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AN EXCEPTIONAL CARADOC SPONGE FAUNA FROM THE LLANFAWR QUARRIES, CENTRAL WALES AND PHYLOGENETIC IMPLICATIONS

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SYNOPSIS An abundant sponge collection from basal Caradoc mudstones of the Llanfawr Quarries, Llandrindod, Powys is the most diverse fine-sediment sponge fauna recorded from the British Palaeozoic. It is dominated by reticulosans, but includes some lyssakids and demosponges. Eight new genera and 11 species are erected and one new family proposed: *Xylochos palindromica* gen. et sp. nov., *Pirania llanfawrensis* sp. nov., *Heminectere minima* gen. et sp. nov., *Asthenospongia cambria* sp. nov. (Asthenospongidae nov.), *Acutipuerilis spinosus* gen. et sp. nov., *Granulispongia obscura* gen. et sp. nov., *Hemidiagoniella tenax* gen. et sp. nov., *H. caseus* sp. nov., *Solusrectus rosetta* gen. et sp. nov., *Cyathophycus loydelli* sp. nov., and *Dilatispongia tumidus* gen. et sp. nov. Some specimens are preserved with organic or pyritic films representing soft tissue and most have high-fidelity preservation of spicule external moulds, although iron oxide spicule replacement obscures details prior to cleaning. *D. tumidus* shows a thickened wall with specialised dermalia, while retaining some degree of quadruling and represents a lineage that may have given rise to the brachiospongiods. Others, such as *S. rosetta*, appear close to the ancestral state of the modern Lyssacinosida. The hexactinellid taxa are interpreted in a reasoned phylogenetic framework that stresses the importance of root tuft structure, the presence of zero-order spicules and the number and nature of spicule layers. It also attempts to link extant and Lower Palaeozoic palaeontological classifications. The parallel evolutionary development of thick walls and strong attachment structures is interpreted as being due to an offshore-onshore expansion, contrary to many other groups.

KEY WORDS hexactinellid, rossellid, Reticulosa, demosponge, pyritisation, palaeoecology

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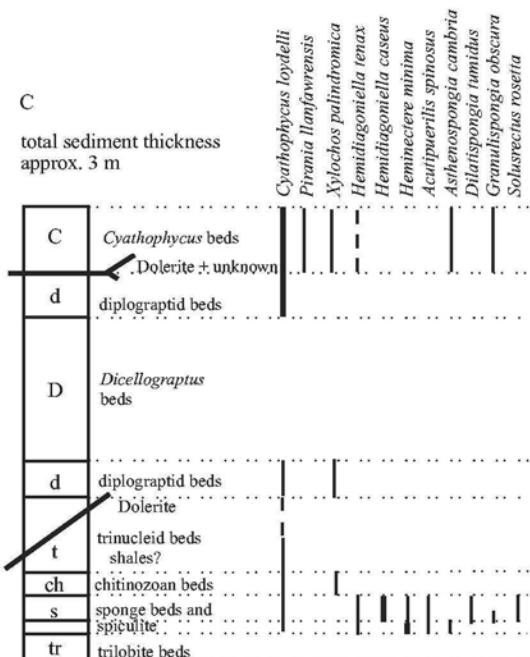
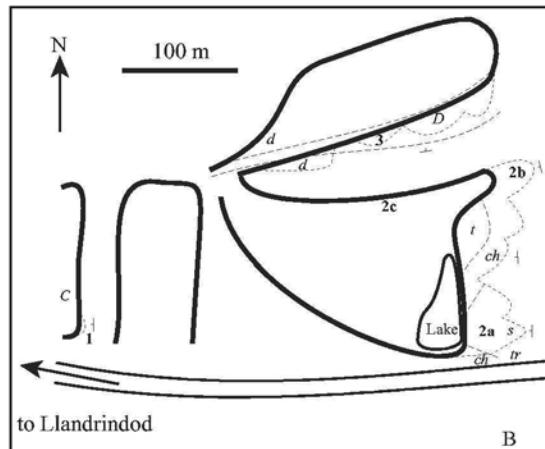
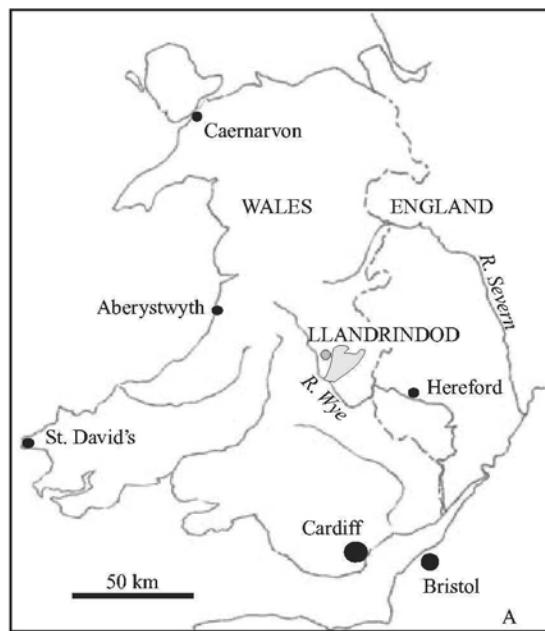
INTRODUCTION

Non-lithistid siliceous sponges are becoming recognised as important or dominant members of many Ordovician siliciclastic ecosystems. Their diversity and abundance in Cambrian deposits has been well described (e.g. Walcott 1920; Rigby 1978, 1986; Chen, Hou & Lu 1989; Chen, Hou & Li 1990), and several diverse assemblages are known from the Ordovician and Silurian of North America and elsewhere (Rigby 1971; Rigby, Hannun & Frest 1979; Rigby & Webby 1988; Mehl, Rigby & Holmes 1993). However, most occurrences consist of very distinct, largely endemic faunas (e.g. Rigby & Chatterton 1994), reflecting patchy preservation and, probably, life distribution. It is possible that sponges were much more abundant than is presently recognised, since almost all non-cemented sponge skeletons are disarticulated and inconspicuous as fossils. Siliceous spicules are also highly prone to dissolution in shallow marine environments (Land 1976). In spite of this, many Lower Palaeozoic sequences contain horizons or intervals where spicules comprise a significant proportion of the sediment and they are often extremely abundant on individual bedding planes. In general, however, these are of no taxonomic use due to the similarity of basic morphotypes in many diverse

taxa, particularly in fine sediment facies, and the impossibility of isolation from the matrix. Preservation is usually either mouldic or as iron oxides (after pyrite), with occasional recrystallisation as silica, or replacement by calcite. Although fresh pyritised material is, in principle, extractable by hydrofluoric acid dissolution of the siliciclastic matrix, this is rarely, if ever, achieved and unpublished studies have shown that pyrite replacement is only partial within at least some examples (A. Roberts, pers. comm., 2001).

Described sponge faunas from the Welsh Basin are limited to isolated occurrences of disarticulated spicule assemblages (Pulfray 1933; Woodland 1939; Lewis 1940) and rare articulated material (Hinde 1887; Owens *et al.* 1982; Botting *in press a*). Shallow-water deposits often contain large elongate monaxons assigned to root tufts of the genus *Pyritonema* M'Coy, discussed by Hinde (1887), Finks (1960) and Reid (1967). Botting (*in press a*) reinterpreted this as a derived hexactinellid, based on silicified Llanvirn material from Llandegley Rocks, Powys.

Isolated hexactinellid spicules are very widespread in siltstone facies of the Builth–Llandrindod Inlier, especially the Llanfawr Mudstone Formation (*sensu* Furnes 1978; Davies *et al.* 1997). Heteractinid spicules are, however, very rare and no articulated material has yet been recovered from



fine sediments; the few isolated spicules are simple hexaradiates and pentaradiates that may have been transported from shallow-water assemblages, or represent the remains of rare individuals after reworking. Sponges were recorded from this formation by Hughes (1969) and Sheldon (1987), but no descriptions were included. Where discussed at all, or labelled in museum collections, they are invariably referred to tentatively (and incorrectly) as species of *Protospongia*. The only non-lithistid genera, in addition to *Protospongia*, that have been adequately described from the Lower Palaeozoic fine sediments of the British Isles are *Phormosella ovata* Hinde, 1888, from the Ludlow of Shropshire, *Amphispongia oblonga* Salter, 1861, *Dictyophyton danbyi* (M'Coy, 1852) and *Plectoderma scitulum* Hinde, 1883, from the Silurian of Scotland and northern England. The attribution of individual monaxons to Recent demosponges such as *Reniera* by some authors (e.g. Lewis 1940) was essentially groundless, due to the indistinctiveness of individual spicules.

