First post-Cambrian records of the reticulosan sponges *Valospongia* and *Hintzespongia* from the late Tremadocian of North Wales

JOSEPH P. BOTTING and LUCY A. MUIR

Botting, J.P. and Muir, L.A. 2014. First post-Cambrian records of the reticulosan sponges *Valospongia* and *Hintzespongia* from the late Tremadocian of North Wales. *Acta Palaeontologica Polonica* 59 (1): 241–252.

A new sponge fauna has been discovered in silty mudstone of the early Migneintian (late Tremadocian, Ordovician) of North Wales. The assemblage is dominated by reticulosan hexactinellids, including several species bearing parietal gaps; this feature is common among Cambrian hexactinellids, but is rare in Ordovician faunas. Of particular significance is *Valospongia bufo* sp. nov., representing the first record of the genus outside the Middle Cambrian of Utah, USA. A single specimen assigned to *Hintzespongia*? sp. is also described, and also represents the first occurrence outside the Laurentian Burgess Shale-type faunas. This fauna indicates that deeper-water hexactinellids from the Burgess Shale-type faunas survived in places into at least the Early Ordovician, in addition to the Cambrian-type protomonaxonid assemblage seen in the Fezouata Biota.

Key words: Reticulosa, Porifera, Silicea, exceptional preservation, Gwynedd, Migneintian, Tremadoc, Cambrian, North Wales, UK.

Joseph P. Botting [acutipuerilis@yahoo.co.uk] and Lucy A. Muir [lucy@asoldasthehills.org], State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China.

Received 6 February 2012, accepted 10 September 2012, available online 24 September 2012.

Introduction

Early Ordovician non-lithistid sponges are extremely poorly known, with very few described taxa. Isolated fragments and partial specimens of protospongioids are widely known from the Tremadocian (Owens et al. 1982; Esteban and Rigby 1998), but few describable taxa have been reported. The only diverse assemblages to date are those from Little Métis, Quebec (Dawson 1896; Dawson and Hinde 1889), which is of uncertain age within the late Cambrian–Early Ordovician interval (interpreted as Late Cambrian by Finks and Rigby 2004b but as Late Tremadocian by Carrera and Rigby 2004), and the Tremadocian–Floian Fezouata Biota of Morocco (Botting 2007a; Van Roy et al. 2010), which is currently under study. The Little Métis fauna includes a range of both simple and more complex reticulosan hexactinellids, many originally assigned to *Protospongia*; the fauna has not, however, been restudied since the original description, and is in need of revision. Several additional species from Little Métis represent other groups, such as the two rather disparate species assigned to *Lasiothrix* Hinde in Dawson and Hinde, 1889, which was interpreted by Finks and Rigby (2004a) as a hamptoniid protomonaxonid, albeit a somewhat aberrant one. Hamptoniids are also common in the Fezouata Biota (Botting 2007a), which is dominated by protomonaxonids (including choiids and piraniids) rather than reticulosan hexactinellids.

The Protomonaxonida Finks and Rigby, 2004a are an enigmatic group of uncertain phyletic status and relationships (Debrenne and Reitner 2001; Botting 2003), which appeared in the early Cambrian (Xiao et al. 2005) and came to dominate the shallower-water Burgess Shale-type assemblages (Rigby 1986; Rigby and Hou 1995; Yang et al. 2003; Rigby and Collins 2004) in the late early and middle Cambrian. The group then appears to have largely become extinct (Carrera and Botting 2008), with the exception of the Fezouata Biota assemblage, and the choiids (Botting 2007b; Beresi et al. 2010) and piraniids (Botting 2004). Other groups of monaxon-bearing sponges, mostly derived from thick-walled hexactinellid lineages, arose to dominate some near-shore siliciclastic habitats by at least the Middle Ordovician (Botting 2005), but these appear to be unrelated groups.

Deeper-water communities from the Middle Cambrian Wheeler Formation (Rigby 1978; Rigby et al. 2010) and

Marjum Formation (Rigby 1969, 1983) host a combination of protomonaxonids (especially choiids) and a high proportion of reticulosan hexactinellids. Many of the reticulosans possessed semi-regular skeletons with parietal gaps (e.g., *Ratcliffespongia*, *Stephenospongia*), clearly bilaminar walls (*Hintzespongia*) or complex walls with both multiple layers and pronounced mounds (*Valospongia*). Some of these taxa also occur as rare specimens in the protomonaxonid-dominated Burgess Shale fauna (Rigby and Collins 2004).

Ordovician hexactinellid faunas from offshore settings often consist only of somewhat derived morphologies following a basic reticulosan architecture, or a combination of morphologically derived taxa with very simple Cambrian-like protospongioids such as *Heminectere* (Botting 2004; Botting and Muir 2011). The derived features include hypertrophied or highly modified spicules (e.g., *Asthenospongia* Rigby, King, and Gunther, 1981), or strengthening structures produced by modified (e.g., overlapping or tractose) spicule arrangement (e.g., *Plectoderma* Hinde, 1883; *Cyathophycus* as discussed by Botting 2003, 2004). There are very few examples of the reticulosan groups that are characteristic of the Middle Cambrian hexactinellid faunas, with only rare examples with weak parietal gaps such as *Hemidiagoniella caseus* Botting, 2004, and some species assigned to *Cyathophycus* (Rigby and Chatterton 1994).

Because there are very few records of Late Cambrian and Early Ordovician non-lithistid sponges, we do not currently know when the protomonaxonids declined, or when the hexactinellid faunas changed from typically Cambrian groups to taxa typical of the Middle and Late Ordovician. Further Early Ordovician faunas are crucial for understanding this transition, and perhaps for relating the changes to the Great Ordovician Biodiversification Event. This paper describes the first species from a new Tremadocian sponge fauna from North Wales, UK, and shows that at least some hexactinellid elements of the Burgess Shale-type fauna survived into the Early Ordovician.

Institutional abbreviations.—NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China.

Geological setting

The historical type Arenig in North Wales was defined on the rocks exposed on and around the mountains of Arenig Fawr and Moel Llyfnant (Sedgwick 1852). The stage was originally defined to include what is now the entire Floian, Dapingian, and Darriwilian, but this was eventually reduced (Williams et al. 1972), before being replaced by globally recognised units. The succession exposed in the Arenig Fawr area was described in detail by Fearnsides (1905), and revised by Zalasiewicz (1984), who recognised the Tremadoc succession as correlated with the upper part of the Afon Gam Formation of Lynas (1973), defined in the nearby Migneint area. This formation corresponded to the *Niobe* Beds, *Dictyonema* Band, Nant-ddu (or *Bellerophon*) Beds, Tai-Herion Flags and Amnodd Shales of Fearnsides (1905), which together constitute the lower part of the Tremadoc (Rushton and Fortey 2000). The Afon Gam Formation has now been equated with the Dol-cyn-afon Formation of Snowdonia (Rushton and Howells 1998; Rushton and Fortey 2000), which itself is roughly contemporaneous with the Shineton Shales Formation of the Welsh Borderland (Rushton and Fortey 2000). The material described here is from the Amnodd Shales of Fearnsides (1905) (Fig. 1), which is assigned to the *Conophrys salopiensis* Biozone of the early Migneintian (late Tremadocian) (Rushton and Fortey 2000).

The lithology of the studied beds is primarily hardened blue-grey mudstone with silty and sandy partings and thin siltstone beds throughout. Bedding is pronounced throughout the Ceunant-y-garreg-ddu section (Fig. 2), with discrete bedding surfaces weathering out at typically 10–50 cm intervals. The fauna from these beds has been previously described as dominated by trilobites (Zalasiewicz 1984) with a

Stage		Biozone	Fearnsides 1905	Zalasiewicz 1984		Rushton and Fortey 2000	
Floian	Moridunian	*Tetragraptus phyllograptoides*	Basal Grit Member	Carnedd Iago Formation	Garth Grit Member	Carnedd Iago Formation	Garth Grit Member
Tremadocian	Migneintian	*Araneograptus murrayi*					
		Angelina sedgwickii					
		Conophrys salopiensis	Amnodd or *Shumardia* Shales	Afon Gam Formation		Dol-cyn-afon Formation	★Amnodd Shales
			Tai-Herion or *Asaphellus* Flags		middle siltstone member		Tai-hirion Flags
	Cressagian	*Adelograptus tenellus*	Nant-ddu or *Bellerophon* Beds				Nant-ddu Beds

Fig. 1. Stratigraphy of the study area, showing correlation of traditional and current lithostratigraphy, and correlation with trilobite and graptolite biozones, regional stages and global stages (at left). Fossiliferous localities are within the Amnodd Shales. The star shows the approximate position of the study localities.

