First Post-Cambrian Records of the Reticulosan Sponges Valospongia and Hintzespongia from the Late Tremadocian of North Wales

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

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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.

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Introduction

Early Ordovician non-lithistid sponges are extremely poorly known, with very few described taxa. Isolated fragments and partial specimens of protospongiods 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 Mètis, 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 Mètis 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 Mètis 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 nearshore 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 protomonaxonoids (especially choiids) and a high proportion of reticulosan hexactinellids. Many of the reticulosans possessed semi-regular skeletons with parietal gaps (e.g., Ractilipespongia, 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 protospongiioids such as Hemineceter (Botting 2004; Botting and Muir 2011). The derived features include hypertrichy 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., Plectodorina 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 one of the first species from a new Tremadocian sponge fauna from the studied beds, and shows that at least some hexactinellid elements of the Burgess Shale-type fauna survived into the Early Ordovician.

### 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 Fearnside (1905), and revised by Zalasiewicz (1984), who recognised the Tremadoc successions as correlated with the upper part of the Afon Gam Formation of Llynas (1973), defined in the nearby Migneint area. This formation corresponded to the Niobe Beds, Dictyonema Band, Nant-ddu or (Bellorophon) Beds, Tai-Herion Flags and Annodd Shales of Fearnside (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 Shinetons Shales Formation of the Welsh Borderland (Rushton and Fortey 2000). The material described here is from the Annodd Shales of Fearnside (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 substantial amount of附着性 fauna that includes trilobites, brachiopods, and crinoids. The faunal assemblages are indicative of a coastal or shelf setting, with the presence of diverse marine invertebrates that are typical of the Early Ordovician biofacies.
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 81653747), 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.

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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.
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 Hydnodictyiidae 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.

Remarks.—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 lay-
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; NIGP154633, a small area preserved with a thin reflective film 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) 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 smaller relative to diameter (Fig. 4D). Mounds are covered with a similar irregular mesh (Fig. 4D) 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), 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). 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). 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 gastrical 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.
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 Hintzespongiiidae (Finks and Rigby 2004b),
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 Mignein-tian, Late Tremadocian) of the Arenig Fawr area, near Bala, Wales, UK.

**Family Hintzespongiidae Finks, 1983**

**Emended diagnosis.**—Thin-walled, oboconical, ovate or vasiform Reticulosa in which an inner, gastric layer of parallel, slender-rayed hexactines or derivatives, as in Protospongidea, 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 gastric 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 gastric 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 Stephenspongia 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). Stephenspongia 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. Decoration 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.
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.

**Material.**—NIGP154638, fragment of the body wall preserving detail of both spicule layers, from the Late Tremadocian (early Migneintian), loose block in Cenunt-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 preservation 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 sparingly 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.

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