LOCALITY INFORMATION

The four Llanfawr Quarries are situated about 500 m east of the main road in Llandrindod, Central Wales (SO 065 617) and were excavated for dolerite building stones in the 19th and early 20th centuries. The three excavated bodies are laccolithic (Jones & Pugh 1948) or lopolithic (J. Davies, pers. comm., 2001) and were intruded into fossiliferous mudstones, which are exposed at the quarry margins. Mudstones occur in three quarries, the lower, main and upper (Fig. 1) and each has produced articulated sponges. Precise thicknesses and correlations are complicated by limited, largely strike-parallel, exposures, deformation and thermal metamorphism from the dolerite intrusions as well as local faulting. Nevertheless, several distinct beds are recognised in the succession, on the basis of sedimentology and faunal content (Fig. 1). The utility of sponges in defining such horizons is presently unclear, since the consistency of the distributions cannot be established. Sponge populations are normally patchy in modern deep shelf environments, with localised regions of very high density, where their accumulated spicules can influence the distribution of other organisms (Bett & Rice 1992). Five specific sponge-bearing localities are distinguished.

Locality 1

Lower quarry: small remnant outcrops adjacent to the lane, overlain by dolerite. Approximately 0.7 m of highly trilobitic blue mudstones, including *Ogygiacarella* (large), *Cnemidopyge*, *Barrandia*, *Trinucleus*, orthoconic nautiloids, inarticulate brachiopods and conulariids, with locally abundant graptolites, particularly *Climacograptus brevis brevis*. The

Figure 1 (A) Regional location of Llandrindod, with the Builth-Llandrindod Inlier shaded. (B) Locality map and local stratigraphy of the Llanfawr Quarries complex on the eastern edge of Llandrindod town centre; numbers in bold refer to localities, abbreviations refer to informal stratigraphic divisions. (C) Simplified stratigraphy of the Llanfawr Quarries succession, showing the distribution of the named taxa described in this paper.

sponges include an almost monospecific mass bedding-plane assemblage of *Cyathophycus loydelli* sp. nov. and rare *Xylochos palindromica* gen. et sp. nov., with occasional well-preserved material of the same species at several other levels. Two specimens of *Pirania llanfawrensis* sp. nov., a single specimen each of *Granulispomia obscura* gen. et sp. nov. and *Hemidiagoniella* sp. and additional unidentified fragments, have also been recovered. These exposures are stratigraphically the highest at Llanfawr. Specimens are preserved by spicular replacement by iron oxides, presumed after pyrite, but usually insufficiently hardened to provide detailed spicule moulds.

Locality 2a

Main quarry: extensive scree with thin outcrop at margins, in the quarry corner immediately above the pool. Thin (5–10 cm) ferruginous spiculite containing *X. palindromica*, *Acutipuerilis spinosus* gen. et sp. nov., *Heminectere minima* gen. et sp. nov., *Hemidiagoniella tenax* gen. et sp. nov., *G. obscura* and *C. loydelli* and overlying blue mudstones with *Asthenospongina cambria* sp. nov., abundant *Hemidiagoniella tenax*, *H. caseus* sp. nov., *G. obscura*, *H. minima* and indeterminate protospongiids. Associated fauna consists of trilobites (often articulated), graptolites (sometimes three dimensionally pyritised), chitinozoans (including helical assemblages), inarticulate brachiopods and rare orthoconic nautiloids, gastropods and conulariids. Sponges are preserved with spicules being replaced by weathered iron oxides, presumably after pyrite, but retaining relief; gentle brush-cleaning yields high-fidelity external moulds. In some specimens, the soft tissue is outlined by an iron-rich film that may represent decay by sulphate-reducing bacteria, as in the Hunsrückschiefer (Raiswell, Bartels & Briggs 2001). Only sponges appear to have been preserved in this way, perhaps because of the nucleation sites provided by spicule replacement. Small-scale, high-angle cross-bedding is visible in section, suggesting that burial was by abrupt sediment input. These are stratigraphically the lowest exposures at Llanfawr.

Locality 2b

Main quarry: slope-parallel beds exposed in a narrow cutting above the northeast corner of the quarry. Thin (10 cm) dark, baked mudstone containing sparse chitinozoan–graptolite fauna with bivalves, nautiloids, dendroid graptolites and conulariids; rare soft-bodied organisms have been recovered, including a possible bivalved arthropod. Sponges are represented by frequent specimens of *C. loydelli* and *X. palindromica* (often monospecifically clustered) and rare *G. obscura*. Minimal relief is preserved, spicules are mouldic without ferruginous replacement, but soft tissue outlines can be shown by dark, presumed organic, staining, occasionally with some preserved silica. Although sedimentologically homogeneous, examples of sponges (SM X.41150) and other organisms with *Leptograptus* wrapped around them indicate significant current activity, here and in the trinucleid beds (Fig. 1), from which only disarticulated spicules have been recovered.

Locality 2c

Main quarry: north wall. Rock-fall material (dark mudstones) with abundant graptoloids, chitinozoans, occasional trilob-

ites and brachiopods (primarily inarticulate). Sponge fauna comprises occasional specimens of *C. loydelli* and *X. palindromica*; the preservation is similar to locality 1, but generally with less relief.

Locality 3

Upper quarry: slope-parallel beds incised by scalloped cuttings. Blue mudstones immediately overlying black graptolitic shales, with trilobites, graptolites and brachiopods. Single slab with sponges, preserving three large specimens of *C. loydelli* in poor relief, lacking spicule replacement.

Additional spicules and partially articulated fragments occur at several levels, most notably among the celebrated *Trinucleus*-dominated beds of the main quarry, from which a single pentaradiate, presumed heteractinid, spicule was also recorded. Root tufts are limited to rare specimens from localities 2a and 2b and also from fallen blocks around the northeastern face between localities 2b and 2c. The latter have not yielded any other sponge material, except for rare hexactinellid spicules and correlation between these and the sponge bodies is difficult (but see section on root tufts, below).

The quarries constitute a Site of Special Scientific Interest and permission to collect must be sought from the Countryside Commission for Wales.

ENVIRONMENTAL INTERPRETATION

Establishing the water depth of organic-rich siltstones is notoriously difficult and estimates for the Llanfawr Mudstone Formation range from around 700 m (Sheldon 1987) to 100–150 m (Botting 2000). The trilobite fauna is very similar to the Arenig Raphiophorid Community of Fortey & Owens (1978), which they attributed to the middle or outer shelf. Pelagic taxa (including agnostids) are conspicuously rare, but this could be attributed to offshore, fault-generated elevations enclosing a relatively shallow basin, although this would not explain the ‘Raphiophorid Community’ fauna. No other faunal element is particularly useful, although bivalves are frequent in some beds, such as locality 2b; Ordovician bivalve faunas are rarely found below the inner shelf. Orthoconic nautiloids such as *Alumettoceras* (Evans 1994) have been examined for possible use in estimating water depth from septal implosion (Stridsberg 1990), but most are decalcified and compressed. One specimen was recovered retaining calcitic infill of the chambers and some mouldic specimens retaining partial details of septae, but these yielded only a tentative maximum depth limit of 600 m, having no imploded chambers.