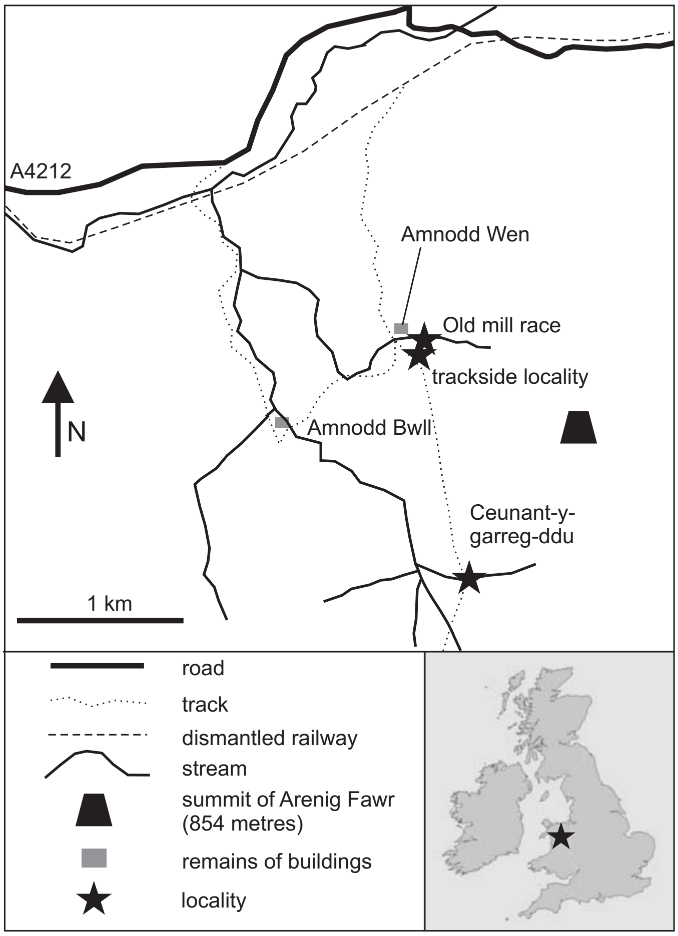


Fig. 2. Locality map showing the positions of the study sites within the local area, west of Arenig Fawr. Ceunant-y-garreg-ddu location marks the base of an extensive section through the upper part of the formation. Inset map shows the position of the localities within the UK.

few other skeletal fossils, notably brachiopods, tergomyans, hyoliths, and the cystoid *Macrocystella* (Fearnsides 1905; Zalasiewicz 1984). Following reports of articulated sponges from Richard. A. Fortey (personal communication 2006), we have recovered a diverse and abundant sponge fauna, which at some levels comprises the most abundant fossil group. The new species described here is the most common in the initial collections, although there are several other hexactinellid-like species, as well as protomonaxonids resembling *Choia* and *Hazelia* (Fig. 3); these will be described in future, when additional material is available.

The environment of deposition is currently unclear. The preserved biota includes some well-preserved non-calcareous algae in addition to a diverse benthic marine community. Frequent torn but articulated sponges indicate brief, violent transport. This conforms with the presence of variable but clearly defined beds with silty and gritty laminae, suggesting a series of transported, perhaps slumped or storm-reworked deposits. The region was volcanically active, although the nearest roughly contemporaneous activity was probably at Rhobell Fawr (Kokelaar 1986), about 10 km from the Arenig area. Volcanic arcs tend to show high sea-floor gradients, and this could explain the repeated abrupt sediment transport.

During the latest Tremadocian and earliest Floian, Avalonia was at high latitude, between 30° and 60° south, with the portion that became Wales being at about 60° south (Fortey and Cocks 2003; Cocks and Torsvik 2004), having broken off from Gondwana around the end of the Cambrian (Fortey and Cocks 2003). This fauna therefore represents a high latitude fauna, nearly comparable with that of the Fezouata Biota, although the latter was nearer to the South Pole (Fortey and Cocks 2003; Cocks and Torsvik 2004).

Material and methods

Material was collected from several locations within the Ceunant-y-garreg-ddu natural stream section on the southwest slopes of Arenig Fawr (Fearnsides 1905; Zalasiewicz 1984, grid reference for base of section National Grid SH 82103600). There are numerous extensive exposures along this stream, but placing beds onto an accurate measured section is impossible due to complex faulting and local deformation; approximate stratigraphic positions based on the left bank exposures are possible for the lower part of the section. Additional loose blocks containing sponges were collected from local glacial drift along the side of the path running north from there to Amnodd Wen (grid reference National Grid SH 81653735), and also from probably locally derived blocks opposite the disused mill-race immediately south of the ruin of Amnodd Wen (Fig. 2, grid reference National Grid SH 81653747). The exact stratigraphic relationships within the succession are unclear, as exposure is very limited between the stream sections, and regional deformation and igneous intrusions have resulted in local faulting.

The sponges from the Dol-cyn-Afon Formation are composed of a combination of reflective films (probably aluminosilicate) with localised pyrite-like sulphides, usually weathered into black or orange iron oxide minerals. Preparation of the material is difficult, as low-level metamorphism has resulted in aluminosilicate recrystallisation throughout the matrix, eliminating planes of easy fracture through the fossils. As a result, specimens often split partially over the fossil, but through the less strongly mineralised areas.

Specimens typically show almost no contrast when dry, and are very difficult to see in the field unless surfaces of split slabs are wetted. The specimens are not susceptible to fragmentation with water, and have already been altered to a sufficient degree that further degradatory oxidation of the material is unlikely. Whole-specimen photographs were taken with the specimens under water, using a Nikon D80 digital SLR camera on a standard lens, and combination of external flash with low angle fibre-optic illumination. Detail photographs were taken with a Canon Eos60D attached to a Leica M125 stereomicroscope.

Systematic palaeontology

Phylum Porifera Grant, 1836

Class Hexactinellida? Schmidt, 1870

Discussion.—Although traditionally classed as hexactinellids, the relationships of many Cambrian–Ordovician hexactine-bearing sponges are now recognised to be unclear, and they may instead represent stem-group hexactinellids or stem-group siliceans. The common ancestor of Silicea + Calcarea is likely to have had hexactinellid-like spicules (Botting and Butterfield 2005), and so it is potentially difficult to distinguish true hexactinellids from basal and stem-group sponges. A full discussion of this is beyond the scope of the paper, but we draw attention to the uncertainty as a matter of accuracy.

Family uncertain

Remarks.—The higher-level classification of complex reticulosans has not yet been fully established. Although several superfamilies and families have been erected (see Finks and Rigby 2004b), these relate only to a few structurally distinct architectures, but even these as currently defined are inconsistent. *Valospongia* was classified by Rigby et al. (2010) as a hydnodictyid dierespongioid. The Hydnodictyidae were defined (Finks and Rigby 2004b) as possessing two non-aligned layers of hexactine-based spicules, each organised in parallel arrays. Their diagnosis of the Dierespongioidea expresses similar concepts, but excludes taxa bearing parietal gaps. Not only are such gaps present in the inner layer of *Valospongia*, but the prominent protuberances are not seen in other taxa in the family. It is also unclear whether the simple presence or absence of multiple skeletal layers with a degree of regularity is sufficient to define groupings on this level, and to what extent it is convergent. We therefore leave the genus in uncertain familial and superfamilial taxonomic position pending a better understanding of early complex reticulosans.

