Original article

'Cambrian' demosponges in the Ordovician of Morocco: Insights into the early evolutionary history of sponges

Demosponges 'cambriennes' dans l'Ordovicien du Maroc : nouvel aperçu de l'histoire évolutive ancienne des éponges

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Abstract

Cambrian spicular sponge faunas are dominated by a distinctive assemblage of demosponges and hexactinellids that are known from Burgess shale-type faunas worldwide. Most of these are previously unknown outside the Lower–Middle Cambrian (and perhaps Tremadoc) and have no obvious close relatives in later sequences. This paper describes examples of *Choia* sp., *Pirania auraeum* sp. nov. and *Hamptonia christi* sp. nov. from the Arenig of Morocco, associated with isolated hexactinellid spicules. A summary of the stratigraphic ranges of the major Cambrian sponge lineages is provided. These indicate an environmental contrast in the Lower Palaeozoic evolution of hexactinellids and non-lithistid demosponges, with demosponges probably undergoing cryptic diversification in nearshore environments during the Upper Ordovician.
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Résumé

Les éponges siliceuses cambriennes se distinguent par des assemblages dominés par les démosponges et les hexactinellidés. Ces assemblages sont connus dans les faunes de type Burgess partout dans le monde. La plupart des éponges étaient auparavant inconnues après le Cambrien inférieur–moyen, et peut-être le Trémadocien, et n'ont pas de formes apparentées dans des séries plus jeunes. Cet article décrit quelques exemples de *Choia* sp., *Pirania auraeum* sp. nov. et *Hamptonia christi* sp. nov. dans l'Arenig du Maroc, en association avec des spicules d'hexactinellidés isolées. Un résumé de l'extension stratigraphique des plus importantes lignées d'éponges est fourni. Ceci indique un contraste environnemental dans l'évolution des hexactinellidés et des démosponges non-lithistidés au Paléozoïque. Les démosponges ont probablement subit une diversification cryptique dans des environnements sub-littoraux à l'Ordovicien supérieur.
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Keywords: Biodiversity; Palaeoecology; Hexactinellids; Non-lithistid demosponges; Burgess shale faunas

Mots clés : Biodiversité ; Paléoécologie ; Hexactinellidés ; Démosponges (non-lithistidés) ; Faunes de type Burgess

1. Introduction

The Ordovician–Silurian fossil record of non-lithistid, spicular sponges is extremely incomplete. Most descriptions of new faunas are dominated by new species, and often new genera, while the recognition of an existing species is remarkably rare. Cambrian sponge faunas, in contrast, are dominated by a characteristic assemblage of distinctive genera that occur in North American, Arctic and Chinese Burgess shale-type faunas (Rigby, 1986; Rigby and Collins, 2004; Chen et al., 1989; Hou et al., 2004), but have little or no record outside them. This has led to the pervasive informal view that Cambrian spicular sponges are largely distinct from later faunas, perhaps having undergone a significant episode of elevated extinction in the Upper Cambrian.

The data on Ordovician non-lithistid sponges are gradually increasing, and show an extraordinary diversity of, particularly, hexactinellids (e.g., Mehl and Lehnert, 1997; Carrera, 1998; Carrera and Rigby, 1999; Botting, 2004a, 2005). Non-lithistid

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demosponges are still, however, extremely rare. The discovery of new Arenig sponges from the Zagora area of Morocco (Fig. 1), dominated by the non-lithistid demosponges *Pirania*, *Choia* and *Hamptonia*, is, therefore, unexpected and provides a new perspective on Ordovician sponge distributions.

Workers studying rare fossils in the Moroccan Anti-Atlas are often partly reliant on the efficient commercial network, either through the direct supply of fossils or through directions to sites. Rare groups such as sponges are encountered only occasionally and from a very wide area so that commercial dealers and amateur collectors obtain a high proportion of the finds. The sponges described here were obtained from commercial collectors (holotype of *Pirania auraeum*, and *Choia* sp.), the amateur palaeontologists Catto (one specimen of *P. auraeum*) and Réboul (two specimens of *P. auraeum*), and also from Lefébvre (one specimen of *P. auraeum*), Van Roy (*Choia*? sp.) and JPB (*Hamptonia christi* sp. nov. and asthenospongiid? indet.), while on fieldwork in the Vallée du Draa, near Zagora. They were excavated from the Arenig Upper

Fezouata Formation, which is intermittently exposed over a wide region, but the precise localities for some of the material are unknown. The presence of *Clonograptus* sp. fragments on the two *Pirania* slabs that are from unknown localities supports the Lower–Middle Arenig age and suggests a region around 10–20 km northeast of Zagora where these graptolites are abundant in a very similar lithology. The specimens provided by Lefébvre and Réboul have full locality data and include specimens from this area and from slightly to the west. The lithology in which the *Choia* specimens occur is somewhat coarser and more micaceous, suggesting a younger (probably Middle Arenig) age, and a locality probably closer to the eastern or northern margin of the Vallée du Draa, where similar rocks are primarily exposed. Radial structures recovered by Van Roy in sandstones from one site in the eastern Vallée du Draa may be poorly preserved choiids, but no spicules are clearly identifiable. Because of the uncertainties over the locality and precise age, the *Choia* specimens (for which no reliable locality information is available) are recorded under open
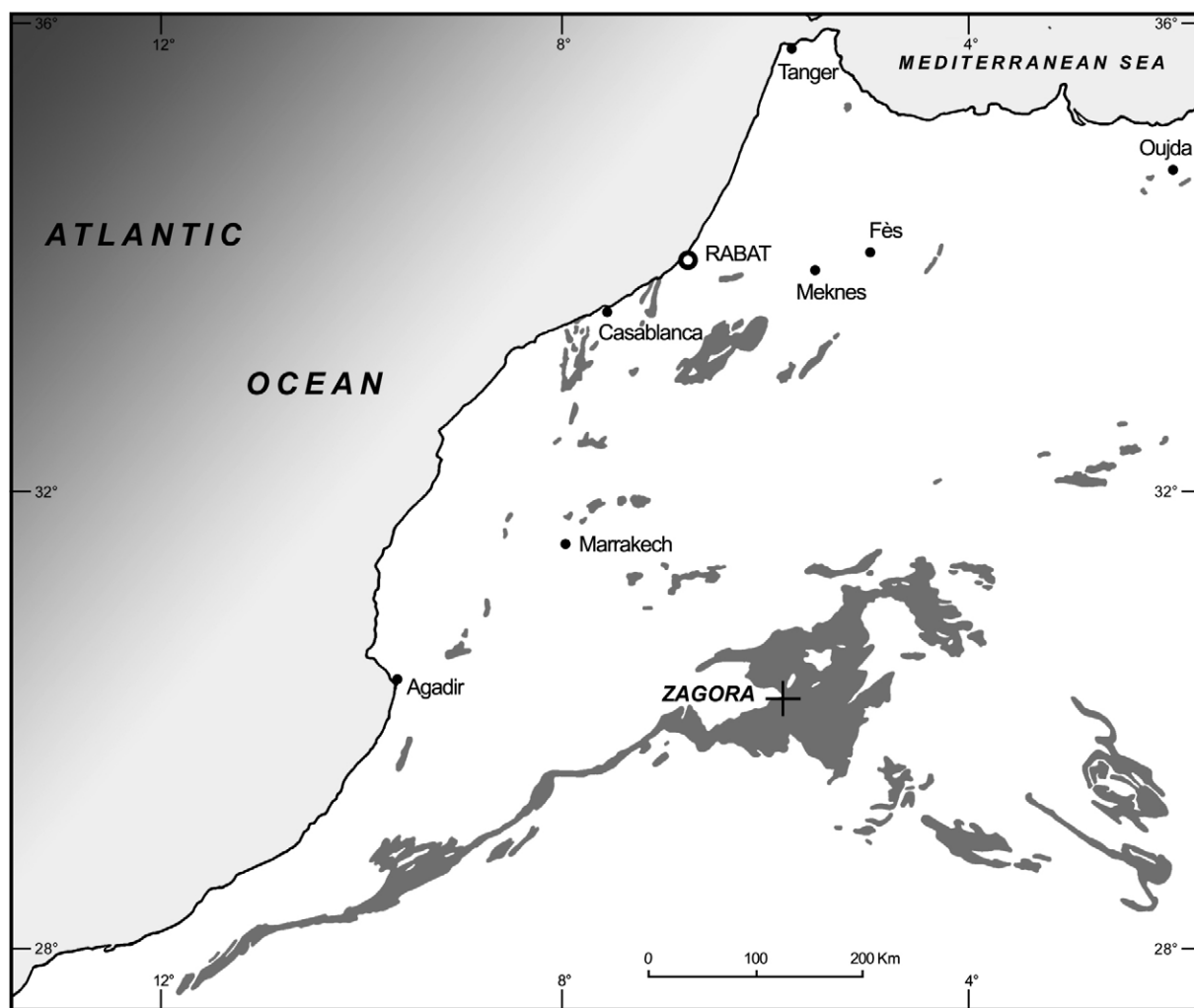