The sedimentary environment became progressively deeper following the Builth Volcanic Formation, deposited during the *murchisoni* Biozone, a sequence that represents both erosion of the quiescent volcanic cone and increasing eustatic sea level. Sediment grain size at Llanfawr is finer than in most localities in the underlying *teretiusculus* Biozone, where there is a higher proportion of mica flakes, but this may reflect proximity to shoreline more than absolute water depth. Sedimentary structures are limited to planar or gently inclined lamination in most beds, although cross-bedding at up to 20° has been observed in some sponge-bearing horizons; the laminations are defined by slight grain

size variations and organic carbon and oxidised iron content, probably related to organic decay. There is little volcanic input, although a single thin ash bed occurs in the main quarry (Huff *et al.* 1993). Benthic oxygenation appears to have been variable, based on faunal colonisation. Trilobites are generally ubiquitous, although absent from an unfossiliferous pyrite nodule horizon low in the trinucleid beds and shales (Fig. 1), while they are rare in the chitinozoan-rich, sponge-bearing bed (locality 2b). Limited oxygenation might be inferred for the latter, supported by the high carbon content, although sponges, dendroid graptolites, inarticulate brachiopods, gastropods, bivalves and the chitinozoan producers were evidently able to tolerate the conditions and other parameters may have been more critical (see section on palaeoecology, below). Articulate brachiopods (*Dalmanella*) are generally rare, occurring locally as disarticulated individuals or very small clusters. Echinoderms have not been certainly recovered from this locality and bryozoans occur primarily as encrustations on orthocone nautiloids, although some of this was post-mortem, occurring on internal and external surfaces. Occasional isolated bryozoan colonies may also represent *in situ* benthic colonisation, or encrustation onto unmineralised organisms such as floating seaweeds or arthropods. At some horizons, numerous subspherical pyrite nodules were developed; although this may be partly related to the dolerite intrusion, pyritisation of sponge soft tissues implies very early mineralisation in some beds.

Overall, the environment appears to have been of middle to outer shelf depth, with typically quiet conditions separated by episodes of sudden sediment input or remobilisation. Oxygenation varied from moderately aerobic to anoxic, sometimes sulphidic. Although consisting entirely of organic-rich silt and mud, the sedimentology and faunal variation indicates a significant range of depositional rates and conditions.

SYSTEMATIC PALAEONTOLOGY

REPOSITORY. All specimens, unless otherwise stated, are housed in the Sedgwick Museum, University of Cambridge.

Class DEMOSPONGIAE Sollas, 1885

Order UNCERTAIN

Family HAZELIIDAE de Laubenfels, 1955

Genus XYLOCHOS gen. nov.

TYPE SPECIES. *Xylochos palindromica* gen. et sp. nov.

DIAGNOSIS. Globular demosponges with thin walls consisting of vertical and horizontal fine monaxon tracts, parallel to wall. Extensive fringe of erect, slightly divergent marginalia and similar broad root tuft, slightly convergent, both of coarser monaxons.

ETYMOLOGY. Greek for copse, thicket, referring to the clustered distribution. Gender *f*.

OCCURRENCE. Known only from the basal Caradoc Llanfawr Quarries, Llandrindod, Powys.

REMARKS. The new genus is easily separated from *Hazelia* by the extensive marginalia and basalia and by the body wall

structure. The latter is similar to *Hazelia*, comprising fine bundled monaxons in a cross-hatch arrangement, but oriented only tangentially and not radially. Because of the basic similarity, however, a close relationship is assumed. Of the other genera of Hazeliidae, *Crumillospongia* Rigby, 1986, has reduced horizontal tracts, whereas *Falospongia* Rigby, 1986, appears to represent a form that is convergent with the rhizomarine lithistids (Rigby 1986). Both are more distinct from *Xylochos* than *Hazelia* is. A similar arrangement is seen in the Leptomitidae, which form elongate cylindrical bodies of long monaxons, but have spaced, rather than pervasive, tracts. Although normally related to the haplosclerid demosponges, de Laubenfels (1955) placed the Leptomitidae tentatively among the protospongoid hexactinellids. Rigby (1986) and Walcott (1920) preferred to classify them as demosponges, but Rigby (1986), in particular suggested a position close to the demosponge–hexactinellid transition. However, the Leptomitidae possess more complex characteristics in the wall itself, such as internal spiral threads, while lacking significant marginalia or basalia; the same is true of the related, but more irregular, Halichondritidae. *Xylochos* therefore appears to be an extremely primitive demosponge, with a globose morphology that may reflect the ancestral state of the Hazeliidae.

The similarity of this genus to the internal layer of *Cyathophycus* is striking and many reticulosans possessed pronounced marginalia and basalia. Reduction and ultimate loss of the hexactine-based dermal layer could have resulted in the appearance of a form similar to *X. palindromica*, so that under phylogenetic taxonomy it would be classed as a hexactinellid. This putative relationship is discussed at length by Botting (in press *b*).

Xylochos palindromica gen. et sp. nov. (Figs 2A–D, 3)

TYPES. Holotype: SM X.39452; obliquely compressed specimen from locality 2c, lacking basalia. Paratypes: SM X.39393, 39353–61, 39363–5, 41078–81.

OTHER MATERIAL. SM X.39362, 39366–77; further poor partial specimens from localities 2b and 2c.

DIAGNOSIS. As for genus.

ETYMOLOGY. From Greek *palin* and *dromos*, yielding ‘palindrome;’ after the difficulty in recognising the correct orientation.

OCCURRENCE. Recorded from localities 1, 2a, 2b and 2c; particularly abundant at 2b and 2c.

DESCRIPTION. Small globular sponges with flattened length: width ratio of 1.2–1.9 in known specimens, typically around 1.5. Maximum observed length = 11.2 mm, obliquely flattened. Maximum width occurs at approximately half height, with width symmetrical across the equatorial plane, until osculum. Main body comprises cross-hatch arrangement of densely-packed fine monaxons, in most cases with individual spicules being obscure. Interweaved structure prevents estimates of spicule length; thickness approximately 0.01–0.02 mm. Cross-hatched on variable scale, but clearest divisions approximately 0.1–0.2 mm per edge of square in adults (for change of skeletal parameters with growth, see Botting 2003). There is no evidence of wall thickness beyond