Genus *Valospongia* Rigby, 1983

Type species: *Valospongia gigantis* Rigby, 1983, from the lower part of the middle Cambrian Marjum Formation of Utah, USA.

Species included: *Valospongia gigantis* Rigby, 1983; *Valospongia bufo* sp. nov.

Emended diagnosis.—Barrel-shaped to vasiform sponges with a complex skeleton composed of at least two layers; continuous inner layer or layers of semi-quadruled, semi-regular hexactines or their derivatives combining to form orthogonal and diagonal elements, and outer layer of similar spicules that is extended into prominent tubercles covered by a fine reticulation, which may or may not be spicular; prominent spicular strands developed in some species.

Remrks.—*Valospongia* is a complex sponge (see diagnosis of Finks and Rigby 2004b), with several apparently unique features, and the diagnosis has been reclarified here in light of the new material. It is unclear whether the two inner layers recognised by Finks and Rigby (2004b) are separate, or whether they form one layer with combined orthogonal and diagonal elements; the two series sometimes do appear distinct, however, and are treated as such here. The nature of the skeletal strands emphasized by Finks and Rigby (2004b) is unclear, but they may represent fusion or close overlapping of elongated spicule rays. The apparent parietal gaps are seen in the new material to reflect abrupt curvature of the wall into the mounds, which appear to be covered by a reticulate meshwork of small hexactine-based spicules in irregular arrangement, but it is possible instead that it represents soft tissues replaced by pyrite (or soft tissues supported by microscleres). The arrangement in these meshworks is not orthogonal, and the lines are irregular and perhaps curved, suggesting a non-spicular origin; it is possible that they were composed of similar material to that of *Vauxia* (e.g., Rigby 1986).

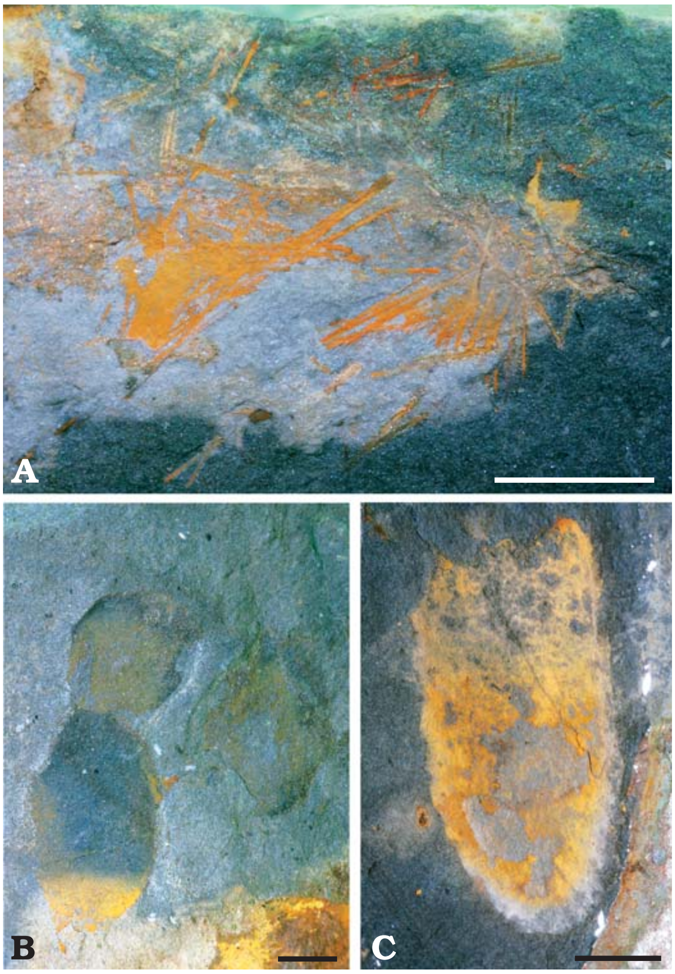


Fig. 3. Examples of undescribed sponges from the Dol-cyn-Afon Formation (early Migneintian, upper Tremadocian, Lower Ordovician), Arenig Fawr. **A**. NIGP 154639, indeterminate choiid, disarticulating, from Ceunant-y-garreg-ddu. **B**. NIGP 154640, three specimens of a *Hazelia*-like sponge, from Amnodd Wen. **C**. NIGP154641, undescribed reticulosan from Amnodd Wen. Scale bars 5 mm. All photographs taken under water.

Despite superficial similarity in appearance of the sponge, there is certainly no dermal quadruled grid as seen in *Hintzespongia* and allies; however, neither is there any obvious reason to assign the genus to the Hydnodictyidae (cf. Finks and Rigby 2004b), representatives of which appear to have possessed neither the multiple layers of *Valospongia*, nor the meshwork-covered mounds. For these reasons, we prefer to leave the family-level assignment of *Valospongia* open. We include the new species within *Valospongia*, as although it does not appear to possess the skeletal strands of *V. gigantis* Rigby, 1983, the remaining structure conforms closely to the type material.

Stratigraphic and geographic range.—Currently confirmed only from the middle Cambrian of Utah,USA and the Early Ordovician of Wales, UK.

Valospongia bufo sp. nov.

Fig. 4.

Etymology: From Latin *bufo*, toad, in appreciation of the pronounced wart-like mounds all over the dermal surface.

Type material: Holotype: NIGP154629 a near-complete specimen showing both skeletal layers. Paratypes: 8 specimens, NIGP154630 to NIGP154637. NIGP154630 a partial, three-dimensional specimen showing outer layer and poorly preserved spiculation from inner layer in some areas; from loose but local block at Amnodd Wen; NIGP154631, a near-complete but weathered specimen found as a loose block beside the track near Amnodd Wen, 100 m up the track towards Ceunant-y-garreg-ddu; NIGP 154632, a partial specimen from Ceunant-y-garreg-ddu approximately 39 m stratigraphically up in the section from where the stream crosses the path; NIGP154633, a small mesh fragment mostly preserving parietal outer layer, and weak spicule preservation from Ceunant-y-garreg-ddu, approximately 18 m stratigraphically up in the section from where the stream crosses the path; NIGP154634, three partial specimens on a loose block from Ceunant-y-garreg-ddu, including profile of margin with protruding mounds; NIGP154635, loose block with two partial specimens, from Ceunant-y-garreg-ddu; NIGP154636, loose block with three partial specimens, from Ceunant-y-garreg-ddu; NIGP154637, near-complete specimen with three-dimensional preservation of the skeletal mesh but weak spicule preservation, from loose but local block at Amnodd Wen; age for all specimens as for holotype.

Type locality: Ceunant-y-garreg-ddu stream section, found as a loose block below outcrops 40 m stratigraphically above the point where it crossed the track (SH 82103600).

Type horizon: Late Tremadocian (early Migneintian).

Diagnosis.—Relatively small *Valospongia* without obvious skeletal strands; walls between parietal gaps in outer layer narrow (less than half diameter of gaps); inner layer(s) of orthogonal and diagonal reticulation densely arranged and sub-regularly quadruled; spicules small relative to parietal gap size.

