, Silicea and probably also Calcarea and Porifera; this spicule type is not diagnostic of hexactinellids in the fossil record. (3) Reticulosans form the stem lineage of Silicea, and probably also Porifera. (4) At least some early-branching groups possessed biomineralic spicules of silica (with axial filament) combined with an outer layer of calcite secreted within an organic sheath. (5) Spicules are homologous within Silicea, but also between Silicea and Calcarea, and perhaps with Homoscleromorpha. (6) The last common ancestor of extant sponges was probably a thin-walled, hexactine-bearing sponge with biomineralic spicules. (7) The stem group of sponges included tetradially-symmetric taxa that grade morphologically into Cambrian fossils described as ctenophores. (8) The protomonaxonid sponges are an early-branching group, probably derived from the poriferan stem lineage, and include the problematic cancelloriids as derived members of the piraniid lineage. (9) There are no definite records of Precambrian sponges: isolated hexactine-like spicules may instead be derived from radiolarians. Early sponges had mineralised skeletons and thus should have a good preservation potential: the lack of sponge fossils in Precambrian strata may be due to genuine absence of sponges. (10) In contrast to molecular clock and biomarker evidence, the fossil record indicates a basal Cambrian diversification of the main sponge lineages, and a clear relationship to ctenophore-like ancestors. Overall, the early sponge fossil record reveals a diverse suite of extinct and surprising character combinations that illustrate the origins of the major lineages; however, there are still unanswered questions that require further detailed studies of the morphology, mineralogy and structure of early sponges.

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1. Introduction

Sponges are one of the key groups for understanding basal metazoan evolution, having traditionally been regarded as the most primitive living animals, both in phylogenetic topology and morphology (Bergquist, 1978; Gehling and Rigby, 1996). Recent molecular and palaeontological work has challenged this view, with a competing scenario emerging that involves secondary simplification from a cnidarian-like or ctenophore-like ancestor (e.g., Botting et al., 2014; Dunn et al., 2015; Ryan and Chiodin, 2015), although this has been both forcefully disputed (e.g., Nosenko et al., 2013; Simion et al., 2017) and supported (e.g., Whelan et al., 2015; Shen et al., 2017) by different research groups applying different analytical approaches. The debate centres on sources of error and the influence of artefacts such as long-branch attraction in the analyses, and despite confidence on both sides, the answer is not yet resolved unambiguously. Among these and other studies, however, there is now a virtual consensus that sponges form a monophyletic group, and that Silicea (Demospongiae and Hexactinellida) form one clade, probably as a sister group to Calcarea + Homoscleromorpha. The topology and branching sequence of the sponge classes, and more particularly of the Porifera and other early-branching animal phyla (Fig. 1), have critical implications for the nature of their last common ancestor and the question of how animals evolved.

Until now, the published debate has been focused almost entirely on the molecular biological evidence. Understanding the origins and derivation of the extant sponge clades is now critical to interpreting the nature of the earliest animals, but molecular work can as yet provide only limited and speculative conclusions regarding early sponge morphology and biology. There has also been a traditional assumption that the fossil record of sponges is severely limited in what information it can provide on the earliest branches, due to late-stage, independent origins of mineral skeletons (Bergquist, 1978; Reitner and Mehl, 1996), despite reviews that clearly illustrated how much evidence can be obtained from the fossil record (Pisera, 2003, 2006). Phylogenetic studies based on extant sponges have generally assumed that spicules are not homologous between the extant classes

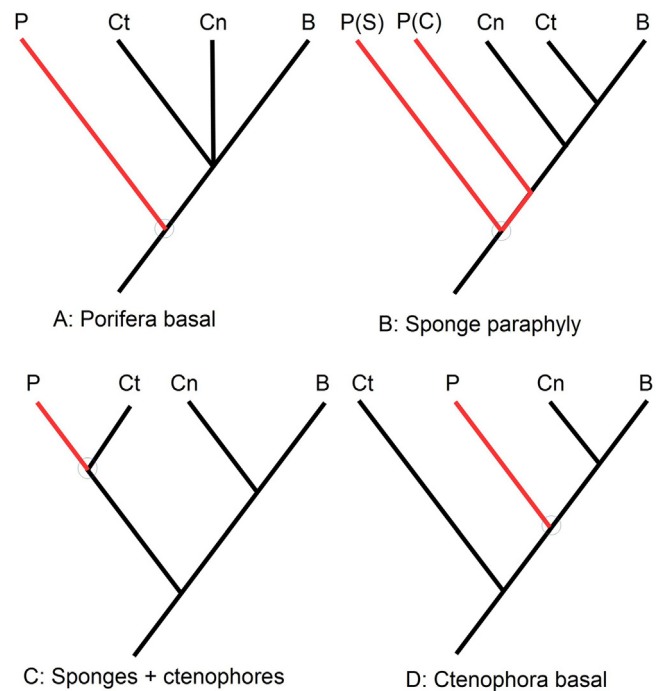


Fig. 1. Competing phylogenetic scenarios (current and recent) for sponge and other basal animal evolution; small circle marks last common ancestor between sponges and the next nearest metazoan group. The monospecific Placozoa are omitted due to further uncertainty over their position (many different published interpretations), and probable secondary simplification from a more complex ancestor of unknown nature. B: Bilateria; Cn: Cnidaria; Ct: Ctenophora; P: Porifera; P(S): Silicea; P(C): Calcarea. (A) The current standard, and traditional view, with monophyletic sponges as the basal animal group; (B) the now-outdated model of sponge paraphyly (e.g., Sperling et al., 2007), which implied that the ancestor of Eumetazoa was a sponge; (C) a rarely-encountered or lower-likelihood result of molecular phylogenies (e.g., Shen et al., 2017), but potentially supported by the fossil record (this paper); (D) the recent competing view of Ctenophora basal, in which either sponges would be secondarily simplified or nervous systems and muscles evolved at least twice.

(e.g., Manuel et al., 2003). In addition, early sponge fossils have been thought to be phylogenetically derived, for example with the assignment of Cambrian taxa to Hexactinellida, albeit the stem-group due to the differences of these taxa from living members of the class (e.g., Dohrmann et al., 2013). Both of these

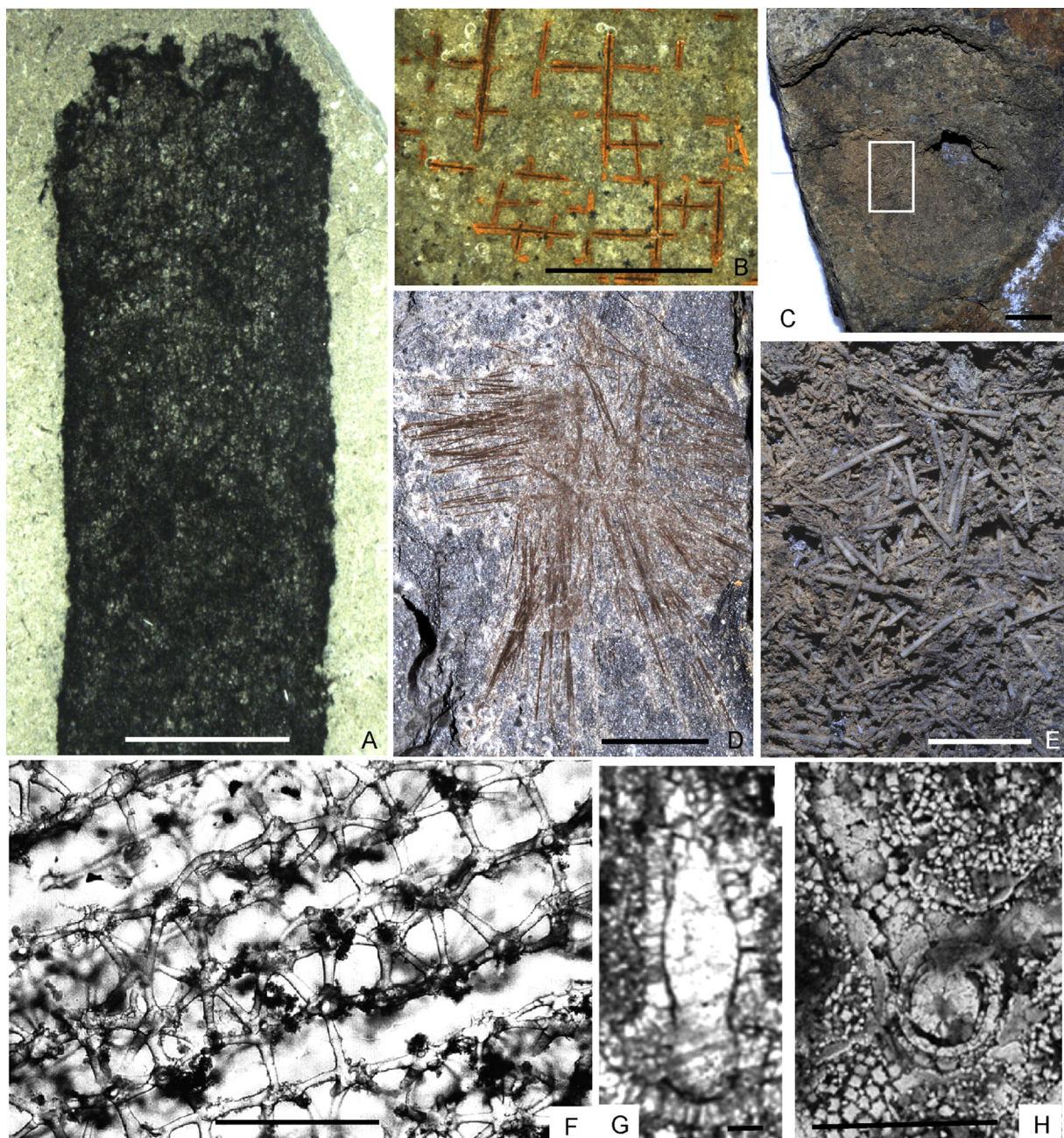


Fig. 2. Examples of the range of fossil sponge preservation. (A) ROM 64298, exceptional preservation of an organic fibre skeleton in an unnamed vauxiid demosponge, middle Cambrian of Monarch Cirque, Canada (photographed in cross-polarised light). (B) ROM 53604, detail of articulated skeleton of *Diagoniella* sp. from the Burgess Shale, Canada, with pyritised spicules showing oxidation haloes (photographed under cross-polarised light). (C, E) LLWLM2016:6474, undescribed brachiospongiid from the Middle Ordovician Llandegley Rocks site (see Botting, 2005), showing preservation of spicules as recrystallised silica (chalcedony); box in (C) shows position of (E). (D) LLWLM2014:5275, undescribed piraniid protomonaxonid from Castle Bank, Llandrindod (modified after Muir and Botting, 2015) with soft tissue and spicule replacement by iron oxides (after early diagenetic pyrite), typical for fine sediments with rapid burial. (F) NRM Sp.4511, *Caryoconus gothlandicus* (Schlüter, 1884; modified after Rhebergen and Botting, 2014), showing preservation of spicule skeleton embedded within clear silica concretion. (G) SMF26163, *Calcihexactina franconica*, replaced (calcitised) hexactine showing radiating void-filling crystals in outer part, and homogeneous replacement of interior (modified after Sdzuy, 1969). (H) NIGP155898, *Cyathophycus loydelli* (modified after Botting and Muir, 2013), showing high-resolution replacement of siliceous laminae by cryptocrystalline pyrite, and coarse crystalline pyrite replacement of organic materials. Scale bar: 5 mm for (A, D, E); 10 mm for (B, C, F); 0.1 mm for (G, H).

hypotheses have been cast into doubt on the basis of fossil evidence, such as the discovery of biminerallic spicules (Botting and Butterfield, 2005; Botting et al., 2012) and the realisation that some reticulans, traditionally assigned to Hexactinellida,

in fact have the axial filament symmetry characteristic of demosponges (Botting and Muir, 2013). It is becoming clear that early sponge evolution can be addressed in surprising detail from the fossil record.

This review summarises the recent discoveries, discusses the key points of interpretation of fossils and remaining problems, and presents an evolutionary framework based on the fossil record. Molecular evidence provides a further constraint on the phylogenetic topology and polarity of character acquisition, which is incorporated into the model as a foundation. Finally, an assessment is provided of the highly contentious Precambrian record of sponges (or lack thereof), with discussion of potential pathways to resolving the discordance between the microfossil record, molecular clocks and biomarker results.

Institutional abbreviations: LLWLM: Radnorshire Museum, Llandrindod, UK; NIGP: Nanjing Institute of Geology and Palaeontology, China; NRM: Naturhistoriska Riksmuseet, Stockholm, Sweden; ROM: Royal Ontario Museum, Toronto, Canada; SMF: Senckenberg-Museum, Frankfurt, Germany.

2. Sponge palaeontology and taphonomy

As with all organic remains, there has been at least some loss of information during the fossilisation of sponges. However, there are numerous different modes of preservation (Fig. 2), and these taphonomic styles must be understood in order to constrain reconstructions of living sponges. In general, soft-tissue structures are highly unlikely to be preserved, except under the most remarkable conditions, and then in most cases only as outlines; this is a significant problem, as many soft-tissue and cytological characters are critical for high-level taxonomy of extant taxa (e.g., Leys, 2003). Skeletal characters are more resilient, but collapse and compression of skeletal architecture following soft-tissue decay, as well as mineralogical replacement, are both very common processes. These processes must be understood in order to reconstruct the original morphology, particularly for non-actualistic aspects of spicule structure or soft-tissue organisation; an assumption of similarity to living taxa is not necessarily reliable.

In general only skeletal characters are preserved, although in sites of exceptional preservation (Konservat-Lagerstätten) soft tissues (Fig. 2A, D, H) are frequently encountered. Usually such tissues are preserved as flattened organic carbon or mineral films that can nonetheless reveal some structure (Botting, 2004; Rigby and Collins, 2004; Rigby et al., 2010; Botting and Muir, 2013). In some cases, notably through pyritisation, some degree of three-dimensionality is preserved (Botting et al., 2011, 2015a; Kühl et al., 2012), and exceptional cases with uncompressed three-dimensional soft tissue preservation are also known (Briggs et al., 1996; Botting, 2005). Putative phosphatised Precambrian sponges with complete three-dimensional preservation (e.g., Li et al., 1998) are unconvincing, as discussed in Section 5.

Where soft tissues are preserved, this is normally through mineralogical coating or replacement, typically by pyrite (iron sulphide; Fig. 2D, H) as a response to bacterial sulphate reduction in anoxic sediments (Briggs et al., 1991; Raiswell et al., 2008), or rarely by silica (Botting, 2005) or phosphate (Brayard et al., 2017). A distinct class of soft-tissue preservation is found in the Cambrian Burgess Shale-type faunas, in which fossils are preserved primarily as organic carbon (Fig. 2A), undecomposed but polymerised into a stable kerogenous composition;

the process by which this happened remains controversial (e.g., Butterfield, 1996; Petrovich, 2001; Gaines et al., 2012). In these situations, sponge spicules are frequently etched or removed by dissolution (Rigby, 1986; Botting and Peel, 2016). In many Burgess Shale-type assemblages (Gabbott et al., 2004; Lin and Briggs, 2010; Van Roy et al., 2010), there is at least a component of pyritisation together with the carbonaceous compressions, leading to a preservational continuum.