Fig. 1. Ordovician outcrop in Morocco, with the location of Zagora in the Anti-Atlas region. The specimens in this study are from the area to the east and north of Zagora.

Fig. 1. Distribution géographique de l'Ordovicien du Maroc et localisation de Zagora dans la région de l'Anti-Atlas. Les spécimens étudiés ici proviennent de la région nord et est de Zagora.

nomenclature, although their presence is significant enough to warrant an otherwise full description. In particular, the presence of an attachment structure has implications for the palaeoecology of the genus. Details of the basal region and gastral surface of *Pirania auraeum* sp. nov. add to existing knowledge of the range of generic characteristics. Also described are *Hamptonia christi* sp. nov. and isolated hexactinellid spicules, collected by the author.

The sponges are associated with diverse shelly and graptolitic faunas, of which the most common elements are trilobites, graptolites, hyolithids, echinoderms (primarily cystoids, 'carpoids' and asterozoans), and brachiopods. Rarer organisms include unmineralised arthropods, worms, machaeridians, bivalves, tergomyids and gastropods, including, in some cases, remarkable preservation (to be described elsewhere). The faunas are distributed throughout the formation, in both the green siltstone that dominates the sequence, and in thin (20 cm) interspersed limestone beds that often contain concentrated deposits of near-monospecific assemblages and represent transported sediments. Sponges are distributed very locally, but in some of the specimens that lack provenance data, there are small fragments of probable sponges on the slabs. It is likely that additional sponge taxa are present in the formation, but from collections to date, the species described here appear to be the most widespread and abundant, and no others have yet been confirmed.

2. Systematic Palaeontology

Specimens are housed in the Sedgwick Museum, Cambridge, UK (CAMSM), the Natural History Museum, London, UK (BMNH), and the UFR *sciences de la Terre, université de Bourgogne*, Dijon, France (UBGD).

Class DEMOSPONGIAE
Order uncertain
Family CHOIIDAE de Laubenfels, 1955
Genus ***Choia*** Walcott, 1920
Choia sp. Figs. 2 and 3(A)

Material: two small slabs (CAMSM X 50108.5, 50108.6) densely crowded with five partial or complete specimens on one, and seven on the other, from the Upper Fezouata Formation, Vallée du Draa, Morocco; probably Middle Arenig. Also two probable specimens from 30°32.436′ N, 005°40.313′ W (CAMSM X 50108.7).

Description: diameter of largest specimens exceeds 40 mm, including prostalia, with the central region approximately 28 mm across. Each is a largely symmetrical array of coronal monaxons, typically 15–20 mm long, with some spicules up to 25 mm, sometimes loosely clustered in groups of two to five; this may be taphonomic. Any asymmetry in the radial form can be attributed to biostratinomic distortion. Spicules in some specimens are slightly curved, in consistent orientation, suggesting transport with friction against the sediment. The distal termination of all spicules is oxeate, but proximal ends are often obscured by an oxidised mass over approximately the central 10 mm of the sponge, apparently resulting from local pyritisation. Where coronal spicules initiated away from the centre, proximal ends are sometimes visibly rounded; these spicules are styles. It is possible that the obscured central region of the sponge represents the extent of soft tissue, which acted as a nucleation centre for pyrite growth; although spicules are also preserved as weathered iron oxides, there is little pyritic overgrowth except in this central area. Although largely flattened, the centres of the sponge bodies are slightly raised on both specimens, producing shallow cones.
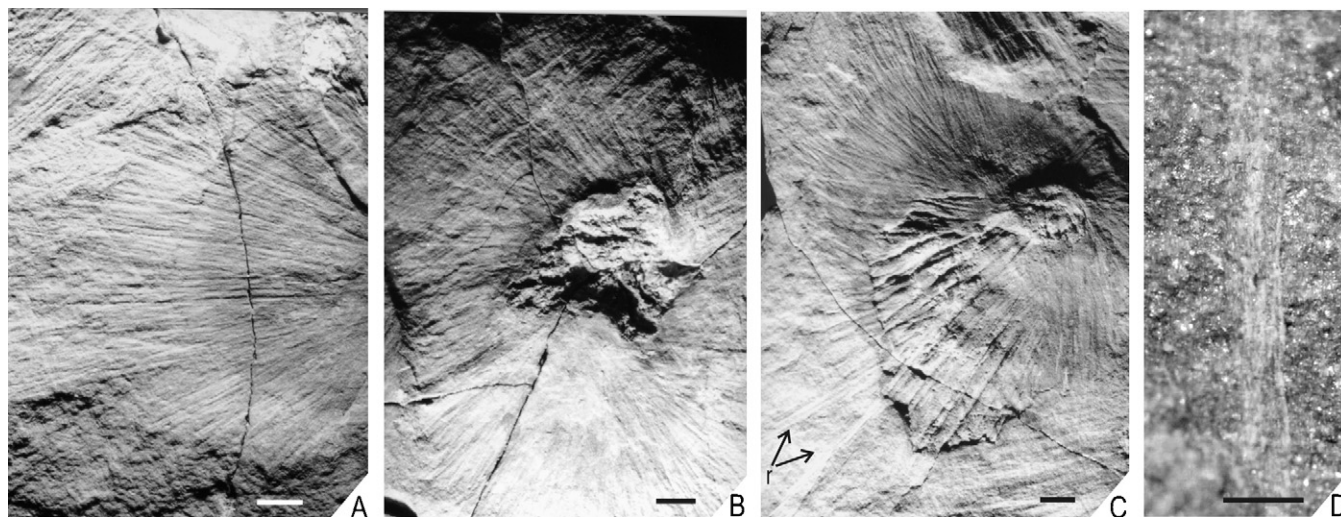

Fig. 2. *Choia* sp. photographs. **A**, CAMSM X 50108.5a, coronal spicules; **B**, CAMSM X 50108.5b, near-complete specimen showing heavily mineralised central region, perhaps indicating region of thick soft tissue; **C**, CAMSM X 50108.6a, near-complete specimen with attachment ropes (r) labelled; **D**, magnification of lower attachment rope in **C**. Scale bars 10 mm in **A**–**C**, 1 mm in **D**. All specimens from the Upper Fezouata Formation, near Zagora, Morocco.