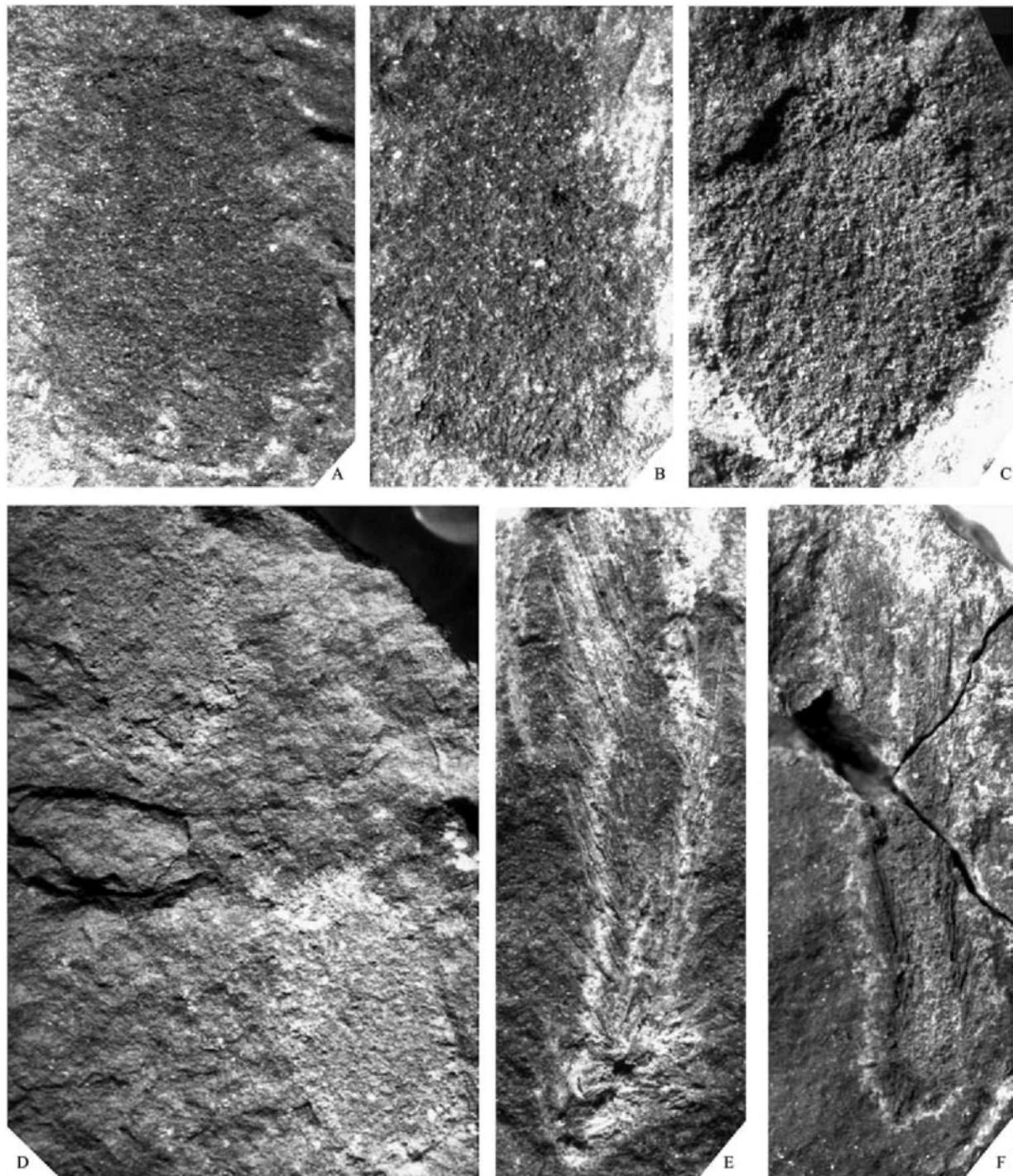


Figure 2 *Xylochos palindromica* gen. et sp. nov. (A)–(D) and *Pirania llanfawrensis* sp. nov. (E), (F). (A) *X. palindromica* SM X.39452, holotype, $\times 6$; (B) SM X.39464, paratype, with basalia, $\times 11$; (C) SM.X.39465, paratype, $\times 10$; (D) SM X.39459–60, paratypes, $\times 3$. (E) *P. llanfawrensis* SM X.39478, holotype, under water, $\times 20$; (F) SM X.41011, paratype, $\times 10$.

that of the spicule mesh, and no other spicules are present, excluding marginalia and basalia. Allowing for the unknown length of monaxons, the skeletal wall thickness is estimated at several to 10 spicule thicknesses (i.e. up to 0.2 mm). There are no obvious ostia or parietal gaps and inhalant canals are assumed to have been 0.2 mm in diameter at most. Osculum revealed by marginalia and was approximately one-half of maximum sponge width. In some specimens (e.g. Figs 2B &

C), the oscular rim is visible as an impression on the spicule mesh, possibly indicating reinforcement of the margin. Orientation of cross-hatching is approximately orthogonal to the sponge axis, leading to a radial pattern in obliquely compressed specimens. All known specimens are completely articulated, excepting basalia, implying a high degree of coherence. There is no evidence for distinct gastralria, which are therefore presumed absent.

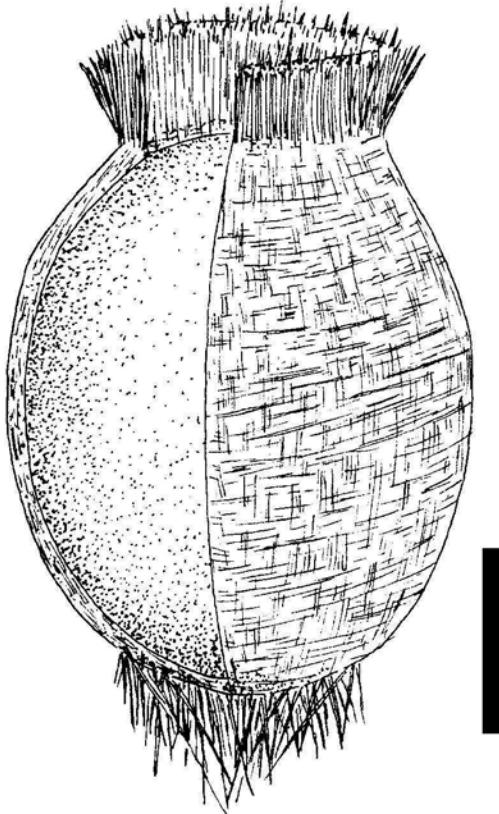


Figure 3 Cut-away reconstruction of adult *Xylochos palindromica* gen. et sp. nov.; scale bar = 2 mm.

All specimens have a broad fringe of marginalia, diameter approximately three times height. Marginalia are fine monaxons, but much coarser than body spicules; length up to 2.8 mm and thickness 0.03 mm in large specimens. Distal terminations oxeate, but proximal terminations are embedded in the body wall and not clearly seen. Marginalia densely packed, but individual monaxons are separable in good specimens, particularly at margins. The fringe was slightly divergent, but not held rigidly; several specimens show convergent vertical flattening, where the sponge body has sunk into the sediment on its side and the marginalia were pushed up by drag against the sediment.

Basal tuft comprises 15–20 monaxons, slightly broader and shorter than marginalia: length 1.5 mm, thickness 0.04 mm. Again, no proximal terminations seen, but distal terminations oxeate. Basalia orientation more variable than body spicules or marginalia, although in general slightly convergent. In some cases, perhaps where damaged, the tuft may be divergent, when it closely resembles the marginal fringe. Overall size of tuft is approximately equal to marginal fringe.

Smallest known example is 3 mm long and morphologically very similar to adults. The marginalia are slightly more pronounced and basalia absent in this specimen (SM X. 39458).

REMARKS. The species occurs among a range of sub-facies at Llanfawr, usually associated with the dictyospongoid *Cyathophycus loydelli* sp. nov., with which it shares several morphological features, although the outer hexactine layer is absent. However, there is no likelihood of confusing the species with any previously described taxon. Where found,

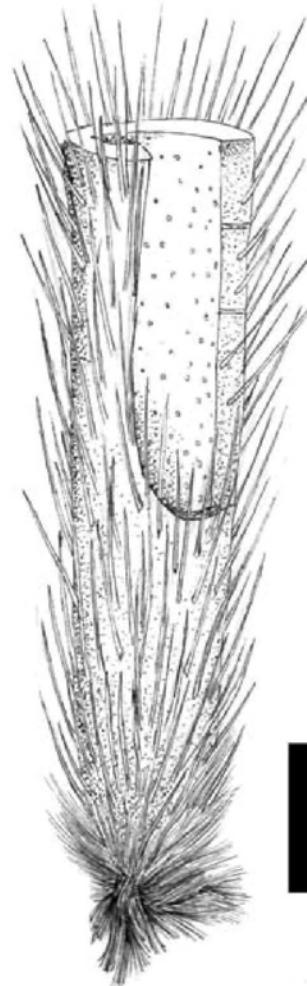


Figure 4 Cut-away reconstruction of *Pirania llanfawrensis* gen. et sp. nov.; scale bar = 2 mm.

X. palindromica tends to be locally clustered, with a very patchy distribution, but is sometimes common. The dense mesh inhibits recognition of the spicule arrangement in poor specimens.

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

TYPE SPECIES. *Pirania muricata* Walcott, 1920, from the Middle Cambrian Burgess Shale, Canada.

OCCURRENCE. Known from the Middle Cambrian of North America and the Middle Ordovician of Wales.

Pirania llanfawrensis sp. nov. (Figs 2E, F, 4)

TYPES. Holotype: SM X.39478; lacking apex. Paratype: SM X.41082; complete but damaged, with less detail preserved than the holotype.

DIAGNOSIS. Small *Pirania* in which the fine dermal monaxons are restricted to the basal region.

ETYMOLOGY. After the Llanfawr Quarries, Llandrindod, Powys; the type locality.

OCCURRENCE. Locality 1 only.

DESCRIPTION. The holotype is a well-preserved proximal region, lacking apex and showing possible broken base of a second branch. The paratype is a complete, larger specimen. Basal region consists of dense, fine monaxons radiating from base of sponge body in all orientations, wavy in places and without individually projecting basalia. Spicules are too densely clustered to specify proximal terminations, but appear to be oxeate distally.