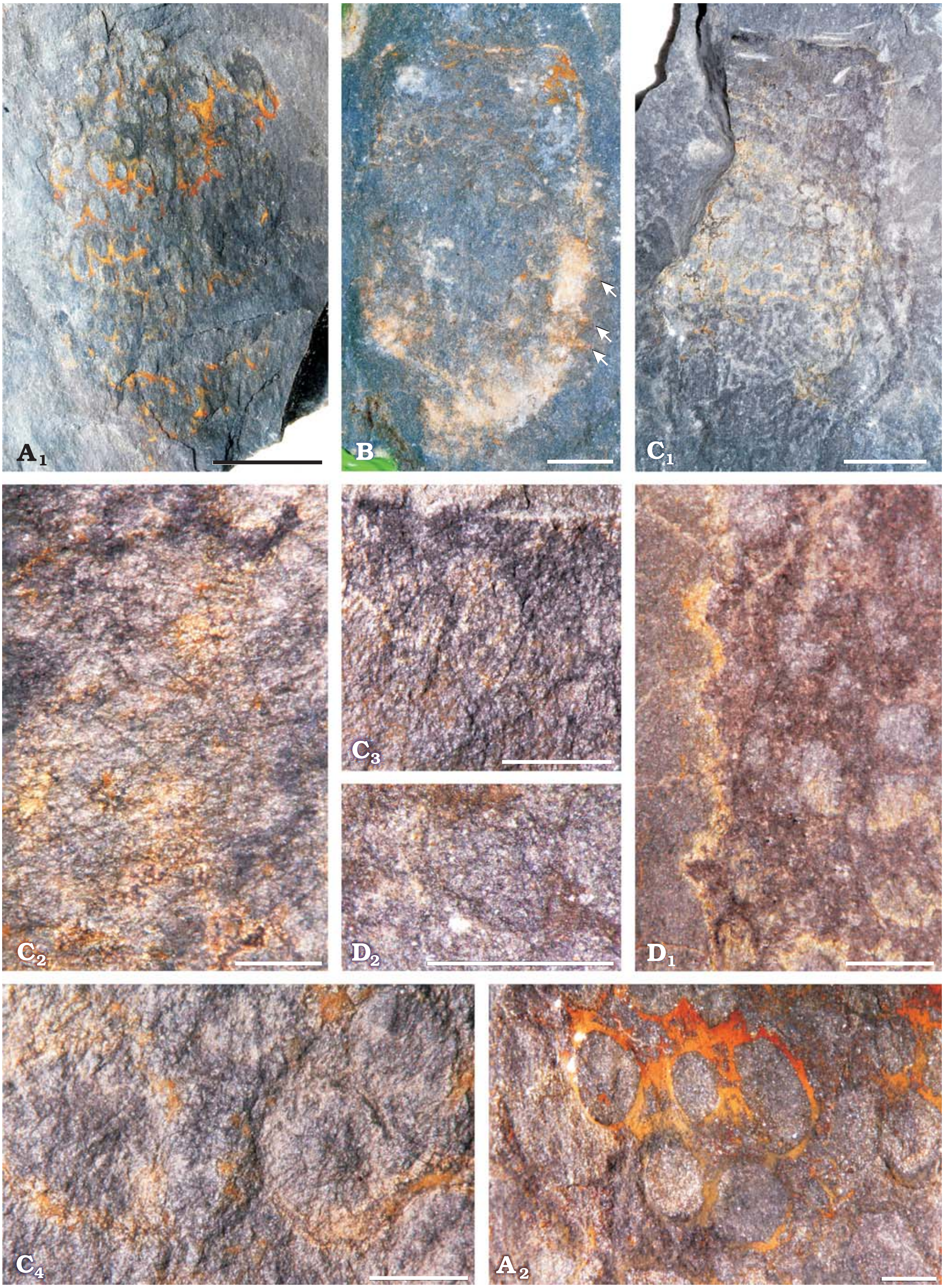
Description.—Rounded, roughly barrel-shaped sponge body (Fig. 4A_1, B, C_1). Holotype (Fig. 4C) 31 mm wide and over 40 mm tall (estimated height c. 45 mm), with other specimens of comparable size. Base broadly rounded. Oscular margin is flat, nearly as wide as widest point of sponge, and slightly irregular. Appearently no distinct marginalia, but very short (0.3–0.4 mm) spicule rays project subvertically from the edge. Weakly-preserved, slightly longer (less than 1 mm) spicule rays also project laterally from the body wall, but do not constitute discrete prostalia.

Body wall consists of a tuberculate primary (outer, probably dermal) layer, and a thin inner (probably gastral) spicule layer. Primary skeletal wall layer with acute rounded mounds (Fig. 4A_1, B, D_1) that penetrate into the matrix, giving the appearance of numerous subcircular spaces, typically 2 mm in diameter (clearest in Fig. 4A_1, A_2) but proportionally smaller in small specimens (around 1 mm in the 18-mm tall NIGP154634; Fig. 4D_1). Some smaller spaces are interspersed irregularly with the larger ones, and occasionally a large gap is subdivided by an additional curving wall (Fig. 4C_4, at right edge), typically leaving one half smaller and with a concave side. At the upper margin of the sponge, these gaps are less clearly defined and smaller, around 1 mm in diameter. Mounds form a disordered array, roughly close-packed, and with skeletal areas between gaps normally 0.5 mm wide at thinnest, widening slightly in triple-junctions but in general maintaining constant thickness (although dependent on degree of compression of specimens); this produces slightly polygonal, rounded spaces rather than strictly circular apertures. The inter-mound areas may be proportionally wider at earlier growth stages, but too few small specimens are available for confirmation.

Mounds, where visible in profile (Fig. 4B, D_1) at the sponge margin, can be up to 2 mm tall in large specimens, and normally around 2 mm wide; this accords with the diameter of spaces described above, indicating that the skeletal wall of the mounds was of negligible thickness. Mounds in early growth stages are proportionally smaller, and perhaps disproportionately shorter relative to diameter (Fig. 4D_1). Mounds are covered with a similar irregular mesh (Fig. 4D_2) to that seen in the body wall near the oscular margin, although nowhere preserved clearly enough to confirm the presence of discrete spicules. Where broken through the domes, the internal section is often preserved with a thin reflective film (Fig. 4D_1), presumed to be composed of aluminosilicates, but fainter than in the skeletal wall. In many of the larger gaps, this surface is slightly domed, with subradial and concentric wrinkles (Fig. 4C_4). This indicates the presence of a thin soft-tissue membrane covering the interior of mounds in life, creating an enclosed space within the mounds.

Spiculation of the outer wall is normally obscured by substantial pyritisation, particularly at the margins of parietal gaps, but individual spicules are visible in places (Fig. 4C_4). Where pyritisation is less extensive, the skeleton is covered by a thin reflective sheet of probable aluminosilicates. Spicules appear to be simple stauractines, although additional gastral or dermal rays cannot be excluded. Rays are straight and simple.

The largest spicules in the primary skeletal layer are centred in the centres of wall areas between parietal gaps, with the largest spicule identified having ray length 1.2 mm (basal ray diameter approx. 0.1 mm, possibly taphonomically enlarged); orientation is irregular. Smaller spicules are distributed largely irregularly except at parietal gap margins, where they are often arranged with rays parallel to the margin, such that one ray projects towards the centre of the gap (Fig.


A1
B
C1
C2
C3
D2
D1
C4
A2

$4C_4$). Typical ray length for smaller spicules is c. 0.2 mm. Near oscular margin, the spicules are arranged to form an irregular polygonal meshwork, oriented roughly diagonal to the sponge axis with spaces approximately 0.1 mm across (Fig. $4C_3$).

Inner layer (possibly layers) composed of locally dense felt of small, fine hexactines or their derivatives in parallel, perhaps quadruled array. Traces of discrete orthogonal and diagonal spicule series, superimposed onto each other, and visible in the holotype (Fig. $4C_2$); the paratype NIGP154631 (Fig. 4B) also shows a small area at the upper right corner with the orthogonal grid visible. The best-preserved regions in the holotype show an apparently regular grid with square spaces consistently around 0.1 mm per side.

No evidence for basalia is seen in any specimen.

Discussion.—If the structure of the sponge is well preserved, as reconstructed in Fig. 5, recognition of the species is straightforward. Separating the species from other known parietal gap-bearing taxa is difficult if the preservation does not show clear spiculation of the inner layer(s) or the skeletal structure of the mounds, but several features are useful. The parietal gap size appears to be tied consistently to body size, and is larger than that in co-occurring taxa. The near-circular, slightly polygonal form of the gaps, arrangement into locally clear transverse rows, and the occasional division of a large gap by a curving wall, are also characteristic. The narrowness of the walls between the gaps produces a relatively high proportion of space in this layer. Where spiculation is visible, the irregularity of the orthogonal and diagonal layers contrasts with that in *Hintzespongia* Rigby and Gutschick, 1976, in which the regular layer is external to the layer with parietal gaps (supported by Rigby 1983). In specimens from Amnodd Wen, the walls are typically preserved with mounds in three dimensions, allowing easy separation from *Hintzespongia*-like forms; the same distinction is visible at the margin of flattened, complete specimens, where mounds are visible in profile.