Fig. 2. *Choia* sp. **A**, CAMSM X 50108.5a, spicules de la couronne ; **B**, CAMSM X 50108.5b, spécimen presque complet dont la région centrale est fortement minéralisée indiquant peut-être la présence de tissus mous ; **C**, CAMSM X 50108.6a, spécimen dont la région centrale est minéralisée et montrant deux cordes d'attachement minces (r) ; **D**, le grossissement de la corde d'attachement inférieure visible dans **C**. Échelles 10 mm pour **A**–**C**, 1 mm pour **D**. Tous les spécimens proviennent de la Formation supérieure de Fezouata de Zagora, Maroc.
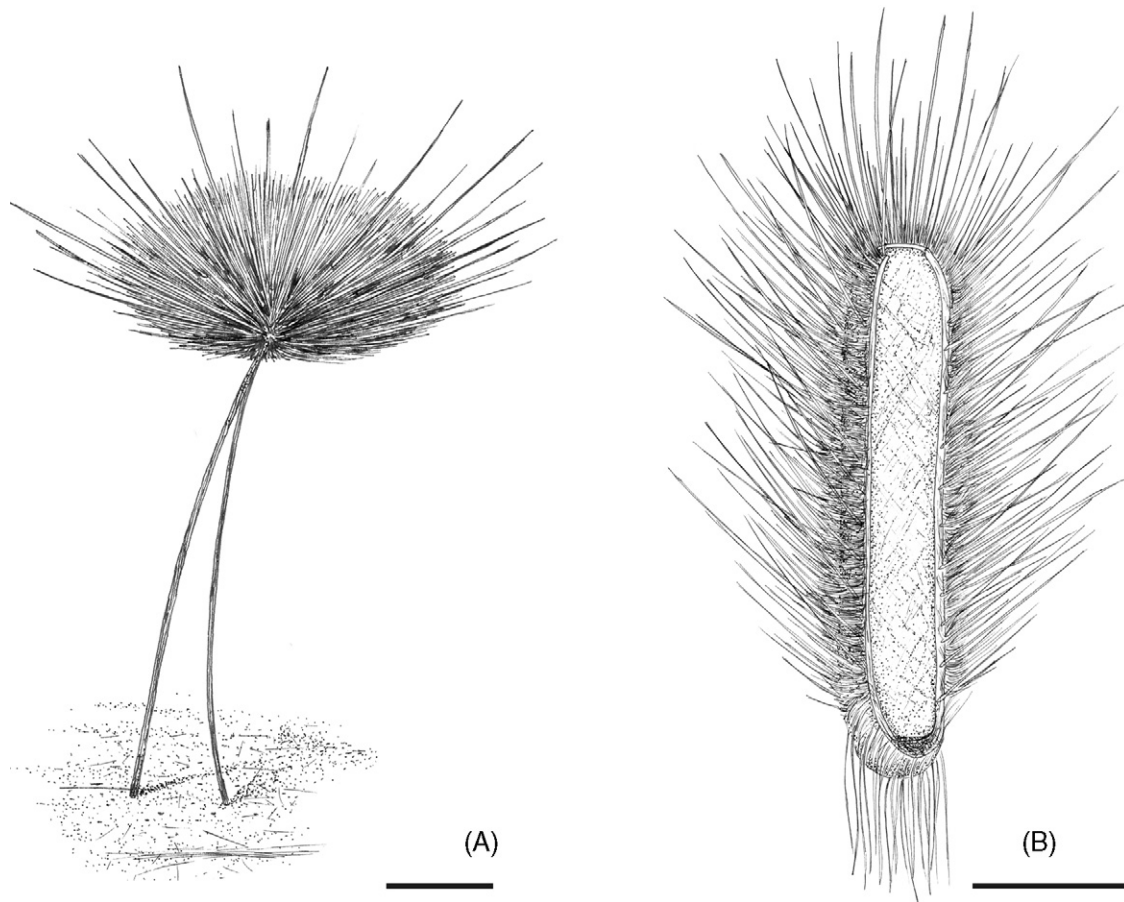
Fig. 3. Reconstructions of **A**, *Choia* sp. and **B**, *Pirania auraeum* sp. nov., showing critical details. Scale bars 10 mm.
Fig. 3. Reconstructions de **A**, *Choia* sp. et **B**, *Pirania auraeum* sp. nov., montrant des détails précédemment inconnus. Échelle 10 mm.

Maximum spicule diameter is 1.5 mm, with the majority much finer; finer spicules are generally also shorter, suggesting continuous or multiple-stage spicule insertion. In one specimen, there are two fine attachment threads, 25 mm long, extending from the centre of the convex surface to beyond the longest spicules. Threads are composed of eight to twelve fine parallel spicules, densely arranged, the thread apparently helically twined albeit with long wavelength. Fragments of what may be other, smaller threads occur nearby, but these are less clear.

The additional, possible specimens on slab CAMSM X 50108.7 show no spicules, but a weak radial structure preserved in a flat, iron-stained cone. The larger has diameter 42 mm, the smaller 20 mm. A heavily mineralised structure, 0.6 mm diameter, in the centre of the larger specimen may possibly be a cross-section through the top of a stalk. The specimens are preserved in fine sandstones.

Remarks: Only one specimen of a choiid sponge (Lower Silurian of Scotland Botting, 2007) has been recorded above the Tremadoc, from which the only recorded occurrence is the Little Metis section (Dawson and Hinde, 1889). However, they are among the most distinctive and widespread of all Cambrian sponges, known from many localities in North America, and from Greenland and China, and their disappearance in the basal Ordovician has previously been taken to represent extinction.

The species described here could easily be regarded as large examples of *C. ridleyi* or a small *C. carteri*; although the ratio of disc to corona radius differs slightly from each, it is not clear how strongly affected this is by ambient conditions. Rigby (1986) discussed the separation of *Choia* into a range of species based effectively on size, concluding that the polymodal size distribution at any locality, and the general exclusion of other sizes in each assemblage was sufficiently reliable evidence to support their separation. It is, however, possible that the patchy, perhaps opportunistic distribution could cause the apparent polymodality through the establishment of a series of dense populations arising in succession, especially given that rapid burial at a single time is essential for their preservation. Maximum sizes are also likely to be strongly dependent on conditions, such as nutrient supply and temperature, and ecophenotypic effects must be considered when interpreting apparent differences between population size distributions. The present species may be separable from the Cambrian species on the basis of the attachment stalks, but these may also have become detached, or simply not been recognised, in other occurrences. Even without the uncertainty over potential type localities, formal description would perhaps not be appropriate without a greater sample size.

The presence of an attachment stalk significantly changes our interpretation of the mode of life of the genus. Rigby (1986)

reconstructed *Choia* with apex upwards on the basis of greater stability, in contrast to previous reconstructions with the apex embedded in the sediment. The stalks are here attached to the convex side of the apex, implying a conventional orientation with concave surface upwards, but probably raised substantially above the sediment surface. The presence and dimensions of such attachment structures could potentially be used to constrain environmental parameters such as ambient turbulence, given better material.

Family PIRANIIDAE de Laubenfels, 1955
Genus *Pirania* Walcott, 1920

Pirania auraeum sp. nov. Figs. 3(B) and 4

Etymology: latin *auraeum*, curtain, describing the basal spicule arrangement.

Diagnosis: *Pirania* with rounded apex, and curtain-like array of basal monaxons attached to the sides of rounded base; prostalia are long and abundant, with intervening small monaxon tufts. Body wall includes wall-parallel monaxon array with diagonal spicule impressions on internal surface.