Skeletal preservation of sponges is more common, but differs significantly between different palaeoenvironments and taxonomic groups. Hypercalcified sponges are much more abundant and diverse in the fossil record than are living sclerosponges (Senowbari-Daryan and García-Bellido, 2002; Vacelet, 2002; Wörheide, 2008). Some groups were major reef-building organisms in, for example, the Silurian (stromatoporoids; Nestor and Webby, 2013) and Permian (sphinctozoans; Fan and Zhang, 1985; Rigby and Bell, 2009). The Cambrian archaeocyathans are also likely to be sponges (Debrenne and Zhuravlev, 1994; Debrenne, 2007), but this remains somewhat questionable (see Section 3.1.2). In carbonate facies, and particularly reef limestones, calcareous skeletons tend to be well preserved, although the fine microstructure may be lost through various types of recrystallisation (Riding, 1974). Hypercalcified sponges are generally derived groups, however, and although they are often common fossils in Phanerozoic carbonate deposits, they are of little use for reconstructing the early evolution of sponges or for clarifying character polarity. Spiculate, non-hypercalcified Calcareia are potentially much more informative regarding sponge origins, but their fossil record is extremely poor. Calcareous spicules are much more easily dissolved than massive skeletons, even in warm shallow water, due to their small size and the relatively high solubility of Mg-rich calcite (Sethmann and Wörheide, 2008; Wosley et al., 2012); their spicule fossil record is reasonable for young rocks but declines dramatically with age.

Siliceous sponges have the most important fossil record with respect to early sponge evolution, but this too is extremely biased towards certain groups. Silica, in contrast to calcite, is more chemically stable under low-temperature and high-pressure conditions (Alexander et al., 1954; Siever, 1962), particularly in the presence of aluminium (Cheng et al., 2009). Deep-water and offshore environments, which tend to be regions of sediment accumulation and low disturbance, are therefore ideal for the preservation of siliceous skeletons. In warm, shallow water, spicules are rapidly etched, usually by enlargement of the axial canal (Bertolino et al., 2016), which physically weakens the spicule and eventually leads to complete dissolution (Land, 1976). Bertolino et al. (2016) demonstrated that spicules exhibit highly variable dissolution rates between taxa, with hexactinellid spicules apparently more easily dissolved than those of demosponges. Siliceous spicules have a greater chance of geological survival if they are buried prior to dissolution and are not exposed to corrosive pore fluids. Although opal-A is metastable, it readily transforms via cristobalite (Inoue, 1973) to chalcedony in situ, and is normally then recrystallised to crystalline quartz (Carver, 1980; Duffy, 1993), which is stable under most chemical conditions.

Sponges in which the skeleton is fused (many hexactinellids) or rigidly interlocking (lithistids) are frequently well preserved (e.g., Fig. 2F), especially in offshore environments, and sometimes even in reef settings. Siliceous sponges are often preserved by calcite replacement, particularly in the Mesozoic and Cenozoic (e.g., Warnke, 1995; Pisera, 1997; Frisone et al., 2016); this calcitisation may have been associated with degradation of the sponge connective tissue (Neuweiler et al., 2007). In some cases of problematic early lineages, this has led to uncertainty over the original composition of the spicules (Hoare and Sturgeon, 1968), although some indication of recrystallisation can normally be recognised in thin sections (e.g., in the unrecognisable genus ‘*Calcihexactina*’; Sdzuy, 1969; Fig. 2G). In extreme cases, even a trace of the axial canal can be preserved in such replaced spicules, and the detailed structure of the preserved spicules (together with the taphonomic environment) must be taken into account when assessing the original mineralogy.

In contrast, in areas with a degree of local silica supersaturation, sponges can be encased within siliceous concretions. This is the case for the abundant sponges of the Cretaceous chalk flint nodules (Marmaduke Langdale, 1888; Reid, 1958; Świerczewska-Gładysz and Olszewska-Nejbert, 2013), and other examples such as Silurian offshore mud mounds (Rhebergen and Botting, 2014; Fig. 2F). Three-dimensional preservation as impressions in pyritic concretions is also known (Pickett and Plusquellec, 1998), as is preservation by concretionary growths of coralline algae (Baldaconi and Corriero, 2009), by phosphatisation (Olszewska-Nejbert and Świerczewska-Gładysz, 2009) and in calcitic concretions in a volcanic ash bed (Briggs et al., 1996). Early-stage concretionary growths often produce exceptionally well-preserved fossils as a result of early mineralisation, sealing from bacterial decay, and resistance to compaction (McCoy et al., 2015). In volcanic settings, it is possible for even unfused skeletons to be preserved in shallow water by volcanism-induced silicification (Botting, 2005; Fig. 2C, E). In less extreme shallow-water situations, impressions of sponges can be preserved when buried in rapidly-cemented sand, even if the spicules have been dissolved (Hall and Clarke, 1899).

Prior to the Ordovician origin of stromatoporoids and rise of lithistids, most sponges possessed loose spicules in a thin body wall, and are most frequently preserved in offshore, muddy or silty environments. Silica under these conditions is usually preserved as quartz only in the largest spicules (e.g., Botting and Muir, 2012); smaller spicules are frequently replaced by pyrite, or dissolved by pore waters after lithification of the mudstone. This pyritisation process is complex and not yet fully understood for replacement of mineral tissues, despite recent progress (Brand and Morrison, 2011), but seems to have been particularly efficient in replacing silica (e.g., Botting, 2004; Xiao et al., 2005; Pisera, 2006; Botting and Muir, 2013; Mouro et al., 2014; Reolid, 2014). The process is very varied, ranging from dissolution and void infill (Reolid, 2014) to coarse replacement by cubic crystals (Xiao et al., 2005) that destroys all internal structure, to near-perfect replication of the axial canal and outer laminae by nanoscale pyrite (Botting and Muir, 2013). There are suggestions that the propensity of sponges to become pyritised is due in part

to the presence of symbiotic sulphate-reducing bacteria within their tissues (Reitner and Schumann-Kindel, 1997), although since the bacteria still require burial under anoxic conditions in order to be implicated in the preservation, this probably encourages the process rather than initiating it. The pyrite is usually oxidised to a range of iron oxides once exposed to weathering, resulting in further taphonomic loss of ultrastructural information.

In most cases, the skeletons of early sponges are not preserved perfectly intact. Disarticulation began rapidly after death if exposed on the sea floor, and any disturbance by burrowers resulted in loss of detail in the skeletal architecture. These processes sometimes produced partially articulated remains where the sponges were exposed for some time on the sea floor (e.g., Botting and Muir, 2011), but more frequently resulted in disarticulation and winnowing, creating spiculite layers that are of little taxonomic use but can provide insights into palaeoecology, environmental interpretation, or palaeogeography (e.g., Cavaroc and Ferm, 1968; Murchey, 2004). Isolated spicules from Cambrian and Ordovician sequences that can be extracted from limestones, however, often show unusual morphologies with no modern counterparts (e.g., Zhang and Pratt, 1994; Zhao and Li, 2006; Carrera and Maletz, 2014). Although disarticulated remains dominate the skeletal record, abrupt burial is surprisingly common in offshore settings, and apparently perfect spicular skeletons with clear outlines (but without preserved soft tissues) are known from many areas (e.g., Rigby et al., 1991; Rigby and Mehl, 1994; Mouro et al., 2014). Torn sponges with partial but fully articulated wall fragments can be almost as informative as entire specimens, so violent transport prior to burial is not necessarily problematic.

Even in the best-preserved articulated skeletons, however, some information is generally lost. Microscleres are almost never found in situ, although they can be isolated by dissolution of some limestones (Mostler, 1986, 1996a; Kozur et al., 1996; Carrera and Maletz, 2014). One exception is the Carboniferous dictyosponge fauna described by Kling and Reif (1969), which contains hexactinellid-type microscleres, and the related sponge described by Mouro et al. (2014), in which the microscleres were unusually large. In certain other cases of sponge fossils that lack microscleres (e.g., Botting and Muir, 2013), skeletal preservation is sufficiently fine that microscleres can be reliably assumed to have been originally absent. The skeletons of these early sponges collapsed once the soft tissues decayed, or were at least compressed, resulting in superposition of the skeletal layers onto each other. If the layers were structurally distinct the structure could remain obvious (Rigby and Gutschick, 1976), but in more complex sponges, distinguishing dermal from gastral architecture is difficult (e.g., see *Dilatisspongia tumida* Botting, 2004). More generally, even the broad three-dimensional structure in the body wall of loose spicular skeletons is often lost, but can be at least partly reconstructed from multiple specimens in different orientations, or by examining the margins of a complete flattened sponge, in which dermal and projecting spicules become obvious when separated in profile (e.g., Brückner and Janussen, 2005).

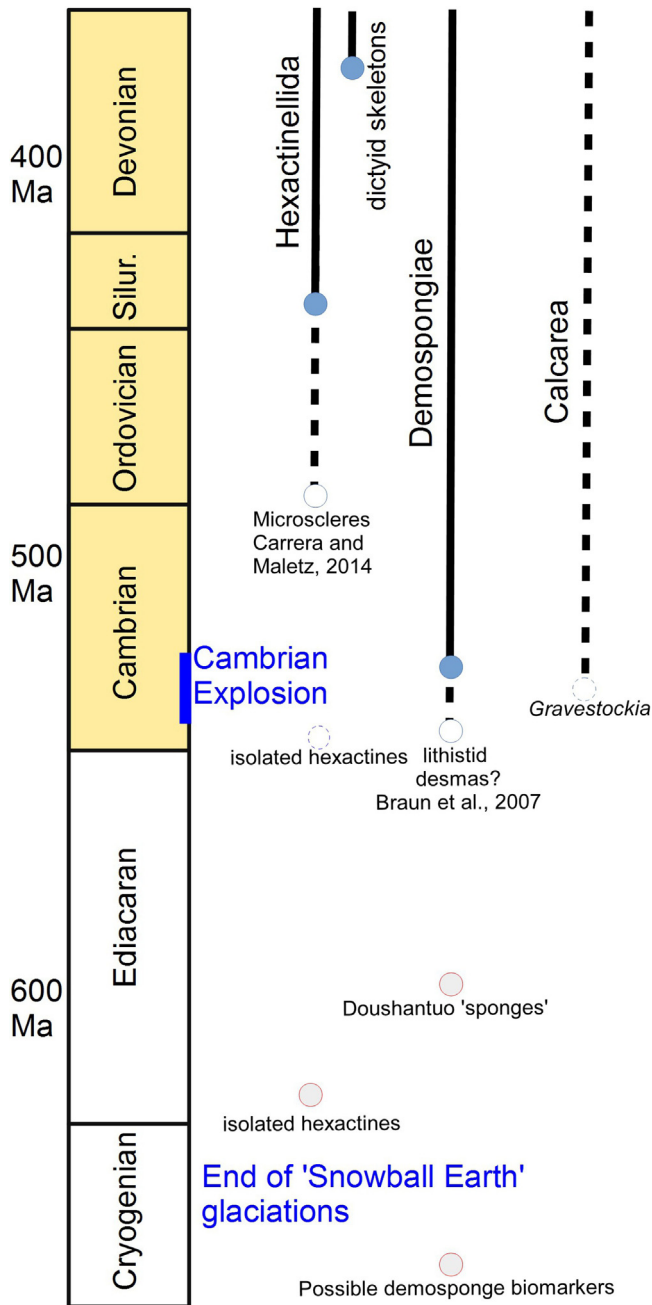


Fig. 3. Timeline with earliest records of crown-groups for extant classes, including high-confidence records of crown groups (filled circles), probable crown groups (open circles) and possible but unlikely crown-group records (dashed circles). Selected discredited and unconfirmable earlier records are also shown (red open circles); see Section 5 for discussion of the Precambrian record.

Overall, interpreting sponge preservation is often challenging, but is not insurmountable. Recognition even of complex original mineralogy can be achieved by comparison of multiple specimens (Botting et al., 2012), and with other fossils for which the composition is known. Interpretation of skeletal structure is more difficult than with living taxa, but can also be achieved with well-preserved material. Some details, such as fine soft-tissue anatomy and microscleres (if present), are usually lost, however, and this presents some challenges when comparing with living groups.

3. Early sponge fossil record

The extant sponge classes are morphologically very distinct, except for the Homoscleromorpha (Gazave et al., 2012), which were until recently included among demosponges. The homoscleromorphs are now generally found to be a sister group to Calcarea (e.g., Gazave et al., 2012; Simion et al., 2017), probably with an early separation between the classes. Differences in the structure, form and secretion mechanisms of the spicules of the different groups have traditionally been regarded as indicators that biomineralisation probably evolved independently within each class, or at least independently between siliceous and calcareous groups (Bergquist, 1978; Uriz et al., 2003; Uriz, 2006; Sethmann and Wörheide, 2008). This hypothesis has the implication that fossil sponges had already separated into these distinctive lineages by the time they appear in the geological record, as non-biomineralised sponges would not be identifiable or interpretable. Biologists might therefore be forgiven for assuming that placement of fossils into extant classes, or at least their stem groups, is a trivial process. However, this is not the case: many early sponge fossils are extremely distinct from living forms in morphology, skeletal architecture and detailed construction. Spicule morphology, which is reliable amongst living sponges, is ambiguous in ancient taxa (Botting and Butterfield, 2005; Botting and Zhang, 2013), with many problematic spicule forms also described (e.g., Zhang and Pratt, 1994; Zhao and Li, 2006; Castellani et al., 2012). The recognition of the clade Silicea (Erpenbeck and Wörheide, 2007; Philippe et al., 2009) has also led to some acceptance of the homology of siliceous spicules in demosponges and hexactinellids (Sperling et al., 2010), although this has been questioned by others based on differences in the enzymatic secretion process (Wörheide et al., 2012).

Continuity of spicules among stem-group siliceans has been viewed more favourably by palaeontologists (e.g., Mehl-Januszen, 1999; Botting, 2003a; Botting and Butterfield, 2005; Harvey, 2010). This is because such continuity can be demonstrated from the fossil record, even though the details of the silicification process have clearly evolved over time. Even the present-day clear distinction between siliceous and calcareous spicules is broken in several fossil taxa (Botting et al., 2012). Among modern taxa, some hexactinellids also break the traditional rules, with siliceous acanthohexactines containing calcite in the cores of their spines (Ehrlich et al., 2011). These aspects are discussed further in the sections on stem groups below, but recognition and definition of even crown-group classes in the fossil record presents some difficulties. Table 1 summarises some of the critical characteristics of the extant classes, where they are actually or potentially visible in the fossil record, emphasising the distinctiveness of the living clades.

3.1. Recognition of the crown groups

Definition of the extant sponge classes is straightforward, due to the major differences that have evolved in the different lineages. However, the common ancestors of the classes were already sponges, and those differences had not developed by the

Table 1

Modern sponge classification: crown-group distribution of major characters. X marks presence for presence/absence characters.