The new species is distinctly separated from *Valospongia gigantis* Rigby, 1983 by the lack of spicular strands, the denser packing of the parietal gaps, and perhaps also by the expression of the dermal spiculation over areas outside the mound surfaces; the holotype of the type species shows the fine-scale reticulation only over the mound surface rather than also within the inter-pariety wall region as seen in *V. bufo* sp. nov. The type species is also an order of magnitude larger than any specimen in the present collection, and with disproportionately larger spicules, although it is possible that the proportions of a juvenile *V. gigantis* would be similar to those of *V. bufo*. Other parietal gap-bearing taxa from the Burgess Shale-type faunas include *Stephenospongia* Rigby, 1986, which is known from fragments only; this species is assigned to the Hintzespongiidae (Finks and Rigby 2004b),

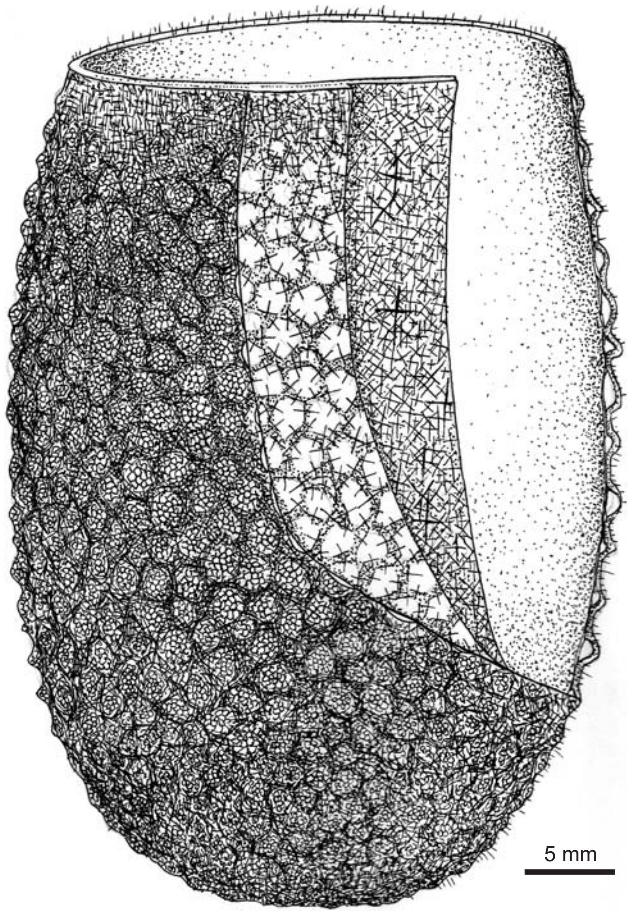


Fig. 5. The hexactine-bearing sponge *Valospongia bufo* sp. nov. Cut-away reconstruction, showing (left to right) outer surface including reticulate covering of mounds; outer layer with apices of mounds cut off, as seen in the majority of specimens due to partial compression of the skeletons; inner layer (or perhaps two layers superimposed) with combination of approximately diagonal and orthogonal elements of the skeletal mesh.

← Fig. 4. The hexactine-bearing sponge *Valospongia bufo* sp. nov. Dol-cyn-Afon Formation, upper Tremadocian, Lower Ordovician, Arenig Fawr, North Wales, UK. **A**. Paratype NIGP154637 from loose but local block at Amnodd Wen. A_1, overall view of specimen in incomplete margin but good preservation of mound array (low-angle illumination); A_2, detail showing bases of mounds with three-dimensional preservation, walls curving upwards until cut off by plane of breakage (intense oronge colouration composed of weathered framboidal pyrite). **B**. Paratype NIGP154631, complete but weathered specimen showing general form and profile of mounds (arrowed) at right margin; block found beside the track near Amnodd Wen, 100 m up the track towards Ceunant-y-garreg-ddu (high-angle illumination). **C**. Holotype NIGP154629, Ceunant-y-garreg-ddu stream section, found as a loose block below outcrops 40 m stratigraphically above the point where it crossed the track. C_1, overall view showing near-complete outline and broad, flat oscular margin; C_2, detail of skeleton, showing dense semi-regular inner spicule grid including semi-quadruled array; C_3, detail of spicules at oscular margin, showing loss of pronounced mounds and irregular, sub-polygonal diagonal organisation; C_4, detail of outer skeletal layer, with clear mound bases and showing wrinkled internal with radiating spicule rays projecting inwards towards centre (right middle). **D**. Paratype NIGP154634 from Ceunant-y-garreg-ddu. D_1, left lateral margin, showing well-preserved arrangement of mound bases, moderate spiculation, and several dermal mounds in cross section; D_2, detail of single mound, showing reticulate mesh over flattened mound surface (contrast significantly enhanced). Scale bars A, B, C_1, 10 mm; C_2–C_4, D_1, D_2, 1 mm. All photographs taken under water.

but may also show a reticulating grid over the parietal gaps, as in *Valospongia*. It can nonetheless be distinguished by its elongate parietal gaps, by the large size of the spicules relative to the parietal gaps, and by the lack of a regularly ordered grid. The allied *Ratcliffespongia* Rigby, 1969 is a difficult genus; the type species, *R. perforata* Rigby, 1969, appears to have possessed only a single wall of spicules in an irregular array, and with transversely-elongated parietal gaps. Neither this nor the Chinese species *R. multiforamina* Wu, Yang, Janussen, Steiner, and Zhu, 2005 shows the reticulation-covered mounds or the regularly-oriented inner layer(s) of *Valospongia*. *Ratcliffespongia wheeleri* Rigby and Church, 1990 is discussed below, where we reassign it to *Hintzespongia*.

Stratigraphic and geographic range.—Known only from several sites within the upper part of the Dol-cyn-Afon Formation (*Conophrys salopiensis* Biozone; early Migneintian, Late Tremadocian) of the Arenig Fawr area, near Bala, Wales, UK.

Family Hintzespongiidae Finks, 1983

Emended diagnosis.—Thin-walled, obconical, ovate or vasiform Reticulosa in which an inner, gastral layer of parallel, slender-rayed hexactines or derivatives, as in Protospongioidea, is overlain by a layer of slender-rayed hexactines or derivatives in nonparallel orientation that surround closely spaced, circular gaps or aporhyses.

Discussion.—The only material of *Hintzespongia* consists of the holotype of *H. bilamina* Rigby and Gutschick, 1976, and additional fragments of *Hintzespongia* from the Wheeler and Marjum formations described by Rigby et al. (2010). Another potential specimen is the holotype of *Ratcliffespongia wheeleri* Rigby and Church, 1990, if that species should be placed in the genus. A fragment of a similar sponge from the Burgess Shale was described by Rigby and Collins (2004), and assigned to *H. bilamina*, but re-examination (JPB, personal observations) shows this specimen to be a different, undescribed sponge with a single spicule layer. The only non-Laurentian sponge recorded as *Hintzespongia* (Yang et al. 2010) appears to show no evidence of a secondary spicule layer, and is likely to represent instead *Ratcliffespongia* or a related genus.

The relative positioning of the two spicule layers in *H. bilamina* could not be stated with certainty by Rigby and Gutschick (1976) due to the fragmentary nature of the specimen, and none of the subsequent discoveries provides a near-complete specimen in which the two layers are clearly distinct. As a result, the dermal and gastral placement of the two spicule layers has never been confirmed.

Genus *Hintzespongia* Rigby and Gutschick, 1976

Type species: *Hintzespongia bilamina* Rigby and Gutschick, 1976, from the middle Cambrian Marjum Formation of Utah, USA.

Species included: *Hintzespongia bilamina* Rigby and Gutschick, 1976, *Hintzespongia wheeleri* (Rigby and Church, 1990).