Holotype: a single near-complete specimen, CAMSM X 50108.3, part and counterpart, with slight relief; shows details including basal region and gastral surface.
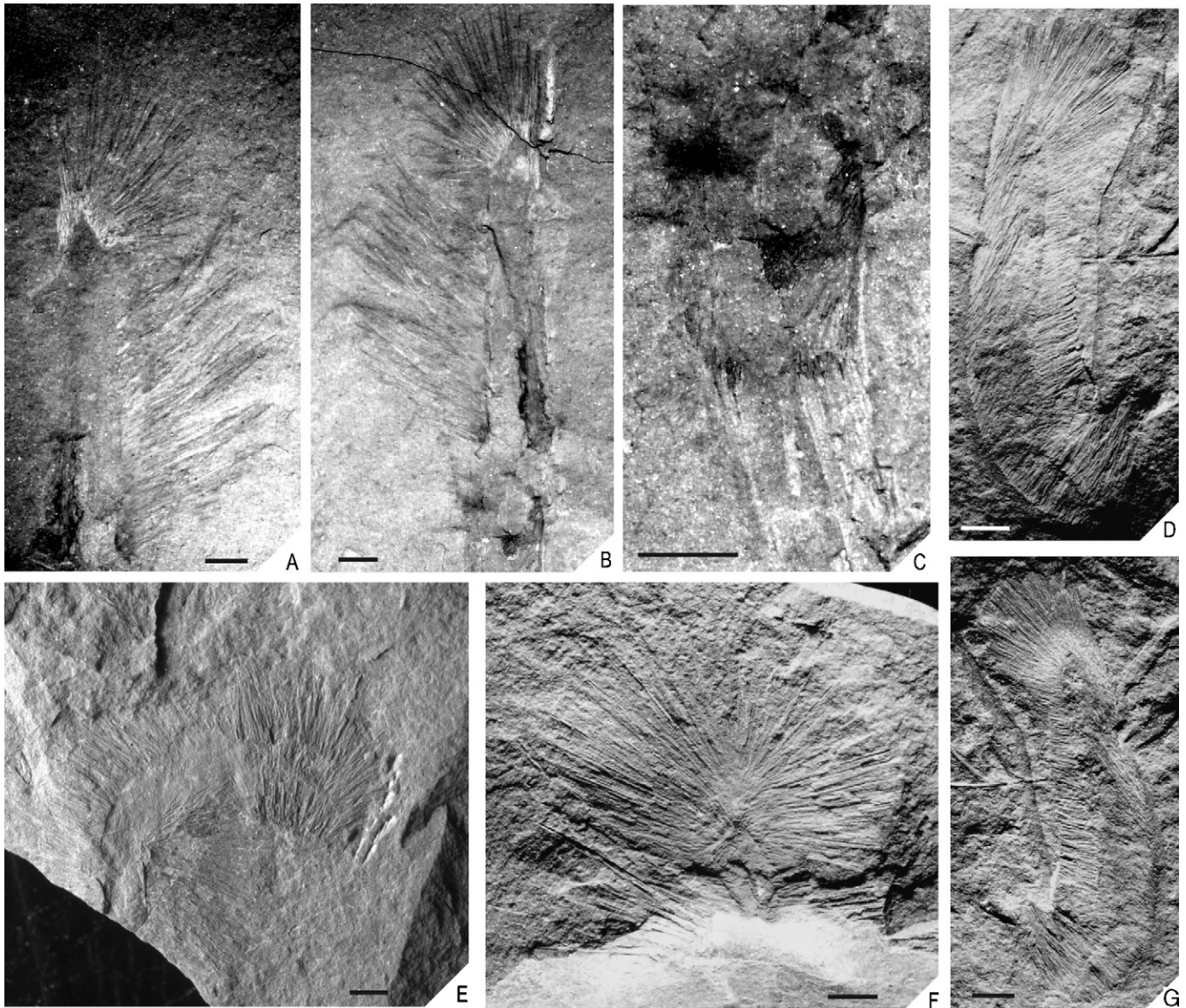

Fig. 4. *Pirania auraeum* sp. nov., from the Upper Fezouata Formation near Zagora, Morocco. **A–C**, Holotype; **A**, CAMSM X 50108.3.2; **B**, CAMSM X 50108.3.1, overall view; **C**, CAMSM X 50108.3.1, detail of basal region, showing 'curtain' arrangement of spicules, and dense structure of the thickened basal part of the body wall; **F, G**, paratype; **F**, CAMSM X 50108.4.1, **G**, CAMSM X 50108.4.2; **E**, BMNH PO 12071; **D**, UBGD 20928, paratype, showing oscular region only, the rest distorted or absent. Scale bars 2 mm.

Fig. 4. *Pirania auraeum* sp. nov., de la Formation Fezouata Supérieur de Zagora, Maroc. **A–C**, Holotype ; **A**, CAMSM X 50108.3.2, la forme générale du corps ; **B**, CAMSM X 50108.3.1, vue générale ; **C**, CAMSM X 50108.3.1, grossissement de la région basale, montrant la préservation remarquable des structures ancitomiques et de l'attachement basal. **F, G**, paratype ; **F**, CAMSM X 50108.4.1, **G**, CAMSM X 50108.4.2 ; **E**, BMNH PO 12071 ; **D**, UBGD 20928, paratype, montrant la région osculaire. Échelle 2 mm.

Paratypes: UBGD 20928, partial specimen from near Beni Zoli, Ouaoufrout, Zagora (30°31′15″ N, 05°56′44″ W), collected by Lefébvre; CAMSM X 50108.4, near-complete specimen from uncertain locality in the region of Zagora, Morocco, donated by Catto; BMNH PO 12072, Oued Beni Zoli (30°28′54″ N, 05°52′03″ W), donated by Réboul; BMNH PO 12071, Jbel Tizagzaouine, Zagora (30°31′00″ N, 05°49′37″ W), donated by Réboul.

Type locality: Lower–Middle Arenig, Upper Fezouata Formation, near Zagora, Morocco. The precise locality of the holotype is unknown, but based on lithological similarity and the presence of fragmentary specimens of unusual fossils (probably an undescribed sponge, but more detail is required), it is likely to be from the same area as that of paratype UBGD 20928. Paratype BMNH PO 12072 was recovered from very close to the type locality of *Hamptonia christi* sp. nov.

Description: total height of holotype 34 mm including marginalia, with longest prostalia up to 8 mm long and 0.09 mm diameter. Body tubular, 3 mm wide, with rounded top, and grades into distinct basal structure, described below. The osculum is inconspicuous, and probably very narrow. Prostalia densely arranged over lateral and upper surface, diverging at 60–80° to sponge surface, except towards apex, where they become near-vertical. Prostalia are assumed to be tylostyles, as in other species of *Pirania*, but this could not be confirmed. On one side of the specimen, prostalia are aligned parallel to the body wall, presumably a biostratinomic effect resulting from transport. Lateral prostalia appear to be absent in the basal 5 mm of the sponge body. Tufts of small monaxons occur between prostalia, often oriented in radiating cushions from the surface, rather than being parallel. Gastral surface is an irregular thatch of small monaxons arrayed near-vertically and obliquely, indicating a three-dimensional arrangement of the small monaxons with a broadly diagonal wall-parallel mesh.

The basal region involves a smooth transition zone from the described spicule thatch to a vertical tuft, 7 mm long. The vertical component of the thatch appears to be continuous across the transition, while some of the oblique portion bends downwards to parallel the vertical elements. The remainder of the oblique spicules form a rounded base to the sponge body wall, at the centre of which is a small, confused mass of short spicules that do not appear to extend far into the tuft itself. The tuft is essentially a cylindrical curtain of basalia formed of extended body-wall spicules.

Remarks: *Pirania muricata* is reasonably common in the Burgess shale and Stephen Formations (Rigby and Collins, 2004), but the genus has not been recorded from the Chengjiang faunas or the Sirius Passet fauna. However, two specimens of *P. llanfawrensis* Botting, 2004a, are known from the Caradoc (Upper Ordovician) of Wales, demonstrating a wider distribution. The extension into Morocco further indicates a greater geographical range, and suggests that its rarity is due to preservational factors rather than very restricted occurrence. *P. auraeum* displays what appears to be a more primitive condition than in *P. llanfawrensis*, being similar to *P. muricata* in several respects; the tufts of shorter monaxons interspersed with the prostalial tylostyles, and the rounded apex with

reduced osculum, are both similar to the type species. The basal structure of *P. muricata* is poorly known, but in some cases, it appears to attach to other organisms, indicating some form of rigid or manipulable base. The peculiar basal structure seen here is unique, while *P. llanfawrensis* possessed a simple tuft of radiating fine spicules (Botting, 2004a). It is possible that the wall-parallel spicules, which have not been observed in *P. muricata* or *P. llanfawrensis*, are a primitive feature related to the suggested origin of the group among the hazeliids (Botting, 2003a), which in some cases had monaxons in three orthogonal orientations. If so, then the differences between *P. auraeum* and the type species appear to be substantial; this would imply significant hidden diversity within the distinctive piraniid body-plan.