Crown-group characters	Hexactinellida	Demospongiae	Calcarea	Homoscleromorpha
Hexactines	X			
Triactines/tetractines		X		X
Monaxons	X	X	X	X
Spicule composition	Silica (some calcite)	Silica	Mg-calcite	silica
Microscleres	X	X		
Spongin skeleton		X		
Axial canal	X (square)	X (hexagonal/triangular)		
External spicule sheath	(X)		X	
Aquiferous system	Sycon/leucon	Leucon	Ascon/sycon/leucon	Leucon

point at which the lineages separated; all the distinctive features of each class are therefore derived features that appeared in the stem group of that class. These features may have arisen around the base of the crown group, or just after the last common ancestor with its sister group, and thus cannot be used to recognise stem groups versus crown groups. Identification of the base of crown groups is reliant on identification of characters that are shared by a subset within the crown group, but not by the stem lineage; this is often extremely difficult when close to the crown base. Nonetheless, being able to identify these classes is critical to interpretation of evolutionary histories and calibration of molecular clocks. The oldest clear records of the major groups are summarised in Fig. 3, together with more circumstantial evidence that is discussed in Section 5. The extant classes are discussed individually below.

3.1.1. Hexactinellids

Modern hexactinellids are immediately recognisable by their hexactine spicules; however, this characteristic cannot be applied uncritically to fossil taxa, because hexactines occur in many disparate groups of early sponges (Botting and Butterfield, 2005; Harvey, 2010; Botting and Muir, 2013; Botting and Zhang, 2013; Botting et al., 2013; see Section 3.2.1 for details). Other major synapomorphies are also unsatisfactory for fossils: neither syncytial nor cellular soft tissues can be recognised in any sponge fossil thus far described, and microscleres are very rarely encountered, especially in situ.

Within the extant Hexactinellida, there are numerous lineages with very distinctive skeletal architectures, but these may all be morphologically derived: many of the earliest-branching clades include fused spicules, despite an unfused (lyssacine) condition being primitive (Dohrmann et al., 2013). Furthermore, a molecular long branch leading to crown-group Hexactinellida (Dohrmann et al., 2008) suggests substantial evolution and perhaps diversification within the stem group. All extant lyssacine hexactinellids share a relatively complex wall (in contrast to single-walled fossils such as *Protospongia* Salter, 1864; e.g., Mehl, 1996a), in which there are morphologically distinct dermal, and often choanosomal and gastral, spicule layers, but it is not currently possible to infer the skeletal architecture of the last common ancestor of extant hexactinellids. At present, recognition of fossil crown-group hexactinellids is dependent on being able to identify specific structural or architectural features of known sub-clades within the class.

The oldest records of hexactinellid-specific microscleres are those described by Carrera and Maletz (2014) from isolated Lower Ordovician material. The oldest definite crown-group hexactinellid known from articulated material is currently the early Silurian *Urphaenomenospongia euplecteloides* Rhebergen and Botting, 2014, which was assigned tentatively to the Lyssacinosa (although similarities to the Euretidae were also noted). Hexactinosan sponges with fused skeletons are known from the Devonian (Rigby et al., 1981a, 2001; Pisera and Bodzioch, 1991); many of the earlier records assigned to specific groups are probably unreliable (Pisera and Bodzioch, 1991). The dominant modern hexactinellid groups, including the Lychniscosida, appear in the fossil record only in the Mesozoic (Mehl and Mostler, 1993).

Many Palaeozoic sponges have been assigned to the Hexactinellida in the past, but there is usually no persuasive indication of crown-group affinities. The ‘Reticulosa’ were erected as an order by Reid (1958) to accommodate an extinct group of hexactinellids with thin, reticulate skeletal walls; however, this grouping is paraphyletic and almost certainly includes most of the stem group of both Silicea and Hexactinellida (Botting and Muir, 2013; see Section 3.2.1). Some reticulosan taxa, especially the more complex ones, may indeed fall near or within the hexactinellid crown group, but this cannot be determined with any certainty. For example, Botting (2004) discussed several features of the skeletal architecture of some Ordovician hexactinellid-like sponges that may indicate crown-group Hexactinellida, such as the development of basal anchoring structures. On this basis, *Cyathophycus* Walcott, 1879 was suggested to be an early amphidiscophoran, but more recent work (Botting and Muir, 2013) has supported a much deeper origin of that taxon within Silicea, related to the basal stem lineage of demosponges. Assignment of some species by Botting (2004) to the stem group of the Rossellidae has since been criticised on the basis of discordance with later origin estimates based on molecular clock dates (Dohrmann et al., 2013).

Isolated spicules assigned to Hexactinellida from the lower Palaeozoic are usually ambiguous with regard to whether they fall into the stem or crown group. One convincing exception, however, is the range of Early Ordovician, hexactinellid-specific microscleres described by Carrera and Maletz (2014), which confirms and enhances the observations of Mostler (1986). They also provided a comprehensive review of potentially similar (but less convincing) examples that had previously been published.

The importance of this assemblage lies in the range of spicule types that are currently diagnostic of single lineages within the crown group, such as the Sceptulophora. While it remains possible that these spicules were evolved within the stem group, a more likely explanation is that crown-group hexactinellids were indeed present in the Early Ordovician.

All prior assignments of Cambrian and Ordovician sponges to the Hexactinellida should be treated with caution, and considered critically, since we now recognise alternative interpretations for hexactine-bearing sponges. In general, putative early hexactinellids should be regarded as probable stem groups, mostly of Hexactinellida or Silicea, unless there is evidence to the contrary. However, the newly-discovered Late Ordovician Anji Biota of Zhejiang, China (Botting et al., 2017a, fig. 2F, H, I) has yielded a diverse assemblage of reticulosans that includes a range of taxa with at least some characteristics reminiscent of specific crown-group hexactinellids. These include taxa with projecting hypodermal pentactines, primarily as marginalia but also including lateral prosthelia, a feature that is typical for extant Rossellidae (Tabachnick, 2002). The spiculation and architecture of the dermal skeleton of these particular sponges differs in several ways from all extant rossellids, suggesting at most a stem-group relationship to the family, but more advanced-looking species are also currently under study by the authors.

Irrespective of their precise relationship to specific crown-group lineages, the Anji Biota hexactinellids are much more complex than other early Palaeozoic taxa, and morphologically closer to extant families, leading to a remarkably long gap in the fossil record before the next (Mesozoic) occurrence of rossellids (Brückner, 2006). The environmental context for the Anji assemblage may be significant, in that it represents an offshore, post-extinction fauna from which deep-shelf benthos had been largely eradicated. Li et al. (2015) described a coeval assemblage from Beigong, Anhui Province, China, and suggested that normally deeper-water taxa had been forced onshore by anoxia in the deep oceans. Such a scenario, combined with utilisation of empty ecospace on the deep shelf, could indicate that substantial evolution of crown-group Hexactinellida occurred on the continental slope or abyssal plain, environments that are not normally preserved in the geological record. Diversification in an effectively ‘invisible’ environment would explain why the origin of crown-group Hexactinellida has remained elusive, especially as the more easily preserved fused skeletons are likely to be an environmental response to colonisation of turbulent, shallow-water environments; fused skeletons apparently did not occur until the Devonian.

3.1.2. Demosponges

In direct contrast to the hexactinellids, the origin of crown-group demosponges appears to be very clearly preserved in the fossil record (Botting et al., 2013), even though demosponge-specific molecular clock studies predict a much deeper origin (Ma and Yang, 2016). Molecular work (Borchiellini et al., 2004; Erpenbeck and Wörheide, 2007) has consistently obtained a fundamental division between the spiculate Heteroscleromorpha (Morrow and Cárdenas, 2015) and the aspiculate Keratosa and Verongimorpha (Erpenbeck et al., 2012). The presence or

absence of spicules in the last common ancestor of demosponges could not be resolved by molecular phylogenetics (Borchiellini et al., 2004), but their presence has been demonstrated in the fossil record, in the *Vauxia*–*Hazelia* complex (Botting et al., 2013; Yang et al., 2017).

The Hazeliidae are a Cambrian group of generally thin-walled sponges with semi-reticulate, tufted skeletons of minute monaxons, and are known primarily from the middle Cambrian Burgess Shale (Walcott, 1920; Rigby, 1986; Rigby and Collins, 2004). *Vauxia* Walcott, 1920 is a very closely related genus with a reticulate organic skeleton, from the same fauna, which was assigned by Rigby (1986) to the Verongida. Although it is not possible to relate this genus so precisely to a living group, its demosponge affinity remains undisputed, especially since the recognition of chitin within fossil *Vauxia* (Ehrlich et al., 2013), following prior recognition of chitin within the fibres of extant Verongida (Ehrlich et al., 2010). Similar but more advanced keratosan demosponges have also been described from later in the Palaeozoic (Luo and Reitner, 2014), with the possibility that they are more common in carbonates (especially microbialites) than has previously been recognised (Luo, 2015).

The Burgess Shale has yielded numerous species of *Hazelia* Walcott, 1920 and *Vauxia* with exquisite preservation, with a clear continuum between the two genera. In particular, the reticulate fibre skeleton can be observed in *Vauxia bellula* Walcott, 1920 to be cored by monaxon spicules (Botting et al., 2013), which have since been confirmed to have been originally siliceous in an undescribed vauxiid from the Cambrian of China (Yang et al., 2017). The dichotomy between spiculate and aspiculate demosponges is therefore visible in the fossil record, and their last common ancestor can be confidently placed within the genus *Hazelia*.

Microscleres have not been found in Burgess Shale sponges, but are present in an early Cambrian sponge from the Sirius Passet Biota of Greenland (Botting et al., 2015b). Microscleres were detected in a disarticulated specimen of a species that appears to have lived on a shallower-water carbonate platform above the depositional site. The most striking aspect is that the microscleres include typical forms (sigmas, toxas and forceps) but are of roughly the same size as the megascleres. This finding suggests that microscleres began as modified megascleres that were secondarily reduced, implying that all living heteroscleromorphs are derived relative to the origin of microscleres.

More derived non-lithistid demosponges have only rarely been recognised in the Palaeozoic fossil record. The best-known is *Saccospongia laxata* Bassler, 1932 (Finks, 1967), which shows a complex structure reminiscent of the modern Desmacididae (Desmacidontidae in Finks, 1967), and plausibly represents a crown-group poecilosclerid. However, despite exquisite preservation of the material, no microscleres have been identified.

Isolated spicules that appear to be assignable to relatively derived demosponges such as tetractinellids have been widely described from Cambrian acid digestion residues (e.g., van Kempen, 1985); these suggest a substantially earlier appearance of the crown group than is currently known with certainty (Botting et al., 2015b). Braun et al. (2007) mentioned abundant

Table 2

The same crown-group characters as in Table 1, applied to the stem-groups of the living classes, subphyla and phylum, as implied by the fossil record. X marks presence for presence/absence characters.

Stem-group characters	Stem-Hexactinellida	Stem-Demospongiae	Stem-Silicea	Stem-Calcareae (? + Homoscleromorpha)	Stem-Porifera
Hexactines	X	X	X	X	X
Triactines/tetractines				X?	
Monaxons	X	X	X	X	X
Spicule composition	Silica	Silica	Silica (+Mg ²⁺ -calcite)	Mg ²⁺ -calcite (+silica)	Mg ²⁺ -calcite + silica
Microscleres	X?				
Spongin skeleton					
Axial canal	X (square)	X (square, hexagonal/triangular)	X (square, amorphous?)	? (amorphous)	?
External spicule sheath			X (basally)	X	X
Aquiferous system	Sycon	Sycon	Ascon [?] /sycon	Ascon?	Ascon?

lithistid spicules from earliest Cambrian acid digestion samples, but these have not yet been illustrated; if genuine, it is likely that they represent anthaspidellids, a group derived immediately from the hazeliid–vauxiid complex (Botting et al., 2013). Other early Cambrian demosponge reports are more ambiguous. Isolated tetractines (Bengtson et al., 1990; Reitner and Mehl, 1995) may be from heteroscleromorphs, but could have a different origin. Caution is needed, because similar spicules with asymmetric, tetractine-like rays are present in other hexactine-bearing taxa such as *Asthenospongia* Rigby et al., 1981b. However, an articulated tetractine-bearing sponge (*Ivantsovia* Zhuravlev in Ivantsov et al., 2005a) from the Sinsk Biota appears to be a genuine tetractinellid demosponge, although the axial canal symmetry has not yet been confirmed. Putative early Cambrian sterrasters (diagnostic of the Geodiidae) described by Reitner and Mehl (1995) are as yet unconvincing, and could be mineral aggregates or recrystallised grains. Possible boring sponges, which are likely to have been demosponges, were recorded by Zhuravlev and Wood (1995) from early Cambrian reefs.

Some comment is needed here on Archaeocyatha: this is an ambiguous group of early to middle Cambrian reef-building organisms with massive, generally double-walled calcareous skeletons. After some debate as to their affinities (e.g., Zhuravleva, 1970), these organisms are now generally accepted to be sponges (Rowland, 2001), following work on their functional morphology (Zhuravlev, 1993), and although sometimes listed as a distinct class (Debrenne et al., 2002), are thought to be specifically related to demosponges based on their immunology, growth and reproductive patterns (Debrenne and Zhuravlev, 1994). Some of the earliest anthaspidellid demosponges were also originally mistakenly assigned to Archaeocyatha before being reinterpreted (Kruse, 1981), illustrating the close morphological resemblance of some of the early examples of each group. However, no spicules have been identified within the Archaeocyatha, except for isolated examples that are presumed to have been incorporated into the skeleton (Reitner and Wörheide, 2002), and there are no obvious structural links to any confirmed demosponge group that could reveal their precise phylogenetic position. Although crown-group demosponges were present at this time, the only lineages yet confirmed are the

vauxiid–hazeliid basal complex, anthaspidellid lithistids and basal heteroscleromorphs, and a single convincing tetractinomorpha, as discussed above. None of these groups provide obvious ancestral conditions for the archaeocyath skeletal construction, and neither do any of the other known sponge taxa from this interval; archaeocyathan origins remain entirely obscure. It is possible that a demosponge interpretation is correct, but the evidence remains circumstantial. It is also possible that they are not sponges at all, but rather a cnidarian-grade organism; although their skeletons could have functioned as sponges if the pores were not obscured by soft tissues, no information on the soft-tissue organisation in these organisms is available, and the interpretation remains speculative. Archaeocyathans must therefore remain of uncertain origin at present, even though a sponge (and possibly demosponge) affinity seems most plausible.

In contrast to the likely deep-water origin of the hexactinellid crown group, demosponges appear to have diversified in shallow water (Botting and Peel, 2016), associated particularly with carbonate platforms. These environments are aerobic and turbulent, factors which probably drove the evolution of the group, but also limited the preservation of articulated material; in both the Burgess Shale and Sirius Passet biotas, the sponges are preserved at the base of an escarpment (Fletcher and Collins, 1998; Ineson and Peel, 2011), whereas the Sinsk Biota tetractinellid *Ivantsovia* was preserved in a shallow-water, platform facies (Ivantsov et al., 2005b).