Dermal skeleton comprises projecting styles or subtylostyles – some spicules show slight basal thickening. Spicules are primarily straight, directed upwards at 30–60° to the axis, some curving towards the axis distally, through no more than 10°. Spicules are up to 2.4 mm long, with basal diameter of 0.03 mm, tapering slowly until near the termination. Style density is approximately 15/vertical mm proximally, changing to 8–10/mm distally. There is no evidence of fine monaxons between the styles except in the basal region, extending for only 1.6 mm distally. Spicule bases are concentrated in a region 0.16 mm thick, presumably representing the soft tissue thickness. The sponge body then consists of a simple tube, 0.6 mm wide at the base, widening slightly to 0.8 mm at the observed length of 7.1 mm. In the paratype, which is approximately twice as large in all measurements, the interior is infilled with microcrystalline quartz, showing that even the basal region was largely hollow. The apex is present in the paratype, but shows no distinctive features; prostalia curve upwards and towards the axis in the described manner.

The fine monaxons at the basal region are 0.7 mm long, with basal ray diameter of 0.01 mm, very densely clustered in radiating tufts. A possible branch base in the root region of the holotype is shown by a blunt projection of similar width to the proximal sponge body, but there is no clear evidence. Fine monaxons in this area terminate abruptly, but due to the variable orientation of basalia tufts, undamaged specimens would be needed to confirm branching. The paratype is certainly unbranched.

REMARKS. The present species differs from *P. muricata* Walcott, 1920, redescribed by Rigby (1986), in that it lacks the dense fine monaxons between the styles over the majority of the sponge body. Although it is also much larger than the present species, only two specimens of *P. llanfawrensis* are known and discussion of size differences, either of body or spicules, is inappropriate. The spicules are otherwise very similar in the two species, as is the overall morphology, relative wall thickness and basal morphology. Although the distal spiculation is clearly distinct from the type species, there is little question that *P. llanfawrensis* belongs to *Pirania*.

De Laubenfels (1955) gave the range of *Pirania* as Cambrian to Silurian, but did not give references. No other record of *Pirania* from above the Middle Cambrian has been found and the present species thus indicates a significant expansion of its stratigraphic range.

Class HEXACTINELLIDA Schmidt, 1870

Order RETICULOSA Reid, 1958

Superfamily PROTOSPONGIOIDEA Finks, 1960

Family PROTOSPONGIIDAE Hinde, 1887

Genus HEMINECTERE gen. nov.

DIAGNOSIS. Protospongiids in which orthogonal quadruling has been partially, but incompletely, replaced by tractose development through extension of spicule rays until extensive

overlap occurs; mesh comprises several orders of stauracts and/or hexacts, but without development of more complex morphologies.

TYPE SPECIES. *Heminectere minima* gen. et sp. nov. from the Caradoc of central Wales.

OTHER SPECIES, REASSIGNED. *Protospongia conica* (Rigby & Harris, 1979).

ETYMOLOGY. Latin *hemi*, half and *nectere*, twine, describing the partial development of spicule tracts. Gender *f*.

OCCURRENCE. Widespread in the Silurian and Devonian of North America and the Caradoc of Wales.

REMARKS. There has been much confusion relating to the assignment of protospongoids that clearly differ from *Protospongia*, while retaining some degree of quadruling and lacking particularly distinctive features. The general difficulty in separating hexactines from stauracts in flattened material, typically with coarse iron oxide replacement, has also led to numerous species being included within *Protospongia*, despite not conforming to the generic diagnosis of Rigby (1986), who emphasised the regularity of arrangement, or of Hinde (1888), who restricted the genus to those whose spicules were entirely stauracts. Rigby (1966) suggested that the genus *Protospongia* could be subdivided on the basis of spicule arrangement, particularly of the first-order, but this suggestion has so far been barely adopted. There are presently no other genera available for such species, until the differences become sufficient for inclusion in forms such as *Cyathophycus* Walcott, 1881, *Asthenospongia* Rigby, King & Gunther, 1981, *Testiispongia* Rigby, 1983, or *Ratcliffespongia* Rigby, 1969. Botting (2003) showed that the variation in tract development could be partly ontogenetic rather than taxonomic. However, in this case, there are sufficient specimens to be assured that the species is not merely an early growth stage of a *Protospongia* species. Although clearly related to that genus, it differs in the spicule morphology, extensive first-order ray overlap and less regular subdivision by low-order spicules. *Heminectere* differs from the Middle Cambrian *Testiispongia* in morphology, lesser regularity and absence of root tuft, although anchoring spicules were recorded in *H. conica* (Mehl *et al.* 1993). It is considered likely that several further sub-divisions of this group of sponges will be adopted in future, perhaps on the basis of quantitative characteristics of the spicule mesh; this is not warranted by the present material, although related but qualitatively different genera are also erected below.

Heminectere minima gen. et sp. nov. (Figs 5, 6)

TYPES. Holotype: SM X.41161. Paratypes: SM X.41162–41185; various complete and partial specimens.

DIAGNOSIS. Very small, stauract-dominated spindle-shaped *Heminectere*, with vertical spicule rays longer than horizontal and at least three orders of spicules, including some clinopentactines.

ETYMOLOGY. Latin, small.

OCCURRENCE. Locality 2a only, from both spiculite and blue mudstone.

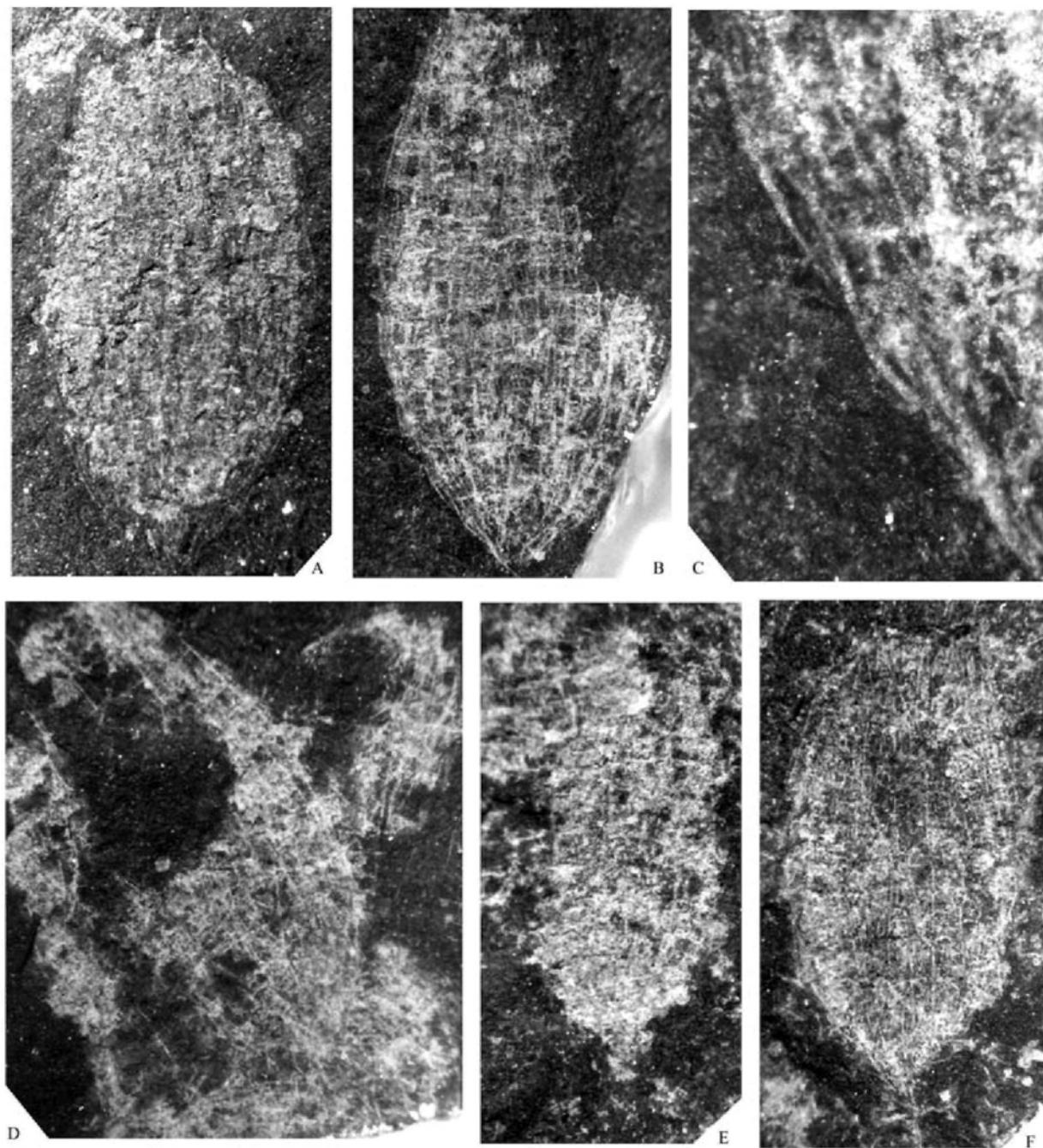


Figure 5 *Heminectere minima* gen. et sp. nov. (A) SM X.41166, paratype, $\times 20$; (B) SM X.41163, paratype, $\times 15$; (C) detail of SM X.42263, $\times 60$; (D) SM X.41178–81, four paratypes in dense association, $\times 15$; (E) SM X.41168, paratype, $\times 19$; (F) SM X.41161, holotype, $\times 13$. All photographs taken under water.