There is also intriguing similarity of the oblique, axial spicules in *P. auraeum* with the wall-parallel mesh in *Wapkia* Walcott, 1920 (Rigby, 1986; Rigby and Collins, 2004). The tufts of projecting spicules are also similar in arrangement, and could be homologous. The basic form of many Cambro-Ordovician monaxonid demosponges is based on three perpendicular spicule axes, with variable development of one or more axes relative to others. If Botting's (2003a) view that demosponge origins lay within the Hazeliidae is correct, then the development of projecting, radial spicules would have allowed the evolution of several of these apparently more complex sponges, with little fundamental modification. Further piraniid-like sponges from the Ordovician of Wales are currently under investigation by the author.

Order uncertain
Family HAMPTONIIDAE de Laubenfels, 1955
Genus *Hamptonia* Walcott, 1920
Hamptonia christi sp. nov. Fig. 5
Etymology: after Christs's College, Cambridge, which funded the Junior Research Fellowship that allowed this research to take place.

Diagnosis: small *Hamptonia* with slightly elongate ellipsoidal form, small radiating monaxons, and occasional transverse monaxons supporting the structure; deep spongocoel (approximately two-thirds of height) and elongated base, often not clearly distinguished and without external spicule tuft.

Holotype: CAMSM X 50108.1, partial specimen showing skeletal architecture, trace of central cavity, and part of basal region.

Paratypes: CAMSM X 50108.2a–d, four near-complete specimens on a single slab, showing range of morphological features and indication of variability.

Other material: twenty-five complete and partial specimens on the slab (CAMSM X 50108.2) containing the four paratypes.

Type locality: all specimens from a small excavation on the southwest edge of Jbel Tizagzaouine, near Zagora, Morocco (30°31.008′ N, 05°49.623′ W); Upper Tremadoc or Lower Arenig, Upper Fezouata Formation.

Description: small (up to 5 mm tall in observed material), ellipsoidal *Hamptonia* with typical height:width ratio (flattened) of 1.8; observed range from 1.5 to 2.5. Maximum
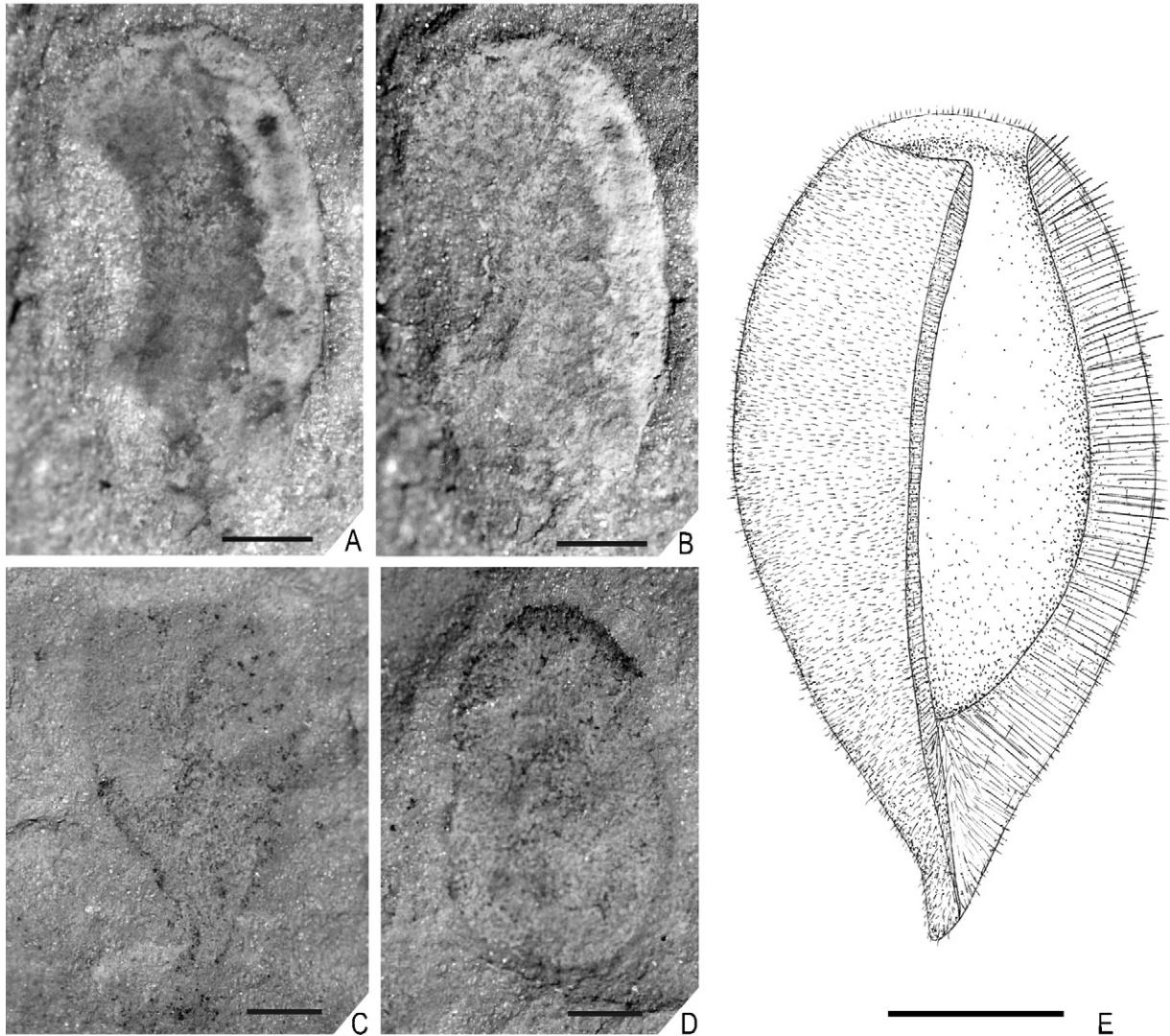
Fig. 5. *Hamptonia christi* sp. nov., from the Upper Fezouata Formation, 20 km north of Zagora, Morocco. **A**, **B**, Holotype CAMSM X 50108.1a, **A**, wet; **B**, dry; **C**, paratype CAMSM X 50108.2a; **D**, paratype CAMSM X 50108.2b; **E**, cut-away reconstruction of *Hamptonia christi* sp. nov. Scale bars 1 mm.
Fig. 5. *Hamptonia christi* sp. nov., de la Formation supérieure de Fezouata, 20 km au nord de Zagora, Maroc. **A**, **B**, Holotype CAMSM X 50108.1a, **A**, spécimen humidifié ; **B**, spécimen sec ; **C**, paratype CAMSM X 50108.2a ; **D**, paratype CAMSM X 50108.2b ; **E**, reconstitution de *Hamptonia christi* sp. nov. Échelle 1 mm.

width usually occurs around mid height, sometimes slightly higher. Walls thick; central cavity one-quarter to one-third of sponge width, but range of variation could not be established. Cavity with smooth, rounded base internally. Top of wall is rounded at the oscular margin, thickness declining over a short distance. Slight annulations of the wall are seen in some specimens, including the holotype, particularly in the lower part. Base either smoothly rounded, or tapered to a relatively sharp point, slightly curved in one paratype. In most specimens, no elongation is visible, perhaps due to variable orientation of compression, so that the base is compressed onto the sponge body.