3.1.3. Calcareae

The fossil record of demonstrable calcareans is very intermittent. There are several hypercalcified groups (reviewed by Pisera, 2006), some of which lack siliceous spicules (e.g., inozoans, from the upper Palaeozoic and Mesozoic); their relationships to crown-group Calcareae remain unclear, but they appear to be derived, for several reasons. Molecular phylogenies of the Calcareae imply that the primitive state of the crown group was asconid, without a cortex (Manuel, 2006; Voigt et al., 2012), and with unfused, triactine or tetractine spicules. Secondary calcification and increasingly complex internal structure would have evolved several times independently. The simple soft-tissue and skeletal architecture of the basal groups agrees

with the traditional view of increasing complexity through time, and implies that the last common ancestor of Calcarea was a thin-walled, tubular to vasiform sponge with triradiate (triacine) or tetrahedral (tetractine) Mg-calcite spicules. Such sponges would have a low preservation potential in turbulent, shallow-water environments, but also in deep-water environments, where the spicules are less chemically stable. Nonetheless, molecular phylogenies and clocks (e.g., [Sperling et al., 2010](#)) suggest that the crown group should have been present by the Cambrian, although there are no convincing Precambrian records of any sponges (as discussed in Section 5).

Articulated material of only one putative Palaeozoic crown-group calcarean has been reported, the pharetronid-like *Gravestockia* [Reitner, 1992](#). This is remarkable given that pharetronids are characterised by secondary calcitization that produces a robust skeleton with high preservation potential. There are differences between *Gravestockia* and living calcareans in skeletal construction ([Pickett, 2002](#)), and it cannot be assigned to the crown group of Calcarea with any real confidence. However, [Reitner and Mehl \(1995\)](#) did describe a range of apparent calcarean spicules, resembling those of modern taxa, incorporated into and preserved within the skeletons of early Cambrian archaeocyaths. These include triactine or tetractine spicules with bifurcating rays, which may be derived from calcaronean and calcinean lineages, but in the absence of any detailed knowledge of the calcarean stem group or basal crown group, could instead fall into the stem groups. The same is true of rare, superficially modern-looking simple triactines ([Mehl and Lehnert, 1997](#)). Even Mesozoic and later non-hypercalcified calcareans are extremely rare as fossils ([Hinde, 1889, 1900](#)), and the origins of the crown group remain unclear.

3.1.4. *Homoscleromorpha*

This group is extremely poorly known as fossils. Their small size, minute siliceous spicules and usually shallow-water, encrusting habits mitigate against preservation, and the spicules are not particularly distinctive. The earliest examples assigned to the group are Plakinidae from the upper part of the Mesozoic, together with isolated Carboniferous spicules that are probably assignable to the class ([Reid, 2004](#)). Recognition of fossil homoscleromorphs depends entirely on distinctive spicules, such as minute tetraxons with bifurcating rays. At present the group is too poorly understood to interpret the likely characteristics of the last common ancestor of *Homoscleromorpha*, and even whether they were spiculate (but see also Sections 3.2.1 and 4).

Some homoscleromorph spicules show a distinctive structure of concentric laminations of silica interspersed with organic matter ([Maldonado and Riesgo, 2007](#)). A similar structure was described in pyritised spicules of the Ordovician reticulosan *Cyathophycus loydelli* [Botting, 2004](#) by [Botting and Muir \(2013\)](#), and was illustrated in hexactine spicules from the lower Cambrian of China by [Hu et al. \(2002\)](#), and may therefore be a primitive feature rather than an autapomorphy of *Homoscleromorpha*.

3.2. Stem-group lineages

Most of the Cambrian and Ordovician sponge record consists of taxa that cannot be confidently assigned to any class-level crown group, or which can confidently be excluded from all of them ([Fig. 4](#)). Understanding of these groups is evolving rapidly based on new information and more detailed studies of spicule structure, morphology and skeletal architecture, but there remain many wide morphological gaps in the known record. This is unsurprising given that most early taxa are delicate, thin-walled sponges with unfused spicule skeletons that require exceptional conditions to be preserved at all, and even more exceptional conditions to preserve the fine details and unaltered mineralogy that are becoming necessary to interpret them fully. Several major lineages of sponges can be recognised, and at least tentatively assigned to the stem groups of particular clades, as discussed below. The distribution of key taxonomic characters within these groups is listed in [Table 2](#).

Discussions of the nature and relationships of each of the groups in the following subsections are combined into the phylogenetic framework described in Section 4.

3.2.1. *Reticulosans* ([Fig. 4C](#))

The dominant group of early Palaeozoic sponges were thin-walled, hexactine-bearing sponges, usually with a semi-regular reticulate skeleton. These were defined by [Reid \(1958\)](#) as a distinct, extinct order of hexactinellids, but this understanding is no longer accepted. The term ‘reticulosan’ remains in common usage, however, and refers to a wide range of thin-walled sponges that cannot be assigned to other groups. The archetypal reticulosan is *Protospongia* [Salter, 1864](#), which possessed an extremely regular skeletal grid that grew by inflation and insertion of spicules ([Botting, 2003b](#)), but many other taxa also fall into this loose assemblage. The genus *Protospongia* is itself used very widely (even very recently) for taxa that have similar spicules and/or a regular grid (e.g., [Henderson and Dann, 2010](#); [Liu et al., 2012](#)), but many of these fossils will eventually need to be reclassified based on details of spicule arrangement and morphology. It is also very unclear whether the strict application of the genus *Protospongia* is recognisable, as it remains unknown as complete specimens, and may therefore be indistinguishable from *Diagoniella* [Rauff, 1894](#) (personal observation). Taxonomy within the reticulosans (summarised by [Finks and Rigby, 2004a](#)) is currently uncertain and inconsistent, with high generic diversity and few obvious evolutionary continua. Distinctive architectures are generally recognised at family level, but many ‘dustbin taxa’ remain to be resolved into a consistent taxonomic system.

Interpretation of reticulosans has been based on a presumed affiliation to hexactinellids. [Mehl \(1996a\)](#) discussed *Protospongia* as a possible stem-group hexactinellid, and concluded that it was primitive but somewhat derived from the ancestral state. Explicit assertion of the stem-group status of these sponges is rare in the literature, perhaps due in part to the difficulties in recognising the base of the crown group. Assignment of reticulosans (or isolated hexactine spicules) to hexactinellids has been based exclusively on the presence of hexactines, and this

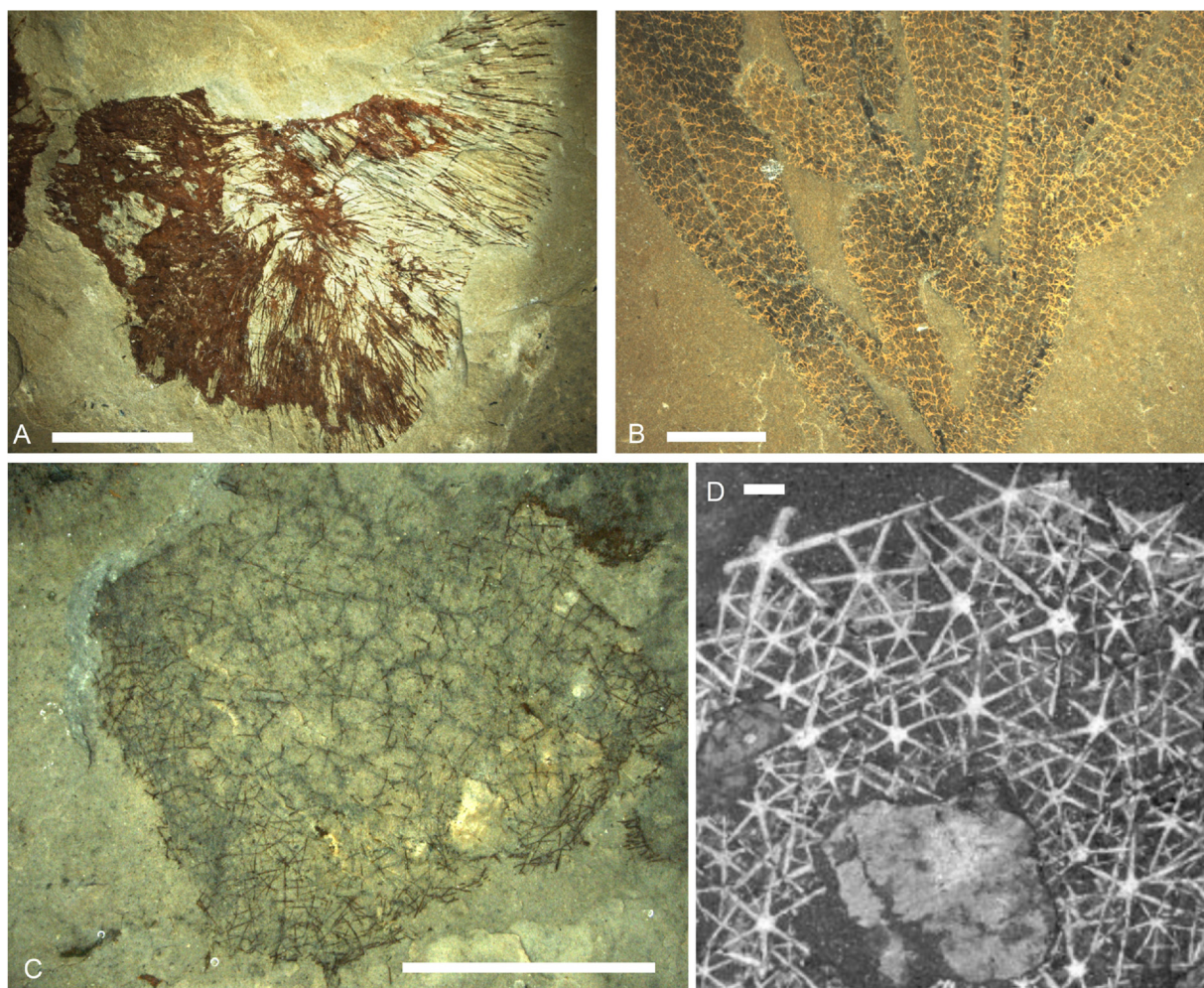


Fig. 4. Examples of sponge stem groups and problematic lineages (see also Figs. 5 and 8). (A) ROM 61914, *Hamptonia* sp. from the middle Cambrian of Monarch Cirque, Canada. (B) ROM 53564, *Vauxia bellula* Walcott, 1920, a vauxiid demosponge from the middle Cambrian Burgess Shale, Canada. (C) Reticulosan described by Rigby and Collins (2004) as *Hintzespongia bilamina* Rigby and Gutschick, 1976, but distinct in skeletal architecture. (D) ROM 57023, the middle Cambrian heteractinid *Eiffelia globosa* Walcott, 1920 (modified after Botting and Butterfield, 2005), showing typical hexaradiate spicules but with additional hexactines. Scale bar: 10 mm for (A–C); 1 mm for (D).

erroneous practice still continues widely (e.g., Beresi, 2013; Antcliffe et al., 2014; Wu et al., 2014; Chen et al., 2015; Chang et al., 2017).

There are several problems with assignment of reticulosans to crown-group (or total-group) hexactinellids. The most important of these is that hexactines are widely distributed amongst early sponges, including in heteractinids (*Eiffelia globosa* Walcott, 1920; Botting and Butterfield, 2005), an extinct group assigned to the stem group of Calcarea (see Section 3.2.3). They are also known from protomonaxonids (see Section 3.2.2), an early-branching monaxon-bearing group (Botting et al., 2012, 2013), which have an entirely distinct architecture from hexactinellids. Furthermore, recent work on exquisitely preserved specimens of the relatively advanced reticulosan *C. loydelli* (Botting and Muir, 2013) has shown a strongly laminated spicule construction seen otherwise only in the Homoscleromorpha (Maldonado and Riesgo, 2007), with hexagonal axial canals that are diagnostic for demosponges among extant taxa (hexactinellid canals being square in cross-section; Reiswig, 1971), and appear to

be a derived feature related to the evolutionary innovation of silicateins within the demosponge lineage (Kozhemyako et al., 2010; Otzen, 2012). *Cyathophycus* also possessed a bilaminar skeletal wall, with an inner layer of fine monaxon spicules that shows a striking resemblance to the morphology and skeletal architecture of the basal hazeliid demosponges (Botting, 2003a). This similarity has been confirmed by the discovery of a hazeliid-like stem demosponge containing hexactines (Botting et al., 2017b). Overall, the very hexactinellid-like reticulosan *Cyathophycus* is best interpreted as being within the demosponge stem lineage.

Even more problematic is the suggestion that the spicules of *Protospongia* itself were in fact calcitic rather than siliceous (Page et al., 2009). Preservation of the spicules as calcite is relatively common, but this has normally been assumed to be a replacement of the original silica (e.g., Church et al., 1999). In some examples, however, there is clear evidence for preservation of axial structures within the spicules (Church et al., 1999, fig. 5.1; Krautter, 2002, fig. 1), and the spicules are preserved

as calcite despite deposition in siliciclastic settings rather than carbonates. The axial structures may indicate a siliceous core to the spicules, but the taphonomic detail has not yet been studied; at present it is clear only that *Protospongia* possessed at least a component of calcite in its spicules, and is therefore not a crown-group silicean. The position of *Protospongia/Diagoniella* is discussed further in Section 4, in relation to similarities to problematic, possible stem-group poriferans.

If the relatively complex architecture of the bilaminar, strongly reticulate *Cyathophycus* approximates to the base of the crown group of Silicea, but the simpler, thin-walled construction of the distantly related *Eiffelia* also includes hexactines in the same quadruded arrangement (Botting and Butterfield, 2005), then many examples of simple, quadruded, single-walled reticulans such as *Heminectere* Botting, 2004 probably fall into the silicean stem group. Reticulosa therefore must be assumed to be paraphyletic with respect to Hexactinellida, Demospongiae, and probably also Calcarea and Homoscleromorpha, and even Porifera as a whole.

3.2.2. *Protomonaxonids* (Fig. 4A)

A major group of sponges during the Cambrian, which appear to have subsequently declined but with some representatives surviving until at least the Jurassic (Keupp and Schweigert, 2012). The protomonaxonids were considered to be demosponges by Walcott (1920), and defined as an order of demosponges by Finks and Rigby (2004b) purely on the basis of possessing only monaxons. This unsatisfactory definition led to the inclusion of a wide range of very different morphologies, including the Hazeliidae, which were considered to be basal crown-group demosponges by Botting et al. (2013). That revision separated the Hazeliidae from large-spiculed ‘protomonaxonids’, which appear to form one or two groups of very different sponges. These form a broadly continuous lineage of species with a fundamentally longitudinal array of long (often several centimetres) monaxons, either parallel to the body wall or projecting from it; in the Leptomitidae, however, there is a transverse component to the skeleton, and that group may have a different origin. There has long been discussion of the nature of these sponges, with some authors (de Laubenfels, 1958; Reitner and Mehl, 1995; Debrenne and Reitner, 2001) noting a closer similarity of structure to that of certain monaxon-based hexactinellids.

Two major features of the protomonaxonids preclude a close relationship with any modern group. Firstly, several of the earliest examples incorporate small, short-rayed, irregular hexactine-like spicules within the skeleton (Steiner et al., 1993; Botting et al., 2013). These spicules are morphologically very distinct from the hexactine spicules of Cambrian reticulans, and have no regular arrangement; even the growth pattern is unclear, as they remain small and appear to be of broadly consistent size. Secondly, there is direct evidence in the larger spicules of *Lenica Goryanskii*, 1977 (Botting et al., 2012, 2013; Botting and Peel, 2016) for a biminerallitic composition with an inner layer of silica (with axial canal) surrounded by an outer region of a distinct phase that was almost certainly calcite, and an organic envelope surrounding that (Botting et al., 2012). This duplicates the structure seen in some heteractinids (Section 3.2.3).