DESCRIPTION. Fusiform sponges with maximum height around 6 mm in observed material and 1.5–2.5 times as high as wide (close to twice in the best-preserved specimens). Maximum flattened width is at around two-fifths of sponge height and equal to half of sponge height. The oscular width is approximately half of the maximum width. Outline smoothly curved, with maximum convexity in the lower third. Spicules parallel to sides, almost exclusively closer to orthogonal than diagonal; fewer than 5% are strongly inclined.

Spicules form a single layer except for overlapping rays, with certainly three, perhaps four orders. All spicules

with at least four rays, and some first-order, are certainly clinopentactinal. No definite hexactines observed, although small orders are unclear; no large hexactines at margins. Spicule rays are straight, or slightly curved proximally in clinopentactines; there are no spines, branches, expansions or other visible modifications. Rays taper evenly, from basal diameter of one-fifteenth of ray length. There are no zero-order spicules (*sensu* Botting 2003). Larger spicules have approximately 30–50% longer vertical rays than horizontal, corresponding to a vertically elongated rectangular first-order grid. First-order spicule rays overlap by at least 50%,

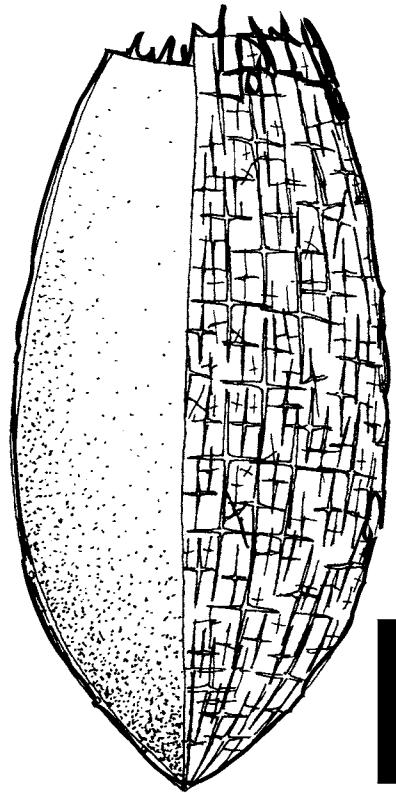


Figure 6 Cut-away reconstruction of *Heminectere minima* gen. et sp. nov.; scale bar = 1 mm.

sometimes entirely, with adjacent spicules. The smaller size orders have all rays of subequal length, but are difficult to distinguish clearly; rays are generally non-overlapping.

The smallest well-preserved specimen is 3.0 mm high, with six or seven first-order squares in the flattened half-diameter. In the largest specimens, there are 13–16 squares, indicating interstitial addition of one lower size order into the first-order grid between these growth stages, in the manner described by Botting (2003).

No basalia are preserved in any specimen. The proximal first-order spicules have ray apices overlapping or adjacent, forming a sharp point, of approximately 90° when flattened, which may have been the only attachment structure. The oscular margin is simple, without distinct marginalia.

REMARKS. The morphology and structure of *H. minima* most closely resembles the larger *H. conica* (Rigby & Harris 1979), also described by Mehl *et al.* (1993), but differs in several features. The smaller size is regarded as a reliable feature due to the substantial number of specimens. The nature of the spicules is seen here to be, in at least some cases, clinopentactinal, whereas *H. conica* is reported to possess only stauracts or hexactines, although imperfect preservation may have resulted in misdiagnosis of spicule morphology. The spicule arrangement, however, is similar; *H. minima* is slightly less bundled, with a smaller ray overlap in adult specimens. The number of spicule orders is probably the same, although the holotype possesses only two (Rigby & Harris 1979), but *H. conica* also possessed anchorage spicules (Mehl *et al.* 1993).

Family ASTHENOSPONGIIDAE fam. nov.

DIAGNOSIS. Protospongoids with partially retained quadruling and containing an enlarged hexactine morphotype (simple or modified), which acts as prostalia. Spongocoel partially enclosed by sharp break in body wall from subconical to horizontal upper surface, significantly reducing oscular diameter.

INCLUDED TAXA. *Asthenospongia* Rigby *et al.*, 1981, *Acutipuerilis* gen. nov. Also ‘*Protospongia*’ *spina* Mehl *et al.*, 1993 and, questionably, *Granulispongia obscura* gen. et sp. nov.

REMARKS. Finks (1983) included only the Protospongidae within the Protospongioidea and no further families have since been added. The morphology and the distinctive characteristic of well-developed prostalia derived from modified first-order spicules are here considered sufficient to separate *Asthenospongia* and *Acutipuerilis* gen. nov. from other protospongids. They appear to represent a coherent group with no obvious descendants. The phylogenetic significance of zero-order spicules is considered in the concluding section.

Genus ASTHENOSPONGIA Rigby *et al.*, 1981

TYPE SPECIES. *Asthenospongia acantha* Rigby *et al.*, 1981, from the Arenig of Idaho.

OTHER SPECIES. *A. cambria* sp. nov and, questionably, *Protospongia spina* Rigby & Mehl, 1994.

DIAGNOSIS. (Emended after Rigby *et al.* 1981.) Thin-walled, conical to cylindrical, with moderate to regular spicule orientation, primarily orthogonal; rough quadrangles formed by first-order spicules. Large zero-order hexactines with non-orthogonal but sub-equal length rays are dispersed around the body wall, producing substantial prostalia; these are concentrated around the dorsal wall flexure, such that non-orthogonal rays are parallel to the wall.

OCCURRENCE. *Asthenospongia* is known from the Middle Ordovician of Wales (Caradoc) and the Lower Ordovician of Idaho. ‘*P.*’ *spina* is from the ? Lower Devonian of Nevada.

REMARKS. Not previously known with a sufficient degree of articulation for a full description of overall morphology. ‘*P.*’ *spina* Mehl *et al.*, 1993, is almost certainly a member of this family, but differences in low-order spicule arrangement and body morphology prevent certain assignment to *Asthenospongia* itself.

Asthenospongia cambria sp. nov. (Figs 7, 8)

TYPES. Holotype: SM X.39479. Paratypes: SM X. 39397, 39480–82, 39484, 39486–9, 39491.

OTHER MATERIAL. SM X. 39483, 39485, 39490. Fair specimens, disarticulated, but not certainly of *A. cambria*.

DIAGNOSIS. High conical *Asthenospongia* with osculum occupying approximately one-half to two-thirds of dorsal diameter; body wall retains quadruled mesh with local regularity maintained over 1–2 first-order squares. Large hexactines with ray length 2–3 times first-order ray length.