Skeletal structure is of monaxons only, with individual spicules poorly preserved in iron oxides. The largest measured spicules are 0.3 mm long and approximately 0.02 mm wide; it is likely that some are substantially larger, even with the small body size. In flattened specimens, the spicules radiate from the axis, perpendicular to the body walls. This corresponds in life to a radiating array, with spicules occupying entire thickness of body wall, perpendicular to the sides; it is likely that some spicules are as long as the wall is thick. Many of the spicules projected slightly from the surface, but there are no distinct prostalia. It is not known whether they also project into the central cavity. In the basal region, spicules are small (except axially), densely packed, and sometimes at oblique angles to the tapering surfaces, to accommodate the spicule length within the tissue.

In some specimens, vertical spicules support the structure, either as discrete elements internally or as an inconsistent surface lamina. The presence or absence of transverse spicules could not be determined.

Discussion: the skeletal architecture and body form mostly closely resemble, and cannot be distinguished from, those of *Hamptonia*. However, *H. bowerbanki* Walcott, 1920 has

inosculating spicule arrangement in the upper parts of the sponge and is very much larger, both in body and spicule size (absolute and relative). The spicules are also noticeably more bundled than in *H. christi*. The growth form of *H. elongata* Rigby and Collins, 2004 is radically different from that of *H. bowerbanki* and *H. christi*.

It is difficult to separate *Hamptonia* clearly from the diverse taxa ascribed to the Hazeliidae, which also have a tufted, sometimes largely orthogonal monaxon skeleton. The Hamptoniidae, as defined by Rigby and Collins (2004), includes only *Hamptonia* and *Hamptoniella*. Their spicules tend to be much larger than those of the Hazeliidae, at least in part, and the degree of dominance of the radial spicules over vertical and transverse elements is greater. However, spicule size is notoriously unreliable as a character, and there are some vertical and transverse spicules in *Hamptonia*, so these differences must be imposed on a continuum. The separation of these two families is, therefore, effectively arbitrary as a result of an unusually continuous range of species, and they are almost certainly closely related. For example, Rigby and Collins (2004) report that specimens of *Hazelia* from the Chengjiang (Chen et al., 1997) are probably referable to *Hamptonia*, based largely on the size of the spicules.

Class HEXACTINELLIDA
‘Order’ RETICULOSA?
Family ASTHENOSPONGIIDAE? Botting, 2004a
Genus and species uncertain
Indet. reticulosan Fig. 6

Material: disarticulated, pyritised spicules on slab CAMSM X 50108.2, from a small excavation 10 km northeast of Zagora, Morocco (30°31.008′ N, 05°49.623′ W), associated with *Hamptonia christi* sp. nov. Upper Tremadoc or Lower Arenig.

Description: thin-rayed triactines and hexactine-based spicules with a reduced vertical axis, approximating to pentactine or stauract (only one side of each spicule is visible). Rays are usually curved; in some cases, all are curved towards one pole, as in *Granulispongia obscura* Botting, 2004a, but others have opposing pairs of rays recurved towards opposite
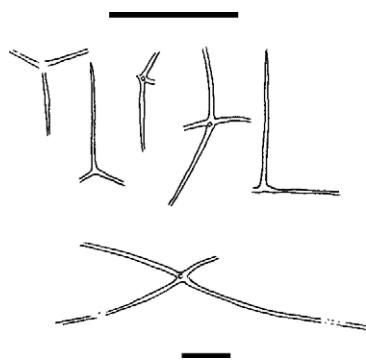

Fig. 6. *Camera lucida* drawings of isolated hexactinellid spicules, possibly from disarticulated asthenospongiids, on slab CAMSM X 50108.2 from the Upper Fezouata Formation, 20 km north of Zagora, Morocco. Scale bar 1 mm. Fig. 6. Dessins à la chambre claire de spicules isolées d'hexactinellidés appartenant peut-être à des asthenospongiidés désarticulés, plaque CAMSM X 50108.2, Formation supérieure de Fezouata, 20 km au nord de Zagora, Maroc. Échelle 1 mm.

poles. Maximum observed ray length 4 mm, with corresponding width 0.08 mm. Triactines are typically triradiate, but there is also T-shaped triactine (tauactine), similarly fine-rayed, and with a slight inflection of the primary axis at the junction with the secondary axis.

Discussion: the unusual curvature of the spicules, and the broad size range, is characteristic of the Asthenospongiidae (Botting, 2004a). However, none so far described also contains tauactines, nor has the precise form with curvature towards two opposing poles been previously recorded. It is possible that the spicules were derived from more than one species, especially given the co-occurrence of triactines, but the rarity of spicules at the locality, and the similar slenderness of the rays suggests that a single species is likely. Dawson and Hinde (1889) reported triradiate spicules occurring among disarticulated spicule associations assigned to their *Hyalostelia metissica*, and although their discussion of affinities is dubious, they do appear to have belonged to a hexaster-bearing hexactinellid. Triactines are not currently known from any asthenospongiid, but their characteristic spicule variety makes such forms plausible. A more detailed discussion of the affinities of this species is currently impossible, but it is significant in being the first record of hexactinellid sponges in the Ordovician of Morocco.

3. Distribution of ‘Cambrian’ sponge taxa

With the recognition of Arenig choiid and hamptoniid sponges, and the geographical range extension of piraniids, the most distinctive elements of the Burgess shale-type fauna sponges are now becoming widely known from later deposits, and a summary is appropriate (Fig. 7). Although the Ordovician–Silurian record of spicular sponges is still sparse, many Cambrian lineages are now known from a broad range of times and locations. The eiffeliid heteractinids *Zangerlispongia* (Rigby and Nitecki, 1975), *Gondekia* (Rigby, 1991) and *Toquimella* (Rigby, 1967) were described from the Late Carboniferous of Illinois, the Devonian of New York and Ontario, and the Arenig of Utah, respectively, and isolated spicules indistinguishable from *Eiffellia* occur widely, but rarely, in Ordovician siliciclastics of the Builth Inlier of central Wales (e.g., Botting, 2004a, and pers. obs.). Reticulosan hexactinellids assigned to *Protospongia* are widespread in the Lower Palaeozoic, although *Protospongia* s.s. is probably restricted to the Cambrian, and perhaps Tremadoc; similar taxa are known from Little Metis (Dawson and Hinde, 1889), but most of these also are probably not true *Protospongia* s.s., and the age of the deposit is still uncertain. Among the early demosponges, Botting (2004a) described the hazeliid *Xylochos palindromica* from the Caradoc of Wales. Although not otherwise known outside the Cambrian, the Hazeliidae was widely dispersed during that time, with the Lower Cambrian *Saetospongia* Steiner et al., 1993, showing a plumose-reticulate pattern characteristic of the group. Reitner and Wörheide (2002) mentioned similar undescribed species from the Lower Cambrian Sirius Passet fauna, making this group present in all regions from which appropriate preservation of Cambrian sponge faunas is know. *Vauxia* Walcott, 1920 is believed to be
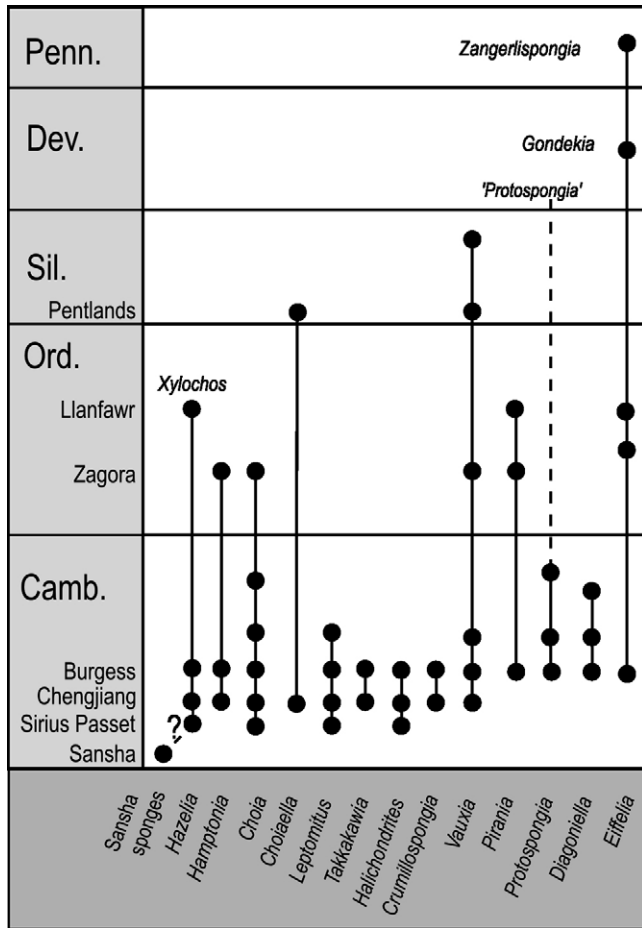
Fig. 7. Summary of the known temporal ranges of the most characteristic Cambrian sponges. Occurrence data for Llanfawr from Botting (2004a), and for the Pentlands from Botting (2007). There is no evidence for elevated extinction during the Late Cambrian–Early Ordovician interval.