The more derived parts of this lineage include *Halichondrites* Dawson in Dawson and Hinde, 1889 and *Pirania* Walcott, 1920 (Rigby and Collins, 2004; Botting et al., 2013), in which projecting spicules are highly developed, and show a strongly organic composition of at least the outer layer. Some spicules of *Pirania* are preserved as organic films exhibiting twisting (Botting et al., 2013, fig. 4.5) that is incompatible with a primarily mineral composition. Equally unexpectedly, the derived members of this lineage, which includes *Lenica*, possess spicules that are open at the base (Botting et al., 2012, 2013), seen particularly clearly in *Pirania muricata* Walcott, 1920 (Fig. 5A). The structure of these spicules is remarkable, and appears to have been derived from the biminerallitic structure, with enhancement of the organic outer lamina (Botting et al., 2012), especially in the basal region, to produce effectively a conical sclerite. Silica and carbonate deposition within the basal part of the spicule appears to have been reduced (see *Lenica unica* Goryanskii, 1977 in Botting and Peel, 2016), producing a partly hollow, organic structure.

These derived, sclerite-like spicules of *Pirania* (Fig. 5A) bear a striking resemblance to the sclerites of cancelloriids (Fig. 5B, C), a controversial group of Cambrian organisms that have been described as sponges (Walcott, 1920; de Laubenfels, 1955; Sdzuy, 1969; Butterfield and Nicholas, 1996; Conway Morris and Chapman, 1997; Botting and Butterfield, 2005), ascidians (Mehl, 1996b), cnidarians (Randell et al., 2005), and armoured slug-like organisms (Coeloscleritophora; Bengtson and Missarzhevsky, 1981; Li, 1999; Bengtson and Hou, 2001; Porter, 2008) or regarded as occupying an indeterminate position among the Epitheliozoa (Janussen et al., 2002). Others (Kloss et al., 2009; Vinther, 2009) wisely stated no certain preference, but discussed the range of prior interpretations. The Coeloscleritophora concept has gained significant support, due largely to the differences in sclerite secretion mechanism from that of sponge spicules, despite acceptance of a sponge-like overall morphology with an apparent apical osculum (Bengtson and Collins, 2015). However, the non-actualistic spicule structure observed in *Pirania* and other protomonaxonids implies an identical mode of secretion to that of cancelloriids, derived from the primitive process of biminerallitic spicule construction, which also has no modern counterpart. Furthermore, the epithelium-like surface described by Janussen et al. (2002) is effectively identical to the surface texture of the Burgess Shale sponge *P. muricata* (Walcott, 1920; Rigby, 1986; Botting et al., 2013); the nature of this surface texture remains unclear, but it appears to have been an evolutionary innovation of that group, as it is not seen in more basal protomonaxonids. The multi-pronged sclerites of cancelloriids are also unlike any known sponge spicules, but a recent study (Hou et al., 2014) of a cancelloriid from the Chengjiang Biota describes short, single-pronged sclerites that differ only in proportions from those of *Pirania* and other, unnamed protomonaxonids (Botting et al., 2013, fig. 4.3). Another undescribed example of a cancelloriid with single-rayed sclerites was noted by Hu et al. (2013, p. 60). These findings resolve all the problematic perceived differences between cancelloriids and sponges; thus, cancelloriids can be regarded confidently as a derived lineage of protomonaxonid sponges.

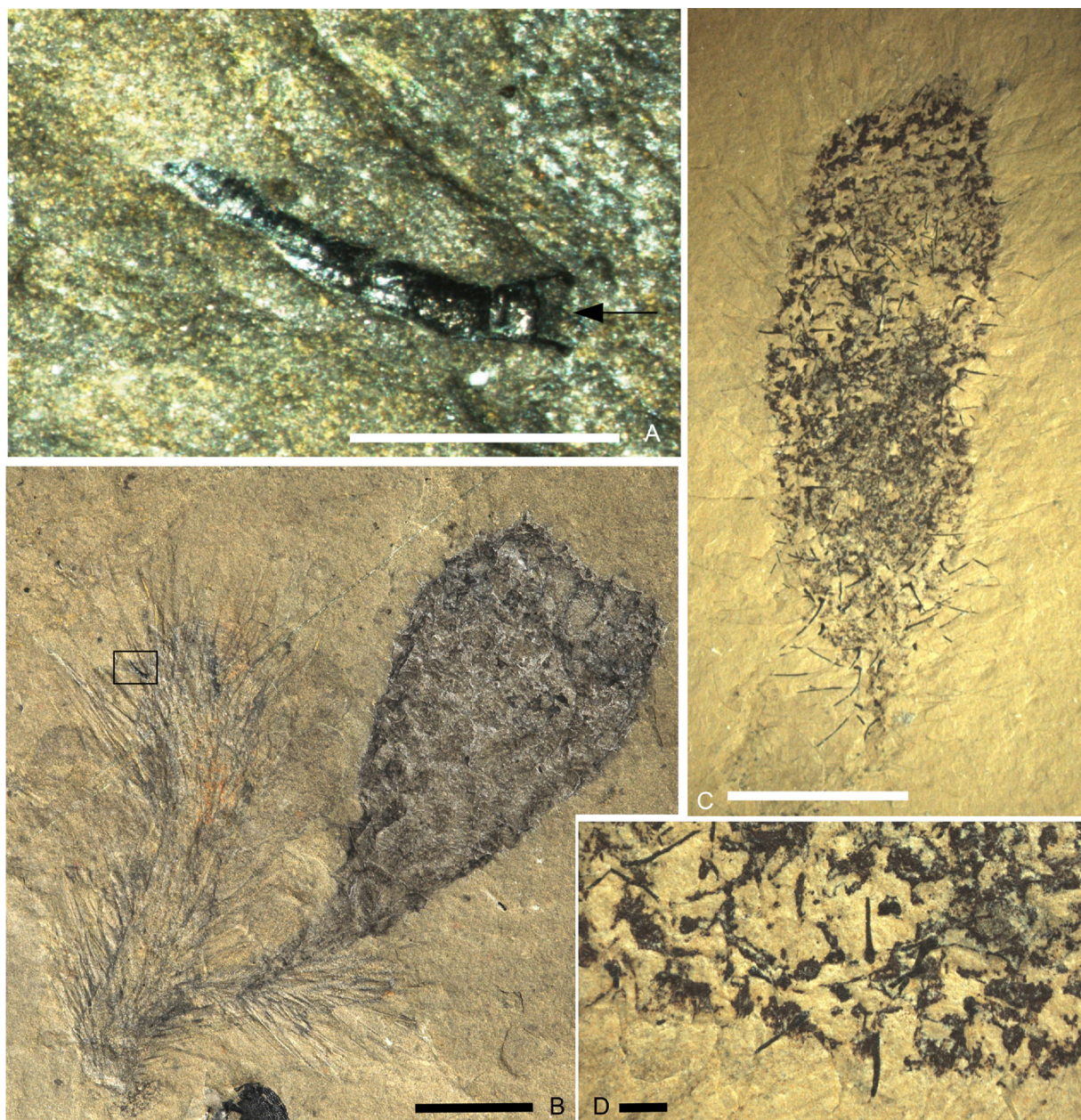


Fig. 5. Piraniids and cancelloriids. (A, B) ROM 56249, *Pirania muricata*, overall view of specimen (B) with attached cancelloriid, and with box showing position of detail (A) with three-dimensional preservation of spicule base, showing open base (arrowed) and sclerite-like morphology. (C, D) ROM 64299, undetermined cancelloriid, showing overall form (C) and details of three-dimensionally pyritised sclerites (D). Scale bar: 1 mm for (A, D); 10 mm for (B, C).

The Leptomitidae, in contrast, show a potentially different origin revealed by the Ordovician *Heteractenigma* Botting and Zhang, 2013 from Zhejiang, China. In this species, which has the fundamental architecture of *Leptomitus* Walcott, 1886, minute pentaradiate, tetra-radiate and triradiate spicules are also present. These spicule morphologies have no counterpart today except in certain calcareans (Rossi et al., 2006), but are also present in the equally enigmatic heteractinid *Petaloptyon danei* Raymond, 1931 (Rigby, 1986; Rigby and Collins, 2004). It is tempting to suggest that leptomitids therefore originated from stem-group calcareans, but the existence of biminerallitic spicules in *Lenica* and *Eiffelia* implies that an origin in the early stem group of

Silicea, or the late stem group of Porifera, is also possible. *Heteractenigma* also contains stauractine (presumed to be modified hexactine) spicules, and is thus another example of a hexactine-bearing sponge that cannot easily be accommodated within the Hexactinellida, because of the presence of spicules only found in other groups at the present day.

3.2.3. Heteractinids (Fig. 4D)

The heteractinids are a group of Palaeozoic sponges with anomalous spicules containing a non-actualistic number of rays (de Laubenfels, 1955; Rigby and Nitecki, 1975; Kozur et al., 2008). In almost all cases, the spicules are based on a hexara-

diate pattern, sometimes with an additional pair of rays in the perpendicular plane (octactines), or additional radial rays (Kozur et al., 2008). Although no such spicules are known in any living calcarean, the symmetry pattern is based on the triradial symmetry of calcite crystals, which appears to influence the growth form (Jones, 1970). Furthermore, some Ordovician and Silurian heteractinids have robust skeletons of coarse spicules that are often well preserved, and demonstrate an unambiguous calcitic composition (Mehl and Reitner, 1996; Rhebergen, 2007). In the absence of Palaeozoic crown-group calcareans, heteractinids have long been presumed to represent the stem group of the class.

The discovery of hexactine spicules within the Burgess Shale heteractinid *E. globosa* (Botting and Butterfield, 2005) opened a new set of possibilities for evolutionary homology of the spicules with those of siliceans. Their suggestion of the spicules of *Eiffelia* being originally bimineralic was confirmed by Bengtson and Vinther (2006) and Bengtson and Collins (2015), who documented *Eiffelia* spicules with a silica core surrounded by a calcite layer. Subsequently, robust organic sheaths around acid-derived Cambrian hexactines were discovered (Harvey, 2010). External sheaths are particularly characteristic of calcarean spicules (Jones, 1967; Ledger and Jones, 1991), again suggesting an extinct character combination linking hexactines with the calcarean lineage. The combination of spicule morphotypes, together with the same bimineralic structure as seen in the protomonaxonid *Lenica*, implies either implausible levels of structural and morphological convergence, or homology of silicean and calcarean spicules (Botting et al., 2012).

The lower Palaeozoic *Calcihexactina* Sdzuy, 1969, which is a spicule of hexactine morphology preserved as calcite, has been widely reported (e.g., Lindström, 1979; Ding and Qian, 1988; Brock and Cooper, 1993; Wrona, 2004). *Calcihexactina* probably represents replacement of original silica; however, it is possible that these spicules were originally calcitic (Sdzuy, 1969). If so, this would mean that some early sponges possessed hexactine spicules composed partly or wholly of calcite.

Post-Cambrian heteractinids appear to have been dominantly or exclusively calcitic (e.g., Mehl and Reitner, 1996), supporting a placement in the stem group of Calcarea, although the preservation of *Microastraeum tenuis* Botting, 2005 in the silicified volcanogenic sandstones of Llandegley Rocks (Botting, 2005) appears incompatible with an originally calcitic composition; this example needs to be re-examined. Another anomalous example is the *Contignatiospongia* sp. spicules described by Carrera and Maletz (2014, fig. 8H–K). These were described as having been originally calcitic, but replaced by silica diagenetically; however, there are clear axial canals present in their fig. 8J, implying that the siliceous composition is original. It is unknown whether a calcitic outer layer was also present, but this represents another spicule with calcarean-diagnostic symmetry but at least partly siliceous composition. The type material of that genus is also preserved as supposed silica replacements of original calcite, and also shows possible axial canals (Kozur et al., 2008, pl. 1, fig. 1). The implication of *Eiffelia* and other anomalous heteractinid sponges is that purely calcitic spicules

are a derived condition in which the siliceous component of the spicules in the ancestral lineage has been secondarily lost.

There have been two other problematic heteractinids described to date: *Heteractenigma* (Botting and Zhang, 2013; see discussion of protomonaxonids, Section 3.2.2) and *Petaloptyon danei* (Rigby, 1986; Rigby and Collins, 2004). *Petaloptyon* in particular shows an extremely complex morphology that is very distinct from all other known sponges, but with dominantly pentaradial spicules similar to those of *Heteractenigma*. The phylogenetic relationships of these two taxa to ‘normal’ heteractinids remain to be identified; they may not even be closely related, and the original composition of their spicules has not been identified. It is possible that the pentaradial spicules were independently derived from the hexaradial spicules of *Eiffelia* and allies, or that they represent a deeper branch of sponge evolution from which eiffeliids and reticulosans were both derived; their origins will probably remain unclear until additional taxa that provide morphological links to other groups are described.

A probably related group, the Palaeozoic Polyactinellidae, are characterized by branching triradial calcareous spicules, and do not show any obvious close relationship to other calcarean groups (Mostler, 1996b), although they are generally accepted to be calcareans (e.g., Mehl and Lehnert, 1997). Mostler (1985) suggested derivation of heteractinids from chancelloriids (no longer a tenable relationship; see Section 3.2.2), but regarded polyactinellids as a separate group. Debrenne and Reitner (2001) regarded polyactinellids as calcareans but left their precise interpretation ambiguous; more detailed investigations of their structure may clarify their relationships.

3.2.4. *Takakkawiids*

A poorly-known group of rare Cambrian sponges has recently received significant attention. *Metaxyspongia skelidata* Wu et al., 2005, from the lower Cambrian of China, was originally assigned to the reticulosans due to the presence of hexactines and their derivatives in a thin body wall (Wu et al., 2005). This species differs from typical reticulosans, however, in having the body divided longitudinally by four vertical columns of derived spicules with deflected rays, producing clear tetraradial symmetry (Botting et al., 2014). The pattern is also present in the problematic Burgess Shale sponge *Takakkawia lineata* Walcott, 1920, which was restudied by Rigby (1986), Rigby and Collins (2004), and Botting (2012). Both genera also share distinctive marginalia spicules, confirming a close relationship (Botting, 2012), although there are several differences in the body wall spiculation and arrangement. Burgess Shale sponge material is preserved in a variety of taphonomic styles, including preservation of organic material (Botting, 2012). This organic preservation reveals that vertically-oriented spicules support broad, outward-pointing fins in a manner not seen in any other known sponge (Botting, 2012). The fins are also finely ridged, showing concentric growth with incremental growth of the spicules. There are no distinct basal spicules, and no sign of distinct gastral or endodermal spicules (Botting, 2012).