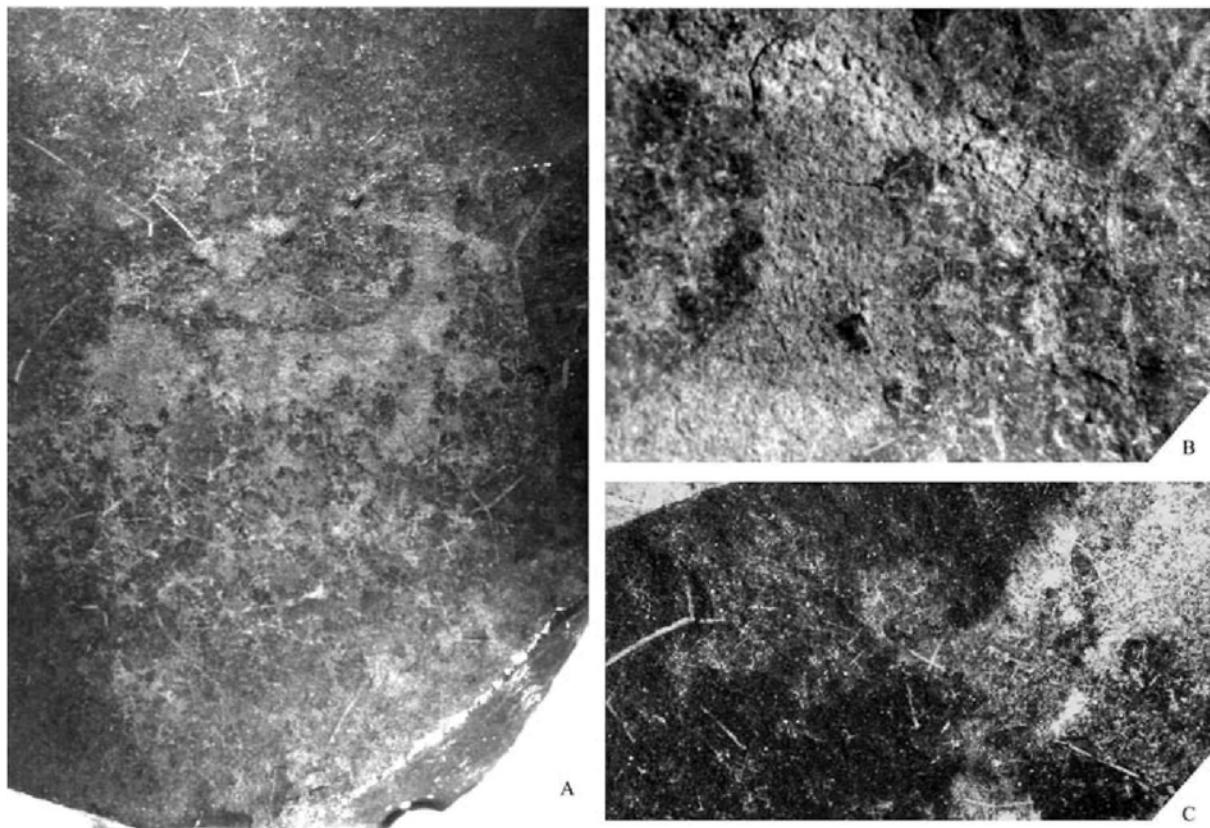


Figure 7 *Asthenospongia cambria* sp. nov. (A) SM X.39479, holotype, overall view, $\times 3.5$; (B) SM X.39479 detail of oscular margin and spicule ray orientation, $\times 10$. (C) SM X.39486, paratype, disarticulated, $\times 5$. All photographs taken under water.

OCCURRENCE. Locality 2b only.

ETYMOLOGY. Latin *Cambria*, Wales.

DESCRIPTION. Details of basal region unknown, but body is high conical to sub-cylindrical with slightly convex sides. The only articulated specimen is 18.3 mm wide and more than 23 mm high, with the maximum width around 5 mm below the upper surface. Osculum approximately 10 mm diameter, in the centre of the upper surface, following inflection to horizontal. The oscular rim is pyritised in the holotype, preventing detailed description of spicule arrangement in that region.

Distal inflection is marked by zero-order hexactines, of which most rays are straight; a few curve smoothly, with radius of curvature around twice ray length. Rays are of sub-equal length within any spicule, distorted in orientation to conform to body wall, with distal ray prostral. Zero-order spicules also present on lateral walls, but less frequent; these also have irregular ray orientations, although generally with coplanar rays parallel to wall.

Smaller size orders are regular hexactines and perhaps some pentactines and/or stauracts, in very loose quadruling. At least five orders of spicules present. All smaller spicules with near-orthogonal, straight rays, tapering smoothly. First-order spicules are dominantly sub-orthogonal to sides of sponge, but with substantial variation. Second-order spicules are of varied orientation, but smaller orders are dominantly diagonal. There is no tract development, or systematic ray overlap. As a result, the wall is very fragile, as also described

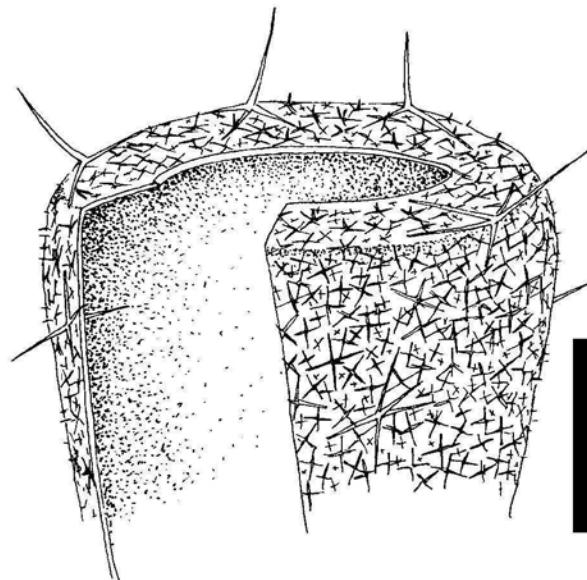


Figure 8 Cut-away reconstruction of *Asthenospongia cambria* sp. nov.; scale bar = 5 mm.

for *A. acantha* Rigby *et al.*, 1981. Although much of the mesh is open space, there is no evidence of distinct parietal gaps.

REMARKS. *A. cambria* can be distinguished from *A. acantha* Rigby *et al.*, 1981, by the more regular arrangement of

zero-order spicules in the latter and the relative sizes of first- and zero-order spicules. There is also a suggestion that *A. acantha* was much shorter, in that some specimens were apparently compressed vertically in the type material. The large hexactine morphology is, at present, sufficient to distinguish the species from all others, including *Acutipuerilis spinosus* gen. et sp. nov.

Genus *ACUTIPUERILIS* gen. nov.

TYPE SPECIES. *Acutipuerilis spinosus* gen. et sp. nov.

DIAGNOSIS. Asthenospongiids in which enlarged hexactines have only one extended, prostomial ray, which is highly developed in the juvenile phase.

OCCURRENCE. Only known from the Caradoc of central Wales.

ETYMOLOGY. From the Latin *acutus*, sharp, violent and *puerilis*, juvenile, for the extreme spinosity of the early growth stages.

REMARKS. This genus is clearly separated from all other reticulosans by the remarkable elongation of prostalia in an otherwise simple protospongiid body wall. It is separated from *Asthenospongia* by the extreme development of one ray of the large hexactines, rather than equal growth of all rays to large size.

Acutipuerilis spinosus gen. et sp. nov. (Figs 9, 10)

TYPES. Holotype: SM X.41083; complete. Paratypes: SM X.39396, 41084–5; two apical specimens and one complete juvenile.

OTHER MATERIAL. SM X.41086. Disarticulated, but appears to be this species.

DIAGNOSIS. As for genus.

ETYMOLOGY. Latin *spinosus*, spiky.

OCCURRENCE. Locality 2a only.

DESCRIPTION. High conical sponge with divergence of wall from axis of 20–30°, generally straight-sided but walls sometimes reducing in angle distally to near-parallel. Ventral surface marked by change in angle to sub-horizontal, forming partial lid over approximately two-thirds of diameter; flexure is rounded, but with small radius of curvature. Flexure is marked by zero-order spicules with hypertrophied distal rays, curving upwards towards axis. The hypertrophied ray is up to 10 mm long in largest specimens, with basal ray diameter of 0.05 mm. The remaining rays are greatly reduced. Zero-order spicules also over body wall surface, also with distal ray curving upwards towards axis, and form isolated basalia near the base, there curving downwards.