Diagnosis (emended after Finks and Rigby 2004b).—Sponge thin-walled, conical to barrel-shaped, with a probably gastral layer of parallel, slender-rayed stauractines of at least four orders of size, underlying a layer of slender-rayed stauractines and hexactines in nonparallel orientation.

Discussion.—Definition of this monospecific genus is complex, and requires a re-evaluation of similar and related taxa. Finks and Rigby (2004b) list *Hintzespongia, Ratcliffespongia*, *Cyathophycus*, and *Stephenosphongia* as being assigned to the family, but some of these assignments are perhaps unsound. *Cyathophycus* is a complex, widely distributed genus that is in need of revision (and probably subdivision), but the inner layer of at least some species appears to be composed of monaxons (discussed by Botting 2003, 2004). *Stephenospongia* is a poorly known genus that may not even have an outer spicule layer, although there are traces of reticulation in some parts (Rigby 1986) that might resemble the reticulating outer mesh of *Valospongia*, discussed above. None of these genera are particularly similar to *Hintzespongia bilamina*, but there are definite similarities between it and *Ratcliffespongia wheeleri* (Rigby and Church 1990).

The taxonomy of *Ratcliffespongia* is complicated, despite being based on only two specimens. Rigby (1969) described *R. perforata* based on a unique, semi-complete specimen from the Wheeler or Marjum formations, of a sponge with prominent, somewhat transversely elongate parietal gaps in a thin wall that was constructed from large, thin-rayed but clearly defined stauractines. The spicule rays do not generally demark the margins of the gaps, which were visible as a soft tissue impression. The sponge apparently consisted of a single layer of spicules, and was assigned to the Teganiidae. Another unique specimen from the upper Wheeler Formation was described by Rigby and Church (1990) as *R. wheeleri*, but although showing prominent parietal gaps, this species differs substantially. The gaps are more circular and irregularly arranged, and the spiculation of the wall is rather obscure, with small hexactines or their derivatives often marking very clearly the margins of the gaps. Most fundamentally, *R. wheeleri* appears to have possessed two layers, with a homogeneous, sub-reticulate grid of small spicules overlying(?) the pariety-bearing layer. The diagnosis of *Ratcliffespongia* was emended by Rigby and Church (1990) to include the double-layered wall, and both species were thereby assigned to the Hintzespongiidae. The similarity was accepted only through the assumption that the holotype of *R. perforata* represents a decorticated inner layer of a hintzespongiid (Finks 1983; Rigby and Church 1990). However, the holotype is apparently well preserved, near-complete (the only damage appears to be due to erosion and distal breakage of the loose block containing the specimen), and fully articulated, even showing traces of the soft tissues marking the margins of the parietal gaps. Decortication seems very unlikely in this case, especially as the fragment forming the holotype of *R. wheeleri* is much less intact and appears to be less well preserved in some areas than others.

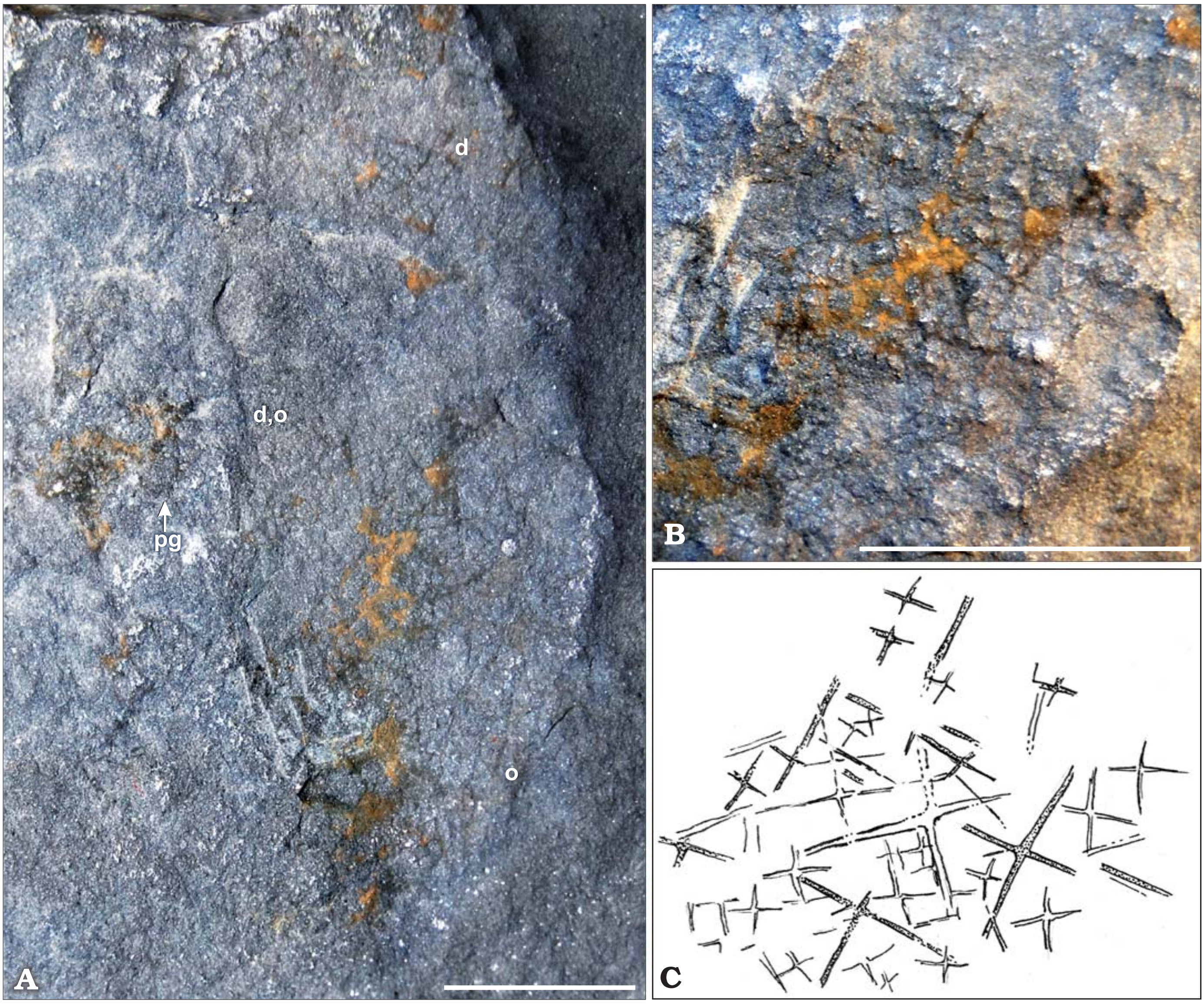


Fig. 6. The hexactine-bearing sponge *Hintzespongia*? sp., NIGP154638, Dol-cyn-Afon Formation, upper Tremadocian, Lower Ordovician, Ceunant-y-garreg-ddu stream section, Arenig Fawr, North Wales, UK. **A**. Overall view of specimen showing several regions with exposed spicules, each revealing skeletal layers interpreted as having originally been dominantly diagonal (d), sub-orthogonal (o) or both (d, o), and with example of possible inner layer parietal gap (pg). **B**. Detail of central part of specimen, showing both diagonal and sub-orthogonal spicule arrays. **C**. Camera lucida drawing of region shown in B, with sub-orthogonal series stippled. Scale bars 5 mm. All photographs taken under water.

The skeletal architecture is fundamentally different in the two *Ratcliffespongia* species, and they have little in common except for being reticulosan hexactinellids with parietal gaps. We therefore do not recognise these two species as belonging to the same genus, and restrict the use of *Ratcliffespongia* to the type species *R. perforata*. Instead, the fundamental structure of *R. wheeleri* is identical to that of *Hintzespongia*, and we therefore reassign it to that species. The separation from *Hintzespongia* by Rigby and Church (1990) was on the basis of differences in the regularity of spicule organisation in the reticulate layer, and parietal gap dimensions; these are superficial differences that do not obscure a close relationship. We therefore include both *R. wheeleri* and the new (open nomenclature) sponge described here in *Hintzespongia*.