Fig. 7. Résumé de la distribution stratigraphique des différentes lignées d'éponges du Cambrien. Données pour Llanfawr d'après Botting (2004a), et des Pentlands d'après Botting (in press). Il n'y a pas de preuves de l'extinction élevée dans l'intervalle Cambrien supérieur–Ordovicien inférieur.

either a verongiid (Reitner and Wörheide, 2002; Rigby, 1986) or possibly an early lithistid (Rigby, 1980), while Botting (2005) considered possible links to the Callyspongiidae. It is still unclear whether their preserved skeleton was spicular or organic, but the skeletal structure is distinctive, and small, simple vauxiids are present in the Silurian of Scotland (Botting, 2007), and the Welsh Borders (under study by the author). Of the major (i.e. abundant and reasonably diverse) groups of Cambrian spicular sponges, only the Leptomitidae are yet to be recorded above the Cambrian. Several rarer and mostly monospecific genera, such as *Takakkawia*, *Crumillospongia* and *Wapkia*, all of which are recorded from both the Burgess shale and Chengjiang, have no record beyond these deposits. There are also a significant number of sponges, such as *Hintzespongia*, *Valospongia* and *Ratcliffespongia*, which are not present in the Burgess shale, but occur in one or more Cambrian localities of North America. Similarly, the majority of the Lower Cambrian Sansha (Steiner et al., 1993) and Hetang (Yuan et al., 2002) sponges are not known outside those

localities, although the presence of *Saetaspongia*-like forms in Greenland (Reitner and Wörheide, 2002) suggests that at least some of these taxa were widely distributed.

The concept of a distinctive Cambrian sponge fauna is supported by the increasing occurrence of very characteristic taxa in widely distributed localities, but its restriction to the Cambrian is now known to be incorrect. There is no longer any indication of a major sponge turnover event in the Late Cambrian or basal Ordovician. The patterns can be regarded instead as the gradual replacement of early taxa by more derived groups, particularly of hexactinellids, as is seen in many organisms at that time. The appearance of a sharp termination to Cambrian sponge lineages has been greatly exaggerated by the widespread distribution of many familiar Cambrian taxa, and the rarity of suitable preservation thereafter. The environmental distributions of early sponge taxa are also likely to have played a critical role in biasing the observed patterns.

4. Ecological transitions in Lower Palaeozoic sponges

In addition to the apparent rarity of 'Cambrian' sponges in later deposits, which may be misleading, there is a contrast in the much higher endemicity and overall diversity of post-Cambrian sponge faunas, particularly of hexactinellids. It is not yet clear whether these are primarily taphonomic biases or real ecological patterns, but the discovery of occasional Ordovician and Silurian assemblages from nearshore environments (e.g., Botting, 2005; 2007) suggests that many additional species probably existed in turbulent, inshore facies at this time. There is no evidence of similar faunas in coarse, shallow-water Cambrian siliciclastics, although there appear to be sponges in some shallow-water Ediacaran sandstones (Reitner and Wörheide, 2002). Hexactinellid spicules have also been recorded in relatively shallow, Early Cambrian deposits, and complete specimens from inshore but quiet-water deposits of the Chengjiang biota, with faunal differences between these assemblages discussed by Wu et al. (2005); all are thin-walled species, in contrast to taxa from coarse Ordovician sandstones. Although it can be argued that sponges diversified from shallow to deep water, based on the Ediacaran and Early Cambrian records (Wu et al., 2005), this is based on the stratigraphic appearance of taxa in a very incomplete early record. The shallow-water sponges seen in the Ediacaran assemblages are either awaiting full description, or possess very unusual characteristics (*Palaeophragmodictya* Gehling and Rigby, 1996). Instead, there are clear trends showing the reverse among later Cambro-Ordovician faunas (Botting, 2004a, 2005), and the environment inhabited by the earliest sponges remains in question. What direct evidence there is for the morphology of the earliest hexactinellids and heteractinids (Botting and Butterfield, 2005) implies a thin-walled construction that is consistent with an offshore origin.

In Ordovician offshore sediments, sponge spicules are often extremely abundant, but the described record is minimal due to the rarity of articulated remains and the lack of specialists to study them. This is particularly true of non-lithistid demos-

ponges, which are only minor components of faunas from facies with the best preservation potential. However, we now recognise that many described Cambrian demosponge lineages continued for a considerable time in offshore environments. This longevity of these early lineages may be a result of the sedimentological and perhaps ecological continuity of fine-sediment facies through the Lower Palaeozoic, combined with very wide dispersal of the earliest, Lower Cambrian groups. During subsequent faunal diversifications, these lineages could then persist in some geographical regions, despite becoming locally extinct elsewhere.

It is tempting to suggest that the presumably Early Cambrian dispersal of the most familiar Cambrian lineages was through a biosphere that lacked diverse sponge communities. The high endemism and patchiness of Ordovician faunas (e.g., Botting, 2004a, 2005) illustrates distribution patterns more typical of recent biotas (e.g., van Soest, 1994). In contrast, the global Early Cambrian homogeneity strongly suggests that these sponges encountered little or no ecological competition during their early expansion, implying that such sponges were essentially absent from shelf environments prior to their rapid Early Cambrian expansion. Although it is possible that they had already diversified in very inshore facies, as suggested by the ambiguous but somewhat dictyosponge-like *Palaeophragmo-dictya* (Ediacaran; Gehling and Rigby, 1996), and a report of Ediacaran demosponges from Namibia and the White Sea (Reitner and Wörheide, 2002), the homogeneous Cambrian distribution suggests either extinction of these earlier forms around the Precambrian-Cambrian boundary, or that the lineages continued, currently unrecognised, in inshore settings. Whatever caused the apparent Precambrian–Cambrian discontinuity in sponges, the 'Cambrian Explosion' was for the Porifera a real phenomenon, at least in offshore shelf settings, involving the sudden diversification of non-lithistid spicular taxa.