In many respects, the takakkawiids represent a very primitive appearance: a thin wall, hexactine-based spicules, no differentiated root tuft and the presence of an organic outer lamina on the

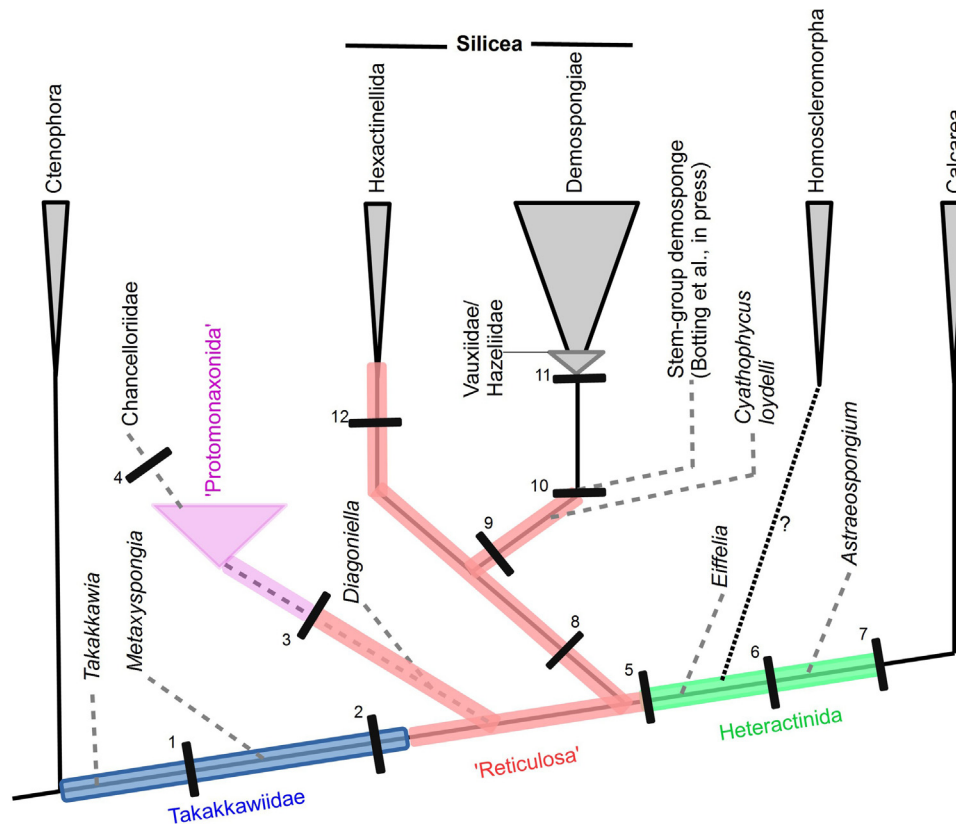


Fig. 6. Summary of phylogeny based on fossil groups, showing stem-group positions of major early sponge lineages. Major character state transitions: (1) origin of hexactines, composition uncertain (but became biminerallic at some point in this lineage, with diffuse axial filament); (2) loss of obvious tetradial symmetry, with skeleton composed of a semi-regular reticulate grid; (3) replacement of biminerallic hexactines by dominant biminerallic monaxons; (4) reduction of biomineral component resulting in partly hollow, organic-walled spicules/sclerites; (5) origin of hexaradiate spicules; (6) loss of siliceous core from spicules; (7) replacement of hexaradiate spicules by triactine and tetractine spicules; (8) loss of calcite from the outer layer of spicules, and origin of square cross-section to axial filament; (9) axial filament symmetry becomes hexagonal/triangular, due to reliance on silicateins in place of cathepsins; (10) loss of hexactines, with secondary monaxon-based skeletal layer becoming dominant; (11) origin of organic fibre skeleton in combination with spicules (microscleres developed later); (12) origin of hexactinellid microscleres and syncytiality. The origin of the Homoscleromorpha is currently unknown, but may relate to loss of calcite from an early, biminerallic heteractinid. The major Cambrian family Leptomitidae (including *Heteractenigma* Botting and Zhang, 2013) is not included because the relationships of this group remain unclear (see Section 3.2.2).

spicules (in this case strongly extended). However, the complex architecture and particularly the structural tetradial symmetry are remarkable features that have no counterpart in other sponges (although elements of tetradiality were widespread among early sponges; Botting et al., 2014). The differences between *Takakkawia* and *Metaxyspongia* indicate that the group was substantially diversified, and does not represent a single aberrant lineage. As yet, the mineralogy of the spicules remains unknown.

The combination of primitive features with unique, complex aspects in takakkawiids precludes a crown-group Silicea affinity, and is also difficult to reconcile with the silicean stem group. The absence of heteractinid spicules also appears to exclude a stem Calcareia/Homoscleromorpha position. However, these features would all be consistent with a stem-poriferan placement, if and only if sponges were derived from a more complex ancestor resembling a ctenophore or cnidarian, rather than originating directly from an amorphous, colonial protistan-grade organism. This is discussed further in Section 4.

4. Phylogenetic framework and reconstruction of sponge ancestors

Although molecular phylogenetics provides a rigorous methodology for creating hypotheses of evolutionary topology, there remain problems with consistency of results, and the method is limited in its ability to illustrate the morphology and attributes of extinct ancestral species. Character mapping onto accepted topologies provides some constraints, but these are often imprecise and assess only particular aspects in isolation. Based only on extant taxa, there is a tendency to make unjustified assumptions about the earliest sponges, such as that they were similar to modern aspicular demosponges (e.g., Luo, 2015). Fossils provide direct evidence of the morphological evolution of a lineage, especially when combined with topological constraints derived from molecular studies. The discussions detailed above can be combined into a phylogenetic framework that arises from the fossil record (Fig. 6; discussed further at the end of this section). The increasing richness and understanding of the sponge fossil record is beginning to illuminate areas that are inaccessible from comparisons of living taxa only. The recogni-

tion of spicule homology within Silicea, and within Porifera as a whole (via biminerallic spicules; see Sections 3.2.2 and 3.2.3), yields unexpected solutions to questions of deep skeletal origins. The improving knowledge of the fossil record illustrates the form, skeletal architecture and occasionally even soft-tissue organisation within the stem lineages, and even appears to be providing strong indications of the wider relationships of the phylum through specific similarities to Cambrian ctenophores (Sections 3.2.4 and 4). This information provides a far more detailed guide to character-acquisition sequences than can be derived from molecular phylogenetics alone, especially in the critical regions below the base of class-level crown groups, and must be taken into account in discussions of basal animal phylogeny.

This framework also allows direct inferences to be made regarding the ancestral morphology of the crown group of Porifera, and of other evolutionary nodes. The biological last common ancestor (LCA) of extant sponges can never be definitively identified as a fossil, but it is potentially possible to constrain its features fairly precisely by comparing characters shared between lineages, and ultimately to recognise fossils that are morphologically similar to the ancestral condition.

Several features of the sponge LCA are immediately clear from the above discussions. Both silicean and calcarean fossil lineages, when traced back to the Cambrian, resolve into thin-walled taxa with a single layer of spicules. These spicules always include hexactines (as in the earliest convincing sponge spicules; Antcliffe et al., 2014; Chang et al., 2017), together with hexaradiate spicules in the Heteractinida, and sometimes also monaxon spicules (in the Protomonaxonida and some reticulosans). Extinct groups such as protomonaxonids and takakkawiids, the phylogenetic positions of which remain somewhat uncertain, also contain hexactines in their earliest forms. The LCA of sponges was therefore almost certainly a thin-walled, hexactine-based sponge that may have additionally possessed heteractinid or monaxon spicules.

Assuming that biminerallic spicules did not evolve multiple times in different lineages, the LCA was probably biminerallic, with siliceous spicule cores secreted onto an axial filament (or diffuse organic region, as in Homoscleromorpha; Uriz, 2006), surrounded by a carbonate (probably Mg-calcite) outer region secreted inside a robust organic sheath. Biminerallic spicules are currently known in eiffeliids and protomonaxonids, but were probably more widely distributed among early sponges; finding more examples, particularly of species with smaller spicules, is dependent on ideal preservational conditions. The LCA's skeletal organisation must, through comparison with eiffeliids and reticulosans, have been semi-regular and reticulate, with a quadrated arrangement of spicules in a body wall that grew by expansion and insertion (cf. Botting, 2003b). If the LCA contained heteractinid spicules, the reticulate organisation may not be obvious.

All these features suggest that the LCA of extant Porifera was morphologically similar to *E. globosa* (Botting and Butterfield, 2005). Whether that species fell onto the silicean branch (Botting and Butterfield, 2005) or the calcarean/homoscleromorph branch (Harvey, 2010), or near the late stem lineage of Porifera,

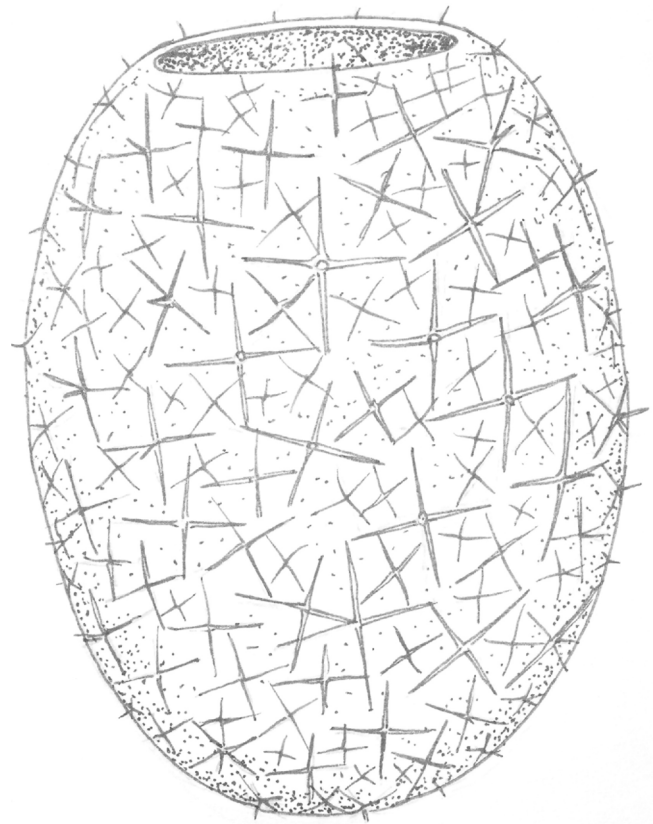


Fig. 7. Hypothetical construction of the morphology of the last common ancestor of Porifera, based on phylogenetic framework of Fig. 6, and comparison with known taxa. Key points: (i) thin-walled skeletal construction (single spicule layer); (ii) globose to ovoid outline; (iii) spiculation primarily hexactines, with projecting (perhaps short) distal rays; stauracts may also be present; (iv) semi-regular quadrated arrangement with localised subdivision of spaces between evenly-spaced large spicules; (v) lack of discrete basalia, marginalia, or modified prostalia; (vi) lack of parietal gaps.

cannot be definitely resolved at present. However, the absence of heteractinid spicules in reticulosans and takakkawiids suggests that these spicules were an innovation of the calcarean stem lineage. This conclusion implies that the LCA would have resembled *Eiffelia* but lacked heteractinid spicules, being constructed almost entirely from hexactine-based spicules. A hypothetical reconstruction of the skeleton of this ancestral sponge is provided in Fig. 7. This architecture most closely resembles that of the early Cambrian genus *Triticispongia* Mehl and Reitner in Steiner et al., 1993, which may be the closest known fossil taxon to the sponge LCA.

The presence of hexactines deep in sponge evolutionary history, rather than as an autapomorphy of Hexactinellida, is undoubtedly contentious; however, it is also extremely strongly supported by the fossil record. Although two additional losses of hexactines are required in this scenario (in basal demosponges and the early stem lineage of *Calcarea/Homoscleromorpha*), the traditional view would require that all taxa with hexactines are hexactinellids. This would imply that the hexactinellid total group previously included taxa with: (i) calcitic spicules; (ii) biminerallic spicules; (iii) hexaradiate, pentaradiate and triactine spicules; (iv) demosponge-like arrays of fine monaxons; (v)

tetradial symmetry; (vi) thick organic spicule sheaths; (vii) hexagonal axial canals; and other features that are presently exclusive to other groups and absent from hexactinellids (see Section 3.2 for details). While a deep origin of hexactines may be surprising, it is also unambiguous, and far more parsimonious than the numerous parallel gains of specific characters needed in the traditional view.

The stem lineage of Porifera initially appears to be less well constrained, particularly as the sister group is not yet identified with certainty. Molecular phylogenies have moved away from sponge paraphyly (e.g., Sperling et al., 2007, 2010) towards monophyly (Pick et al., 2010), but there is still uncertainty over whether sponges are the earliest-branching phylum (Philippe et al., 2009; Pick et al., 2010; Simion et al., 2017) or are more derived than ctenophores (e.g., Dunn et al., 2008; Ryan et al., 2013; Shen et al., 2017). Some analyses have suggested that the data remain ambiguous and ultimately dependent on analytical methods (Philippe et al., 2011; Jékely et al., 2015), but the framework presented here indicates that the latter scenario may be more consistent with the fossil record. This relates in particular to peculiarities of the Takakkawiidae (Fig. 8), and their similarity to certain fossil ctenophores.

Ctenophore fossils are surprisingly well-known in Cambrian Burgess Shale-type faunas (Conway Morris and Collins, 1996; Hu et al., 2007; Tang et al., 2011) and phosphatised microfossils (Chen et al., 2007), with several lineages represented. Assignment of most of these to the Ctenophora is uncontested, but one recent paper (Ou et al., 2015) includes fossils that are more problematic. A range of species from the Chengjiang Biota are discussed in that study, several of them showing organic preservation of an apical organ and/or statolith. Comb rows are clearly preserved also, but with no evidence of cilia, despite the fact that these might be expected based on the fidelity of preservation. Most problematic, however, is the inclusion of *Thaumactena ensis* Ou et al., 2015, which, although appearing to form a continuum with the other ctenophore taxa, is also extremely close in morphology to *Takakkawia*. This similarity includes octoradial symmetry (in *Takakkawia*, the four primary columns divide above the base to produce superficial octoradiality), transverse bars between the longitudinal structures (comb rows in *Thaumactena*, transverse spicule rays in *Takakkawia*), flaring apex ('oral skirt' in *Thaumactena*, oscular marginalia in *Takakkawia*), and the overall morphology (see Botting (2012) for details of *Takakkawia* morphology and Ou et al. (2015) for *Thaumactena*). Because of taphonomic differences between the Burgess Shale and Chengjiang biotas, it is difficult to reliably assess whether spicules were once present in *Thaumactena* (in Chengjiang fossils silica is often dissolved, with sponges preserved largely as iron-stained ghosts of pyritised spicules and soft tissues; Rigby and Hou, 1995; Forchielli et al., 2012), but the visible morphology is effectively identical.

So far as can be judged from the limitations of the preservation, fossils such as *Thaumactena* fall into a morphological continuum between undoubted ctenophores (showing organic preservation of organs that are not present in sponges), and undoubted sponges. Whilst it is always possible that these similar morphologies evolved convergently and differences are

disguised by different taphonomic processes, distinguishing ctenophores from takakkawiid sponges is not straightforward. The simplest (but most controversial) explanation of this is that these groups form an evolutionary continuum, with sponges being secondarily simplified from a more complex, ctenophore-like ancestor. This scenario is in accordance with a substantial body of recent molecular work that suggests loss of eumetazoan characters in the sponge stem lineage and that ctenophores are more basal (see Moroz et al., 2014; Ryan and Chiodin, 2015; Shen et al., 2017, and references therein), and resolves difficulties in the placement of takakkawiids among early sponges. In this arrangement, the Takakkawiidae represent the early stem lineage of Porifera, and shared a common ancestor with extant ctenophores. Whether this common ancestor was exclusively with Ctenophora (Fig. 1C) or Porifera form a sister group to the remaining animals (Fig. 1D), the LCA of Ctenophora and Porifera is likely to have possessed at least some ctenophore-like characters.