Stratigraphic and geographic range.—The confirmed range for *Hintzespongia* is restricted to the middle Cambrian Wheeler and Marjum formations of Utah, USA, together with the probable new record from the Tremadocian of Wales, UK.

Hintzespongia? sp.

Fig. 6.

Material.—NIGP154638, fragment of the body wall preserving detail of both spicule layers, from the Late Tremadocian (early Migneintian), loose block in Ceunant-y-garreg-ddu stream section.

Description.—Fragments of a partial specimen patchily exposed over 24 mm of roughly broken surface, and with spicules often partly replaced by iron oxides. Spicules are distributed through a thickness of matrix, rather than splitting precisely along a plane, producing intermittent overlap of the skeletal mesh from inner and outer layers. The best preserved region displays a dominant diagonal fabric superimposed on a somewhat irregular orthogonal array with major spicule rays visible. Entire individual spicules are difficult to observe, due to the irregular surface and replacement of spicules by iron minerals and reflective films (probably aluminosilicate).

Largest spicules observed with ray length exceeding 3 mm, but no complete rays of largest spicules seen; maximum ray diameter (probably near-basal) approximately 0.20–0.25 mm, but preservation makes exact width difficult to assess. At least three (probably four or five) size orders visible, but few complete spicules. One of the smallest has ray length 0.6 mm and basal diameter around 0.1 mm in broadest ray (around 0.05 mm in narrowest), with rays evenly tapered. These proportions suggest that spicule rays became more elongate as they grew, but better specimens would be required to confirm this. Spicules of orthogonal layer less clearly preserved, but appear to be consistently narrower for given spicule length, with some rays in excess of 1 mm long, but only 0.05 mm in diameter, and not obviously tapering over exposed length. Fewer small spicules are visible in the inconsistently exposed orthogonal array, which may be entirely due to preferential preservation, but might indicate the presence of obscure parietal gaps in that layer. One area (Fig. 6A, pg) shows what may be the pyritised margin of a parietal gap, around 1 mm in diameter.

Discussion.—The limited material available for this species prevents a categorical assignment even at genus level, but the structure appears to be diagnostic of *Hintzespongia*. Although normally described with the two planes of spicules clearly distinct (e.g., Rigby and Gutschick 1976), specimens are known in which the layers are less clearly defined and spicules are superimposed (Rigby et al. 2010). This is a preservational effect that complicates recognition of the sponge, but does not in itself necessitate reconsideration; the specimen was probably originally preserved in a similar manner to the type material, but authigenic aluminosilicate growth during low-level metamorphism is likely to have caused disintegration of particular sedimentary laminations. The preservation is entirely consistent with a regular diagonal layer of spicules overlying a somewhat less regular, sub-orthogonal layer. The only other significant difference from the previously described material is the rarity of obvious parietal gaps in the inner layer, but at least one probable example is visible, and the spicules interpreted as representing that layer in our material are much more sparsely preserved.

The skeletal structure is somewhat similar to that of *Valospongia bufo* sp. nov., but specimens are in general easily separated by preservational differences; in *V. bufo*, the most prominently preserved feature is the array of apparent gaps, the margins usually heavily pyritised. In side view these are clearly seen to be mounds in *V. bufo*, but profile views are not often available due to fragmentation of the sponge skeletons. This difference is not dependent on exact bed; a fragment of *V. bufo*, preserved in the typical way, is present on the edge of the *Hintzespongia*? sp. slab. If only a spicule array is present, there are differences in the spicule dimensions, with the largest spicules in *Hintzespongia*? sp. having rays several times longer than the largest seen in *V. bufo*. Growth stage must be taken into account, but it also appears that parietal gaps in *Hintzespongia*? sp. are substantially smaller than the apparent gaps in *V. bufo*, even when the spicules are substantially larger.

Concluding remarks

Hexactinellid sponge faunas from the Tremadocian–Floian interval are extremely rare, and it has been impossible to reconstruct even such basic faunal dynamics as the continuity (or otherwise) of typical Cambrian taxa into the Ordovician. The only exception is the Fezouata Biota (Van Roy et al. 2010), which has yielded a surprisingly Cambrian-like sponge assemblage dominated by protomonaxonids (in particular, piraniids, choiids, and hamptoniids; Botting 2007a). Hexactinellid-like taxa are extremely rare in the Fezouata Biota. This fauna is, however, from near the Ordovician South Pole, and it is unclear to what extent the sponge community accurately represents the global fauna from similar environments, and to what extent it might be an isolated, relict fauna resulting from the cold-water conditions.

The recognition of an entirely different assemblage of sponges from a similar but slightly older deposit, at somewhat lower latitude, allows some wider generalisations. The species reported here are also typical of Cambrian faunas, but in this case of the slightly deeper-water community of Utah (Wheeler Shale and Marjum formations) rather than the escarpment-related Burgess Shale community. Although the remainder of the fauna remains undescribed as yet, *Valospongia bufo* sp. nov. is probably the most common sponge species in the deposit. Other examples of Cambrian-type taxa such as *Hintzespongia* and choiids are also present, together with novel morphologies, but additional material is needed for a full interpretation.

In combination with the sponges from the Fezouata Biota, the composition of the fauna known so far implies not only that several different elements of the Burgess Shale-type communities survived into the Early Ordovician, but also that aspects of the ecological segregation of taxa within those assemblages were conserved. At least in high southern latitudes, the sponge faunas indicate strong continuity of the middle Cambrian communities into the Tremadocian–Floian interval.

Acknowledgements

Many thanks to Richard Fortey (Natural History Museum, London, UK) for initially pointing us in the direction of the site, and Adrian

Rushton (Natural History Museum, London, UK) for helpful discussion. Thanks also to Naomi Jordan (Imperial College, London, UK), Tess Ormrod (Kington, UK), Neil Owen (Leeds, UK), Jennifer Rodley (Leeds, UK) and Christopher Upton (Bath, UK) for assistance on fieldwork, and to Robert Matthews (Countryside Council for Wales, UK) for arranging access. An anonymous reviewer and Joachim Reitner (Georg-August-Universität, Göttingen, Germany) are thanked for their comments on the manuscript. JPB's research is supported by the Chinese Academy of Sciences Fellowships for Young International Scientists Grant No. 2010Y2ZA03 and National Science Foundation of China, The Research Fellowship for International Young Scientists (Grant No. 41150110152). LAM is receiving funding from China Postdoctoral Science Foundation, grant number 20110490136. This study was supported partially by the Project-Oriented Hundred Talents Programme (Grant No. KZCX2-YW-BR-23). This paper is a contribution to the International Geoscience Programme (IGCP) Project 591—The Early to Middle Paleozoic Revolution.

References

Beresi, M., Botting, J.P., and Clarkson, E.N.K. 2010. A new demosponge, *Choiaella scotica,* from the Caradoc (Ordovician) of Wallace's Cast, Southern Uplands, Scotland. *Scottish Journal of Geology* 46: 77–83.

Botting, J.P. 2003. *Cyathophycus* and the origin of demosponges. *Lethaia* 36**:** 335–344.

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

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

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

Botting, J.P. 2007b. Chapter 3: Algae, receptaculitids and sponges. *In*: E.N.K. Clarkson, D.A.T. Harper, and L. Anderson (eds.), *Field Guide to the Fossils of the North Esk Inlier*, 36–49. The Palaeontological Association, London.

Botting, J.P. and Butterfield, N.J. 2005. Reconstructing early sponge relationships by using the Burgess Shale fossil *Eiffelia globosa*, Walcott. *Proceedings of the National Academy of Sciences of the United States of America* 102: 1554–1559.

Botting, J.P. and Muir, L.A. 2011. A new Middle Ordovician (late Dapingian) hexactinellid sponge from Cumbria, UK. *Geological Journal* 46: 501–506.