The skeletal morphology of most known early Palaeozoic spicular sponges was too fragile for colonising high-turbulence environments. The rarity of more robust taxa with unfused and non-lithistid skeletons in the fossil record could potentially be due to shallow-water forms remaining undescribed due to their low preservation potential in very turbulent environments. Trends towards a stronger skeleton are the dominant feature of the Lower Palaeozoic hexactinellid evolution (Botting, 2004a), involving the inshore migration of various lineages as thicker-walled morphologies arose. Hexactinellid genera appear to have evolved more rapidly than demosponges in the Late Cambrian-Ordovician interval, leading to multiple strongly endemic assemblages, and few obvious genus-level links across the period boundary. Their dominance in most deeper-water facies is not likely to be a preservational artefact; where demosponges are preserved, specimens are often more complete than associated hexactinellids (Botting, 2004a and undescribed material), reflecting the more coherent skeleton of most early demosponge groups, and perhaps more supportive soft tissue. In shallow-water facies, however, there does appear to have been a significant preservational contrast between hexactinellids and demosponges. By the middle Ordovician,

all the major groups of Palaeozoic hexactinellids had appeared, including brachiospongiids and dictyosponges, whereas nearshore non-lithistid demosponges are presently limited to a single silicified fauna (Botting, 2005). With the exception of the near-rigid dictyosponges, the Ordovician nearshore hexactinellids developed thick walls and large spicules. Hexactinellids were also successful in shallow water environments during the remainder of the Palaeozoic (discussed by Mehl, 1996; Mehl-Janussen, 1999), and developed several variations on rigid skeletal structures, eventually including fused skeletons.

Reticulosan hexactinellids also begin to dominate deep-water environments during the early Ordovician, with the decline of Burgess shale-type demosponges. At some point in the early Palaeozoic, or possibly before, hexactinellids evolved the syncytiality that is such a successful habit in modern deep-water habitats; it is now broadly agreed that syncytiality is a derived trait (Boury-Esnault et al., 1999; Leys, 2003). Although we cannot infer with any certainty a connection between the success of reticulosans and unpreservable physiological innovations, the possibility should be considered as a potential element in a wider understanding of sponge evolution.

In contrast to the hexactinellids, the limited data on nearshore, Palaeozoic, non-lithistid demosponges (Botting, 2005) suggest that they evolved more towards varied or plastic morphology and incorporation of clastic particles, rather than rigid skeletons, a novelty perhaps allowed by the loss of a regular skeletal grid that had previously constrained their growth (Botting, 2003a, 2003b). Many of these taxa would be difficult to identify as sponges under most preservational styles and require exceptional conditions to be taxonomically describable. In the present day, this morphological flexibility has proven more successful in nearshore environments (shallow-water hexactinellids are currently limited to a single cave-dwelling species in the Mediterranean; Vacelet et al., 1994), but it is unclear at what time the non-lithistid demosponges became dominant. Their presence in the Llanvirn, along with several more abundant 'demosponge-like' hexactinellids (Botting, 2005), suggests that they became dominant during the Middle–Upper Ordovician or later. Although rare in the fossil record, there are a small number of described monaxonid demosponges from various horizons in the Ordovician (summarised by Carrera and Rigby, 2004) and in the Silurian (Llandovery and Ludlow; Botting, 2007, and pers. obs.) shelf sediments of Scotland and England. In the Silurian examples, the fauna contains a mix of demosponges and hexactinellids, with the hexactinellids being primarily represented by rather specialised forms in the Scottish fauna (e.g., *Amphispongia* Botting, 2004b). These faunas, which lack the dominant large hexactinellids of Middle Ordovician assemblages, imply significant demosponge diversification during the Late Ordovician, or across the Ordovician–Silurian boundary. This therefore, appears to have been a critical period during the evolution of non-lithistid demosponges in inshore areas, although it is unclear what role the end-Ordovician extinction played in their development. The discovery of Late Ordovician and Early Silurian faunas, particularly from inshore

settings, is vital for more detailed investigations of this transition.

The Upper Cambrian–Lower Ordovician transition from the demosponge-dominated Burgess shale-type assemblages to reticulosan-dominated faunas in offshore sediments, and lithistids in nearshore facies, was perhaps the most critical episode in sponge evolutionary ecology. The cause of the Cambro-Ordovician revolution in non-lithistid sponge ecology must be presumed to be a fundamental shift in the ecological preferences of the hexactinellids and demosponges. The most fundamental innovative characteristics of the classes are
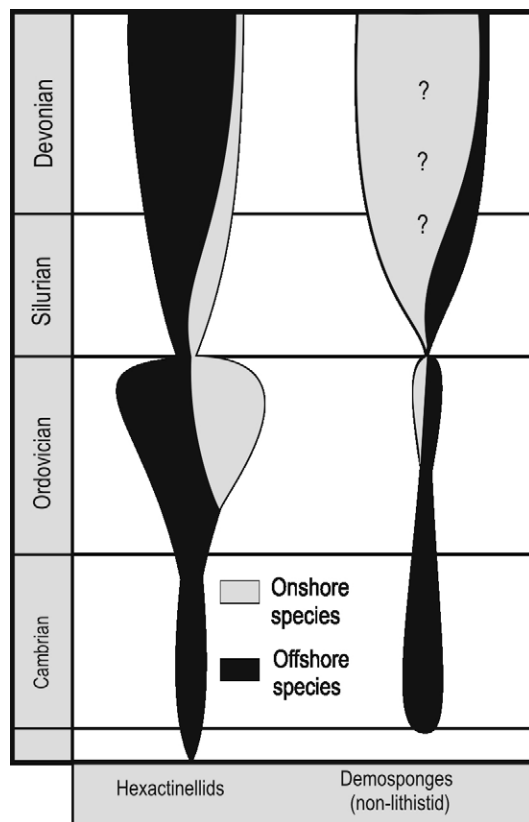

Fig. 8. Schematic comparison of the diversification of hexactinellids and non-lithistid demosponges during the Early Palaeozoic, allowing for taphonomic biases and limited data. Each groups is characterised by onshore expansion, particularly during the Ordovician and Silurian, respectively. Hexactinellids adapted to more turbulent conditions through stronger spicule skeletons, and non-lithistid demosponges by morphological plasticity and organic matrix. These differences produce a strong taphonomic bias towards preservation of hexactinellids in later Palaeozoic inshore environments. Offshore faunas were hexactinellid-dominated by the Silurian, suggesting that their physiological specialisations had evolved by this time (see text, Section 4).

Fig. 8. Comparaison schématique de la diversification des hexactinellidés et des démosponges non-lithistidés pendant le Paléozoïque inférieur, prenant en compte le biais taphonomique et le nombre limité de données. Les deux groupes sont caractérisés par une expansion vers des milieux plus littoraux. Les hexactinellidés se sont adaptés à des conditions plus turbulentes grâce à l'acquisition d'un squelette formé par des spicules plus fortes ; les démosponges non-lithisdités ont développé dans le Silurien, une plasticité morphologique et une matrice organique. Les différences ont produits un fort biais taphonomique favorisant la préservation d'hexactinellidés dans des environnements peu profonds plus tard au cours du Paléozoïque. Les faunes de mer profonde étaient dominées par les hexactinellidés au Silurien, suggérant que leurs spécialisations physiologiques étaient déjà présentes à cette époque.

syncytiality in hexactinellids and morphological plasticity in demosponges. We can observe the latter in the fossil record during the Ordovician–Silurian, but the former must be inferred from ecological observations, so far as is possible. The Cambro-Ordovician shift towards hexactinellids in offshore facies is suggestive of the development of syncytial physiology, although no direct evidence is available. This is particularly likely given that the Burgess shale fauna hexactinellid lineages do not extend far beyond the Cambrian (Fig. 7), unlike many of the demosponges and heteractinids, and those coming to prominence during the Ordovician involve novel morphologies. The earliest hexactinellids, therefore, seem to have been at a disadvantage relative to the newly-evolved Ordovician faunas, despite occurring in the same broad, offshore environments.

In conclusion, observed changes in ecological structure and environmental distribution (Fig. 8) can be used to constrain and educate hypotheses of sponge evolution, perhaps including physiological innovations. Ultimately this could lead to significant insights into early sponge phylogeny, as the distribution of features (e.g., syncytiality) among modern taxa can be compared with the geological distributions of those groups and observed changes in palaeoecology that suggest the presence of these features. Although of less practical utility than molecular and traditional phylogenetic approaches, palaeoecological transitions have the ability to independently constrain hypotheses arising from these other techniques, and have the benefit that significant ecological shifts should be visible without the need for specific, critical taxa being preserved.

Acknowledgements

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