If takakkawiids are stem-group Porifera, then other problematic sponge groups are also more easily resolved. In *Metaxyspongia*, the panels between the vertical spicule rows are composed of an irregular but mostly diagonally-oriented array of hexactines or stauractines (Wu et al., 2005; Botting et al., 2014). Loss or suppression of the longitudinal rows, as must have occurred prior to the LCA of extant sponges, would leave a generally diagonal, quadrupled array of stauracts and/or hexactines. This is the basic reticulosan pattern, as seen in idealised, if diagonal, form in *Diagoniella* (including the possible synonym *Protospongia*). In at least some species of *Diagoniella* (e.g., Dawson and Hinde, 1889; Caron et al., 2010; Rigby et al., 2010), anchoring to the sea floor is achieved by a few long monaxons that are inserted inside the body wall and pass through the sharply pointed base. Multiplication of these monaxons and reduction of the dermal hexactines leads immediately to the 'basal protomonaxonids' of Botting et al. (2013), in which short-rayed hexactines are retained amongst the longitudinal monaxons. The protomonaxonids include biminerallitic taxa (Section 3.2.2), and calcite is present in the spicules of specimens assigned to *Protospongia* (Section 3.2.1), and a phylogenetic origin close to the LCA of sponges is therefore reasonable.

In total, there is now a viable working hypothesis for evolution of the poriferan stem lineage (Fig. 6). The model assumes an origin amongst ctenophore-like takakkawiids, with the apex embedded in the sea floor. The comb rows would have been replaced by development of a pore-based, probably ascon-type aquiferous system, followed by gradual loss of the vertical structural elements that were no longer necessary. Spicules (either calcitic or siliceous) developed at some point within this sequence, with flanged monaxons being eventually replaced by stauractines and hexactines, which provided more structural support through interlinking of the rays. Regularisation of the reticulate grid resulted in the standard reticulosan body plan, as seen in *Diagoniella*. Around this stage, spicules were composed of a combination of silica and calcite, if they had not been before. At this point the first major lineage division occurred. One branch developed robust monaxons, which were multiplied in the protomonaxonids to the eventual exclusion

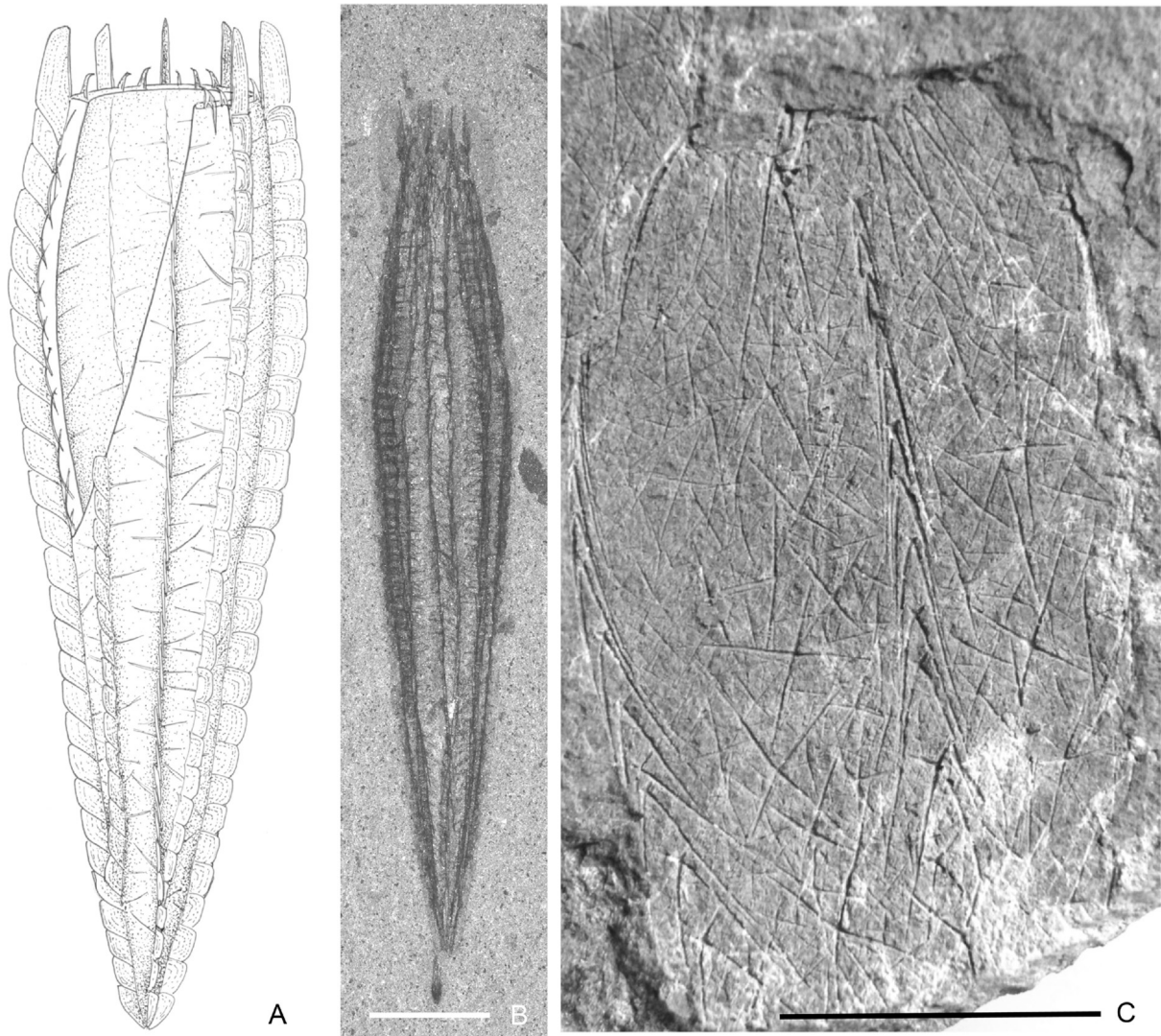


Fig. 8. *Takakkawia lineata* Walcott, 1920, showing tetraradial (secondarily octaradial) symmetry, complex morphology, and spicules with organic outer layers extended into fins. (A) Cut-away reconstruction by Botting (2012). (B) ROM 53568, photographed with crossed polarisers (courtesy of J.B. Caron, Royal Ontario Museum). (C) NIGP154644, upper region of specimen of *Metaxyspongia* sp. from the Hetang Biota (see Botting et al., 2014), showing reticulosan-like primary skeleton and columns of modified spicules defining tetraradial symmetry. Scale bar = 5 mm.

of steadily reduced hexactines; in some members of this lineage, the organic sheath was further exaggerated, resulting in piraniids and chancelloriids. Another branch remained as simple, thin-walled reticulosans, which subsequently divided into stem-group Silicea (with loss of calcite), and stem-group Calcarea (loss of silica) and probably Homoscleromorpha (loss of calcite, or loss of spicules and later reappearance as silica-only).

Later developments within the silicean lineage are well represented in the fossil record, including the division into Demospongiae and Hexactinellida, as discussed above. The calcarean and homoscleromorph branch is much more poorly understood, with critical gaps representing the key transition stages between early calcareous sponges such as heteractinids and living groups.

This model is consistent with the available fossil evidence, even though aspects of it are currently speculative, and some

groups (most notably *Petaloptyon*, *Heteractenigma*, and the leptomitids) remain difficult to relate to other sponges. The proposed phylogeny is consistent with the basic topology of sponge evolution derived from molecular phylogenetics, and with some of the most recent trends in studies of the wider relationships of the phylum. As documented here, the fossil record is strongly supportive of the view that modern sponges are derived from a more complex, symmetric precursor, probably resembling a ctenophore, rather than being the most basal animal group with retained primitive traits. It is possible that further genetic work will disprove a close relationship with ctenophores, or new fossils will suggest alternative interpretations of the affinities of critical early groups, and this review is not intended to be the last word on sponge evolution. Until now there has been no comprehensive hypothesis for early sponge relationships: the present work provides that framework, based

on the most detailed information currently available. The model makes inherent predictions as to the suites of character combinations that should be expected in new discoveries, and is therefore testable by further research. More detailed descriptions of early sponges, particularly of spicule composition and microstructure, are crucial to resolving the uncertainties, and we encourage thorough descriptive studies of existing and future finds, particularly from lower Cambrian and potentially Ediacaran strata.

5. The Precambrian record

5.1. Fossil record

Perhaps the greatest unsolved problem in sponge palaeontology is the absence of Ediacaran sponges. A deep Precambrian history of crown-group sponges is predicted by molecular clocks (Sperling et al., 2010; Erwin et al., 2011; Dohrmann et al., 2013), and by supposed demosponge-specific biomarkers (Love et al., 2009). A large number of putative fossil sponges have been reported from Precambrian strata, but as yet, none are convincing (Antcliffe et al., 2014; Muscente et al., 2015). The review of Antcliffe et al. (2014) refuted virtually all putative Ediacaran sponge fossils, including widely cited, supposed sponges such as those described by Gehling and Rigby (1996), Li et al. (1998) and Brasier et al. (1997). In particular, *Palaeophragmodictya* Gehling and Rigby, 1996 is often referred to as a sponge even in modern molecular biology papers (e.g., Dohrmann et al., 2013), even though it bears little resemblance to extant or early fossil sponges, and has been shown to be merely a holdfast of an Ediacaran frond organism (Serezhnikova, 2007). Other fossils proposed to be sponges by Serezhnikova (2015), however, also show no real evidence of poriferan affinities, and the supposed skeletal structures appear to be only wrinkles in a tough integument. Although it is theoretically possible that some alleged Ediacaran Biota sponges (e.g., the featureless triangle-shaped object *Thectardis* Clapham et al., 2004; Sperling et al., 2011) are in fact genuine, there is no evidence to that effect.

At the time of writing, no reliable or unambiguous specimen of a Precambrian sponge has been described, and there is no convincing evidence even for isolated spicules (Muscente et al., 2015; Chang et al., 2017), even though definite early Cambrian sponge spicules are both very early (Ding and Qian, 1988; Tiwari, 1997; Mazumdar and Banerjee, 1998; Chang et al., 2017) and diverse (Zhao and Li, 2006). The absence is particularly significant given that there are numerous lower Cambrian localities, with a range of environments and preservational styles, that yield entirely unambiguous, fully articulated sponge skeletons (e.g., Steiner et al., 1993; Yang and Zhao, 2000; Yuan et al., 2002; Ivantsov et al., 2005a; Wu et al., 2005, 2014; Xiao et al., 2005; Zhao et al., 2006; Yang et al., 2010; Botting and Peel, 2016). There is a diversity of taphonomic styles and environments in Ediacaran deposits with exceptional fossil preservation, including carbonaceous compressions, preservation in clay minerals, and pyritization (e.g., Xiao et al., 2002; Cai et al., 2012; Yuan et al., 2013; Dornbos et al., 2016). As all these preservational styles are also represented in Phanerozoic sponge-bearing units (e.g., Butterfield et al., 2007; Botting et al., 2011; Kühl et al.,

2012), the absence of sponges from Precambrian strata cannot be easily explained by taphonomic factors.

Three recent publications (not addressed by Antcliffe et al., 2014) deserve additional comment. Du and Wang (2012) described a small number of etched and fragmented hexactine-like spicules extracted from ca. 630-Ma dolostones of the Doushantuo Formation, China. Although some of this material is convincingly spicule-like (Fig. 9C, D; Du and Wang, 2012, fig. 5), there are other options for its origin besides sponges. In particular, early radiolarians (and radiolarian-like fossils) were composed of a framework of spicule-like structures (Won and Iams, 2002; Maletz, 2011), which includes perpendicular (hexactinal) ray junctions, and even axial canals (Afanasieva, 2007; Afanasieva and Amon, 2013; see Fig. 9E, F). Some examples have even been misinterpreted as sponge gemmules (Bengtson, 1986). Radiolarians, like sponges, have a predicted Precambrian origin but an early Cambrian appearance as fossils (Danelian and Moreira, 2004). The small size, broken ends, and in places sharply bent ray of the spicules described by Du and Wang (2012), combined with the broad, irregular axial canal, makes a radiolarian interpretation of these spicules just as likely as a sponge interpretation, and they must therefore remain ambiguous. This point needs reiterating: some radiolarian structures can appear as small but perfectly-formed hexactine or pentactine spicules, complete with axial canals (e.g., Afanasieva and Amon, 2013, pl. 3, fig. 15). Recognition of definite hexactine-based spicules therefore relies on large size, morphological modifications, or (most crucially) articulated preservation. Poorly preserved, small isolated spicules of generic morphology can just as readily be assigned to radiolarians.