Carrera, M. and Botting, J.P. 2008. Evolutionary history of Cambrian spicular sponges: implications for the Cambrian evolutionary fauna. *Palaios* 23: 124–128

Carrera, M.G. and Rigby, J.K. 2004. Sponges. *In*: B.D. Webby, F. Paris, M.L. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 103–111. Columbia University Press, New York.

Cocks, L.R.M. and Torsvik, T.H. 2004. Major terranes in the Ordovician. *In*: B.D. Webby, F. Paris, M.L. Droser, and I.G. Percival (eds.), *The Great Ordovician Biodiversification Event*, 61–67. Columbia University Press, New York.

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

Dawson, J.W. and Hinde, G.J. 1889. New species of fossil sponges from the Siluro-Cambrian at Little Metis on the Lower St. Lawrence. *Transactions of the Royal Society of Canada* 7: 31–55.

Debrenne, F. and Reitner, J. 2001. Sponges, Cnidarians, and Ctenophores, *In*: A.Y. Zhuravlev and R. Riding (eds.), *The Ecology of the Cambrian Radiation*, 301–325. Columbia University Press, New York.

Esteban, S.B. and Rigby, J.K. 1998. Hexactinellid sponges from the Lower Tremadocian Volcanito Formation, Famatima Range, northwestern Argentina. *Brigham Young University Geology Studies* 43: 1–7.

Fearnsides, W.G. 1905. On the geology of Arenig Fawr and Moel Llyfnant. *Quarterly Journal of the Geological Society* 61: 608–640.

Finks, R.M. 1983. Fossil hexactinellids. *In*: T.W. Broadhead (ed.), Sponges and Spongiomorphs. Notes for a Short Course Organized by J.K. Rigby and C.W. Stearn. *University of Tennessee, Studies in Geology* 7: 1101–1115.

Finks, R.M. and Rigby, J.K. 2004a. Paleozoic Demosponges. *In*: R.M. Finks, R.E.H. Reid, and J.K Rigby (eds.), *Treatise on Invertebrate Paleontology, Part E (revised), Volume 3*, 9–171. Geological Society of America and the University of Kansas Press, Lawrence.

Finks, R.M. and Rigby, J.K. 2004b. Palaeozoic hexactinellid sponges. *In*: R.M. Finks, R.E.H. Reid, and J.K Rigby (eds.), *Treatise on Invertebrate Paleontology, Part E (revised), Volume 3*, 320–448. Geological Society of America and the University of Kansas Press, Lawrence.

Fortey, R.A. and Cocks, L.R.M. 2003. Palaeontological evidence bearing on global Ordovician–Silurian continental reconstructions. *Earth-Science Reviews* 61: 245–307.

Grant, R.E. 1836. Animal Kingdom. *In*: R.B .Todd (ed.), *The Cyclopaedia of Anatomy and Physiology, vol. 1*, 107–118. Sherwood, Gilbert, & Piper, London.

Hinde, G.J. 1883. *Catalogue of the Fossil Sponges in the Geological Department of the British Museum (Natural History)*. viii + 248 p., 38 pl. British Museum (Natural History), London.

Kokelaar, B.P. 1986. Petrology and geochemistry of the Rhobell Volcanic Complex: amphibole-dominated fractionation at an early Ordovician arc volcano. *Journal of Petrology* 27: 887–914.

Lynas, B.D.T. 1973. The Cambrian and Ordovician rocks of the Migneint area, North Wales. *Journal of the Geological Society, London* 129: 481–503.

Owens, R.M., Fortey, R.A., Cope, J.C.W., Rushton, A.W.A., and Bassett, M.G. 1982. Tremadoc faunas from the Carmarthen district, South Wales. *Geological Magazine* 119: 1–38.

Rigby, J.K. 1969. A new Middle Cambrian hexactinellid sponge from western Utah. *Journal of Paleontology* 43:125–128.

Rigby, J.K. 1978. Porifera of the Middle Cambrian Wheeler Shale, from the Wheeler Amphipheater, House Range, in western Utah. *Journal of Paleontology* 52: 1325–1345.

Rigby, J.K. 1983. Sponges of the Middle Cambrian Marjum Limestone from the House Range and Drum Mountains of western Millard County, Utah. *Journal of Paleontology* 57: 240–270.

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

Rigby, J.K. and Chatterton, B.D.E. 1994. New Middle Silurian hexactinellid sponge from the McKenzie Mountains, Northwest Territories, Canada. *Journal of Paleontology* 68: 218–223.

Rigby, J.K. and Church, S.B. 1990. A new Middle Cambrian hexactinellid, *Ratcliffespongia wheeleri*, from western Utah and skeletal structure of *Ratcliffespongia*. *Journal of Paleontology* 64: 331–334.

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

Rigby, J.K. and Gutschick, R.C. 1976. Two new Lower Paleozoic hexactinellid sponges from Utah and Oklahoma. *Journal of Paleontology* 50: 79–85.

Rigby, J.K. and Hou, X.-G. 1995. Lower Cambrian demosponges and hexactinellid sponges from Yunnan, China. *Journal of Paleontology* 69: 1009–1019.

Rigby, J.K., Church, S.B., and Anderson, N.K. 2010. Middle Cambrian sponges from the Drum Mountains and House Range in western Utah. *Journal of Paleontology* 84: 66–78.

Rigby, J.K., King, J.E., and Gunther, L.F. 1981. The new Lower Ordovician protosponge, *Asthenospongia*, from the Phi Kappa Formation in central Idaho. *Journal of Paleontology* 55: 842–847.

Rushton, A.W.A. and Fortey, R.A. 2000. Chapter 5, North Wales. *In*: R.A. Fortey, D.A.T. Harper, J.K. Ingham, A.W. Owen, M.A. Parkes, A.W.A. Rushton, and N.H. Woodcock (eds.), *A Revised Correlation of Ordovician Rocks in the British Isles*. *Geological Society Special Report no. 24*, 18–24, The Geological Society, Bath.

Rushton, A.W.A. and Howells, M.F. 1998. *Stratigraphical Framework for the Ordovician of Snowdonia and the Lleyn Peninsula, Research Report No.RR99/08*. 40 pp. British Geological Survey, Keyworth.

Schmidt, O. 1870. *Grundzüge einer Spongien-Fauna des Atlantischen Gebietes*. 88 pp. Wilheim Engelmann, Leipzig.

Sedgwick, A. 1852. On the classification and nomenclature of the Lower Palaeozoic rocks of England and Wales. *Quarterly Journal of the Geological Society of London* 8: 136–184.

Van Roy, P., Orr, P.J., Botting, J.P., Muir, L.A., Vinther, J., Lefebvre, B., el Hariri, K., and Briggs, D.E.G. 2010. Ordovician faunas of Burgess Shale-type. *Nature* 465: 215–218.

Williams, A., Strachan, I., Bassett, D.A., Dean, W.T., Ingham, J.K., Wright, D.W., and Whittington, H.B. 1972. A correlation of the Ordovician rocks in the British Isles. *Special Report of the Geological Society of London* 3: 1–74.

Wu, W., Yang, A.-H., Janussen, D., Steiner, M., and Zhu M.-Y. 2005. Hexactinellid sponges from the Early Cambrian black shale of South Anhui, China. *Journal of Paleontology* 79: 1043–1051.

Xiao, S., Hu, J., Yuan, X., Parsley, R.L., and Cao, R. 2005. Articulated sponges from the Lower Cambrian Hetang Formation in southern Anhui, South China: their age and implications for the early evolution of sponges. *Palaeogeography, Palaeoclimatology, Palaeoecology* 220: 89–117.

Yang, X., Zhao, Y., and Wu, W. 2003. Discovery of Early and Middle Cambrian Choiidae from Guizhou, SW China. *Acta Micropalaeontologica Sinica* 20: 286–295.

Yang, X., Zhao, Y., Zhu, M., Cui, T., and Yang, K. 2010. Sponges from the Early Cambrian Niutitang Formation at Danzhai, Guizhou and their environmental background. *Acta Palaeontologica Sinica* 49: 348–359.

Zalasiewicz, J. 1984. A re-examination of the type Arenig Series. *Geological Journal* 19: 105–124.