Another problematic fossil, *Eocyathispongia*, was described by Yin et al. (2015) from 600-Ma phosphorites, also from the Doushantuo Formation, China. This fossil is a minute specimen with a tubular, chambered form and a granular wall, which is wrapped around itself. The fossil was studied in great detail, and interpreted as a sponge based on the morphology, the supposed cellular preservation of the external pinacoderm, secondary (exhalent?) pores, and other more ambiguous features. *Eocyathispongia* is an extremely interesting fossil, but several features are not easily compatible with sponge biology. The morphology is problematic for a sponge, especially a very small one, as it appears to actively minimise the available surface area for incurrent pores, on which it would depend for feeding. During the Cambrian and Ordovician, small sponges were invariably radially symmetric, were not curved to overlap themselves, and were erect (or at least globose), to enable feeding from a maximised surface area. *Eocyathispongia* is functionally difficult to understand, as much of the surface is covered by other parts of the same organism, and there is no sign of vertical growth. The apparent cellular preservation of pinacoderm is also potentially problematic, in that it is significantly coarser (15–30 μm) than that observed in most extant sponges, which is typically around 5–10 μm in diameter across a wide range of taxa (e.g., Bagby, 1972; Maldonado and Riesgo, 2007; Lanna and Klautau, 2010) — although the cells can reach 15–20 μm in some lineages (Wielspütz and Saller, 1990). However, these structures are on a similar scale to the particles in the agglutinated test of certain tes-

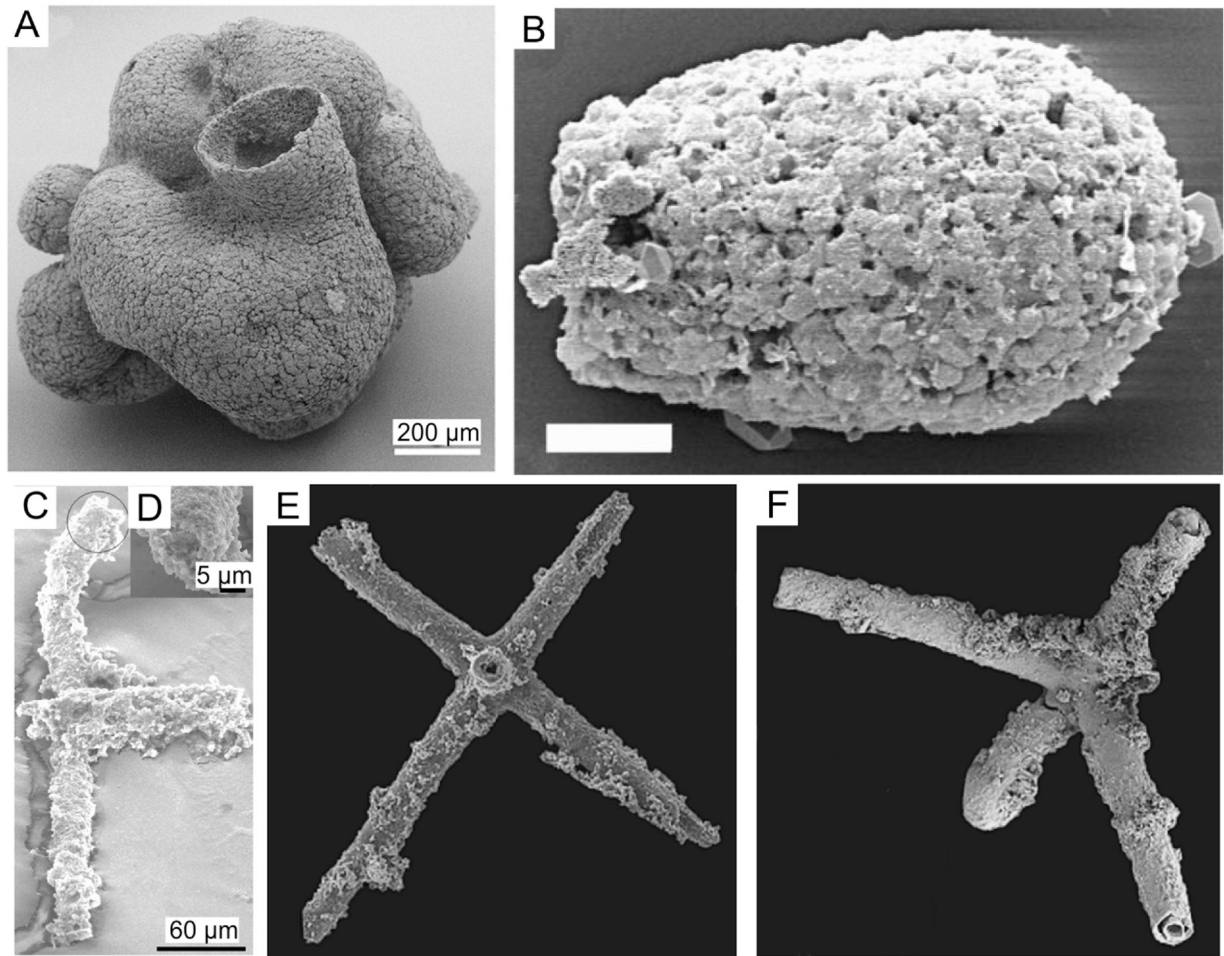


Fig. 9. Putative Precambrian sponges, and alternative interpretations. (A) *Eocyathispongia qiania* Yin et al., 2015 from the Ediacaran of China; reproduction of fig. 1A of Yin et al. (2015), copyright Yin et al. (2015). (B) Testate amoeba from the Neoproterozoic of the USA; reproduction of fig. 7D of Porter and Knoll (2000), copyright the Paleontological Society; scale bar = 20 µm. (C, D) Putative Precambrian sponge spicules; reproductions of fig. 5A, B of Du and Wang (2012), copyright Palaeontological Society of Japan, reproduced with permission. (E, F) Radiolarian spicules; reproductions of pl. 3, figs. 15 and 18 of Afanasieva and Amon (2013), copyright Pleiades Publishing Ltd., reproduced with permission; longest spicule ray is approximately 320 µm in (E) and 600 µm in (F).

tate amoebae (e.g., Bosak et al., 2011), which are known to have existed at that time (Porter and Knoll, 2000; Bosak et al., 2011); a comparison is provided in Fig. 9A, B. Vase-shaped amoeboid taxa are known from the Neoproterozoic, including some with remarkably similar surface texture (Porter and Knoll, 2000, fig. 7D). An amoeba interpretation would explain the absence of any evidence for choanacocytes, which is otherwise a problem for a fossil that appears to preserve three-dimensional cell structures as calcium phosphate. The apparently chambered (or perhaps communal) morphology would be unusual, but the apical aperture is entirely normal for an amoeba. Alternatively, there may also be an argument for interpretation as a multicellular alga, with the apparent apertures being taphonomic artefacts; this also requires more detailed study. Overall, interpretation of this fossil is very difficult, but at this stage there are sufficient problems with a poriferan interpretation that an alternative (agglutinated amoeba, alga or other non-metazoan organism) is more viable.

Finally, there is an undescribed but illustrated specimen from the latest Ediacaran White Sea Biota, described by Reitner and Wörheide (2002, fig. 1B) as a demosponge. The specimen super-

ficially resembles some protomonaxonids (see Botting et al., 2013), and the single photograph is moderately convincing. However, the resemblance is only superficial, as this specimen is a basal fragment of large but typical Ediacaran frond (A. Zhuravlev, personal communication, 2016).

5.2. Contradiction with molecular clocks, and possible explanations

Most of the claims for Precambrian sponges are of fossils that are very different from crown-group Porifera. Nonetheless, based on molecular phylogenies and clock results, the crown group of Porifera should have had a deep Ediacaran or Cryogenian divergence, implying that spiculate, Cambrian-type sponges should dominate Precambrian animal faunas. The assumption that class-level stem lineages comprising most of Precambrian sponge evolution were aspiculate and perhaps amorphous directly contradicts the evolutionary framework derived from the abundant and diverse record of early Palaeozoic sponge fossils presented here, which is itself consistent

with molecular phylogenies, as presented above. This implies that if sponges were present in the Precambrian, then most or all of them should have been spiculate, with clear morphology, and should have included protomonaxonids, reticulosans, and takakkawiids. All of these groups have a good Cambrian record, and are distinctive and obvious fossils, yet none have ever been reported. This is in spite of the discovery of several Ediacaran Burgess Shale-type assemblages such as the Lantian Biota (Yuan et al., 2013), Miaohu Biota (Xiao et al., 2002), Zuun-Arts Biota (Dornbos et al., 2016) and Gaojiashan Biota (Cai and Hua, 2007), which have a range of preservational styles from carbonaceous compressions to pyritisation. Silica itself should also have been more stable in Ediacaran seas, as its saturation in normal seawater was much higher, leading to, or at least enhancing, some of the exceptional preservation seen in the sandstone-hosted Ediacara biotas (Tarhan et al., 2016). The reduction in silica saturation around the early Cambrian appears to have been caused by removal of silica from seawater resulting from increased biosilicification — in which sponges were a major factor (Maliva et al., 1989).

There are few potential explanations for the apparent absence of Precambrian sponge fossils. One possibility is simply collection failure, whereby palaeontologists have collectively overlooked the articulated sponges that are there; however, this does not seem likely. Given the range of different lithologies that have been investigated, the number of exceptionally preserved biotas studied, and the volume of samples dissolved to extract microfossils, total failure to recognise sponge remains is implausible, especially given the number of erroneous reports that have been published (Antcliffe et al., 2014). Taphonomic megabias (e.g., Sperling et al., 2010) is also insufficient to explain the absence of sponges, especially as siliceous fossils should be better preserved in upper Precambrian than in Phanerozoic strata due to the high silica concentration in Ediacaran seawater (Tarhan et al., 2016). Pyritisation is also widespread in Ediacaran mudstones (e.g., Cai and Hua, 2007), representing an extremely common taphonomic mode for Palaeozoic sponge fossils, and at least some early sponges should have possessed both calcite and silica within their spicules, providing two potential pathways to fossilisation under any conditions (see Section 3.2). Taphonomic bias therefore seems impossible; remaining explanations must reflect ecological and evolutionary aspects.

It is possible that sponges evolved in environments with very poor preservation potential, and were restricted to them for the majority of their early history. From our understanding of the fragile nature of the early members of each lineage, shallow-water environments would probably not have been survivable for many early reticulosans (Muir and Botting, 2015). A deep marine habitat, on the continental slope or abyssal plain, would potentially allow a great deal of evolution to have occurred without leaving a palaeontological record. There is some support for this view from the Hirnantian sponge faunas of South China discussed above, which include some unexpectedly derived taxa that may have evolved offshore (Li et al., 2015; Botting et al., 2017a). However, it is unclear how or why such an environmental restriction could have developed during the Ediacaran, given the virtual absence of predators or bioturbators that could have

prevented benthic settlement or growth, or why such limitations would exclude colonisation of the preserved areas of the deep shelf. Some form of competition or chemical exclusion related to the shallow-water Ediacaran Biota may offer some explanation, but no persuasive solutions are obvious. It is more likely that the deep oceans were themselves dominantly or completely anoxic (Fan et al., 2014; Li et al., 2010), rendering long-term colonisation by animals impossible. It is also very difficult to explain how such a mechanism could have operated for over 100 million years. Ecological arguments therefore seem to be unworkable, unless entirely new aspects are discovered.

Changes in phylogenetic understanding, such as the derivation of sponges secondarily from ctenophore-like organisms (e.g., Ryan and Chiodin, 2015), may negate some of the contradiction. Molecular clocks are superimposed on phylogenies, which until recently have usually shown sponges as the most basal group. If the accepted topology alters such that ctenophores are basal (e.g., Borowiec et al., 2015; Dunn et al., 2015), then the origin of sponges post-dates that of animals, reducing the discrepancy between clocks and fossils. How far the discrepancy would be reduced remains to be seen.

5.3. Biomarkers

Biomarker evidence for early radiation of crown-group demosponges is more problematic, as it is completely incompatible with the fossil record. The palaeontological evidence for an early to middle Cambrian diversification of the demosponge crown group is very strong, even if pushed back to near the Ediacaran–Cambrian boundary (541 Ma; Peng et al., 2012) by the putative but undescribed lithistid desmas of Braun et al. (2007). If crown-group demosponges were present even at 600 Ma (Love et al., 2009), then the stem lineage of Silicea, and that of Porifera, must substantially pre-date that point, meaning that spiculate sponges would have been already diverse in the Cryogenian. This discordance with fossil observations suggests that there is a problem with interpretation of the biomarkers, such as suggested by Antcliffe (2013); however, this critique has itself been criticised (Love and Summons, 2015) and some further support for the demosponge biomarker interpretation was provided by Gold et al. (2016a). Nonetheless, it is curious that the relevant biomarkers have not yet been recovered from analysis of fossil sponges themselves (Gold et al., 2016b), and the extremely high Precambrian levels of the steranes combined with a decline at the point where sponge fossils first appear (Love et al., 2009) cannot be anything but problematic. It remains entirely possible that the Precambrian biomarkers record an independent origin of the same steranes in a different organism, such as (but not limited to) pelagophyte algae, in which the relevant sterols are known to occur as trace products (Love and Summons, 2015).

Some evidence inadvertently supporting the possibility of biomarker convergence was presented by Brocks et al. (2016), who interpreted novel but related (probably 26-methylcholestane), pre-Sturtian (ca. 750–800 Ma) steranes as possible demosponge or protistan biomarkers. Only sponges are currently known to methylate steranes in the 26-position, and so this ostensibly supports a demosponge origin. However, this so

far pre-dates the known sponge record, or even recent molecular clock results, that it becomes entirely implausible, and a convergent origin must be the null hypothesis. Brocks et al. (2016) also note that sterane synthesis in living protists is extremely poorly known, and that a much more detailed survey of sterane biosynthesis across the Eukarya is needed. Synthesis of related biomarkers by an unknown group, leaving an abundant record in Cryogenian rocks, at least creates some doubt over the other supposed Precambrian sponge biomarkers that long pre-date the fossil record.

Overall, the use of biomarkers depends on the assumption that the same compound was not independently derived in a different group. Even if a compound is entirely restricted to one group among the living biota, this was not necessarily true in the past. In the case of the sponge-derived steranes, even some living algae are known to produce the same compounds, and therefore it cannot be assumed that convergence is impossible, or even unlikely. Although the modern algal steranes are apparently produced in error in place of their isomer (Love and Summons, 2015), they may have had ancient relatives that made use of the supposedly diagnostic sponge biomarker, together with the 26-methylcholestane. Alternatively, an entirely different group may have evolved the same compound: if this could happen twice, it could happen three times. Overall, the biomarker evidence remains circumstantial as a record of demosponges, and given the complete contradiction with the fossil record, cannot be considered compelling. Rather, these compounds should be regarded as an incentive to look for definite Precambrian spiculate sponges, because according to the biomarker evidence they should have been present in much higher numbers in the Ediacaran than they were when they left an abundant fossil record in the Cambrian.

6. Conclusions

The fossil record provides the only direct evidence of early sponge evolution. Despite limited preservation potential and a correspondingly patchy record, there is now sufficient detail recognised in early sponges to allow reconstruction of the crown and stem-group divergence points, and draw reasonable inferences about the poriferan stem lineage and ancestry. This review combines disparate lines of evidence to produce a model framework for early sponge evolution (Fig. 6), for which most of the major stages are preserved in the fossil record. Most of the early sponge fossils fall outside the class crown groups, although the class-level divergence must have occurred during the early Cambrian. Some Cambrian sponges appear to form a continuum with Cambrian ctenophore fossils, supporting recent molecular work that indicates ctenophores rather than sponges were the basal animals (e.g., Dunn et al., 2015; Ryan and Chiodin, 2015).

The persistent absence of demonstrable Precambrian sponges is exacerbated by this model, as the early stem lineages must also have been spiculate, and morphologically similar to those of the early Palaeozoic, which are abundant and obvious under suitable preservational conditions. The prior focus on amorphous structures with pores, which could have represented early sponges as derived from protistan colonies, is misleading and based on

outdated expectations of what early sponges were related to; any such fossils are now highly unlikely to be primitive sponges. The continued absence of spiculate sponge fossils in the Ediacaran therefore suggests that they were not present until the very end of that interval, either because of ecological restriction to rarely preserved environments such as the deep ocean, or because they had not yet evolved. Which of these options is more likely cannot yet be assessed, but secondary simplification of sponges from ctenophore-like organisms may partly solve the conundrum, in removing the deep origin of sponges implied by a basal position in animal evolution. The origin of sponges would then be a part of the Cambrian Explosion phenomenon, rather than substantially pre-dating it, thereby conforming with the fossil record, although this is yet to be tested by molecular clock analyses constrained to the ctenophore-basal hypothesis.

In order to improve and revise this framework for sponge morphological evolution, more material is needed of articulated spiculate sponges from the lower Cambrian, and ideally also the upper (or lower) Ediacaran. Equally important are detailed studies of the spicule microstructure (especially mineralogy and axial canal symmetry) of a wide range of early-branching groups. These new discoveries will test the outline presented here, in relation to the expected character combinations present in different lineages. By combining information from the fossil record with molecular, embryological and other analyses based on modern sponges, an understanding of their early evolution is finally within reach.

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