Spicules of body wall dominated by small, simple hexactines of at least four orders, possibly some stauracts, but not confirmed. Mesh sparse, with little coherence; first-order spicules separated, arranged irregularly, but each generally associated with locally orthogonal spicules of smaller orders. Approximately one-fifth of smaller orders are diagonal to the associated first-order spicule, the rest more-or-less orthogonal.

Holotype is 10.8 mm high, with maximum width 6.0 mm. Zero-order spicules extend at least 7.6 mm from margins of upper surface and 4.7 mm from base. First-order spicules have ray lengths of up to 0.6 mm, with basal ray diameter of 0.04 mm. The partial paratype X.41085 has maximum width 5.8 mm and zero-order spicules extending at least 9.3 mm distally. First-order spicules have ray lengths up to 0.7 mm, suggesting that although the body width is slightly less than that of the holotype, it represents a later growth stage.

Paratype X.41084 has body length 3.8 mm and maximum width 1.8 mm. Zero-order spicules extend over 4.1 mm distally and 2.5 mm basally, the former probably incomplete. Short, 0.4 mm lateral prostalia also occur. Spicule rays in the disarticulated specimen X.41086 do not exceed 10 mm, despite the much larger array of spicules, which implies a larger body size. This suggests that the importance of the prostalia was emphasised in the early growth stages and growth rate reduced through ontogeny.

Family ?*ASTHENOSPONGIIDAE* fam. nov.

REMARKS. It is unclear whether the large spicules of *Granulispomgia* should be regarded as first-order or zero-order, but they do not appear to be prostomial. However, in all other respects, *Granulispomgia* is similar to the asthenospongiids and may best be questionably included, at least temporarily, within the family. If eventually rejected from the Asthenospongidae, it should fall instead in the Protospongidae, pending further division.

Genus *GRANULISPONGIA* gen. nov.

TYPE SPECIES. *Granulispomgia obscura* gen. et sp. nov.

DIAGNOSIS. Thin-walled protospongidiids with six or seven orders of dominantly hexactine spicules; the largest are of appropriate size to be first-order, but are sparsely distributed and with a greatly reduced radial axis; second-order spicules rare. Spicules are arranged in a coarse grid, but with little regularity at any scale and poor organisation within the approximate squares. Includes spicules with all rays curved in one orientation and others with the two primary axes oblique. Skeleton with numerous small granules, concentrated near the apex.

ETYMOLOGY. Referring to the small mineralised granules that particularly characterise this species, but are lost in more derived protospongiods and their descendants.

REMARKS. Since the genus is currently monospecific, *Granulispomgia* can be identified from the diagnostic spicule morphologies and arrangement. The granules are not unique to this genus, but have so far received little attention, due in part to the difficulty of distinguishing them from embedded spicule rays or entirely diagenetic features.

Granulispomgia obscura gen. et sp. nov. (Figs 11, 12)

TYPES. Holotype: SM X.41087. Paratypes: SM X.39492, 41001–8, 41010. Primarily disarticulated, but containing the diagnostic spicules.

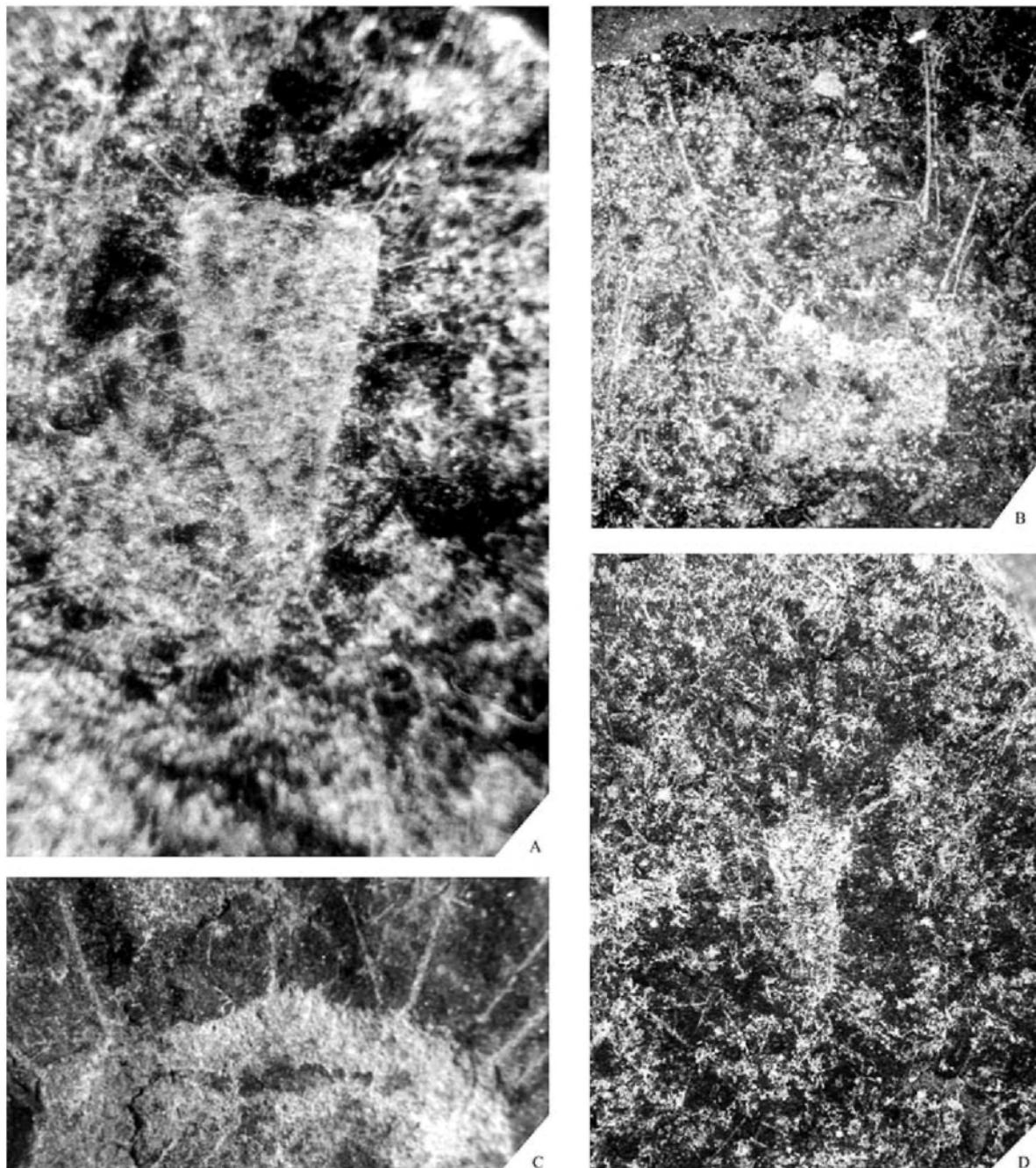


Figure 9 *Acutipuerilis spinosus* gen. et sp. nov. (A) SM X.41083, holotype, $\times 6$, taken under 'dry water' polarisers (Crabb 2001); (B) SM X.41085, paratype, under water, $\times 5$; (C) SM X.39396, paratype, under water, $\times 12$; (D) SM X.41084, paratype (juvenile), under water, $\times 9$. Figure 9(c) reproduced with permission from Botting (2003).

DIAGNOSIS. As for genus.

ETYMOLOGY. Latin, *obscura*, indistinct; referring to the uncertain body morphology.

OCCURRENCE. Localities 1, 2a and 2b.

DESCRIPTION. The available specimens are poorly articulated or consist of associations of spicules only, with the morphology partly visible only on the holotype. Isolated spicules are also known, suggesting that the sponge was not rare, but relatively fragile. Sponge body broadly globose with osculum approximately half of maximum width. Basal region not

seen. Diameter of compressed body approximately 20 mm, although with some disarticulation at margins.

Spicules comprise single layer of hexactines with reduced distal rays, organised in very weak orthogonal quadruiling, only clearly visible around the osculum of the holotype. Only hexactines definitely present, although some with distal ray apparently reduced to a small node. Rays are unusually slender, with ray length to basal diameter ratio being approximately 20–25:1 in observed material. Ray diameter is constant for a large part of the length, then tapers rapidly. Maximum observed length 3.3 mm, corresponding to a width of 0.12 mm. Lower size orders reduce by one-third

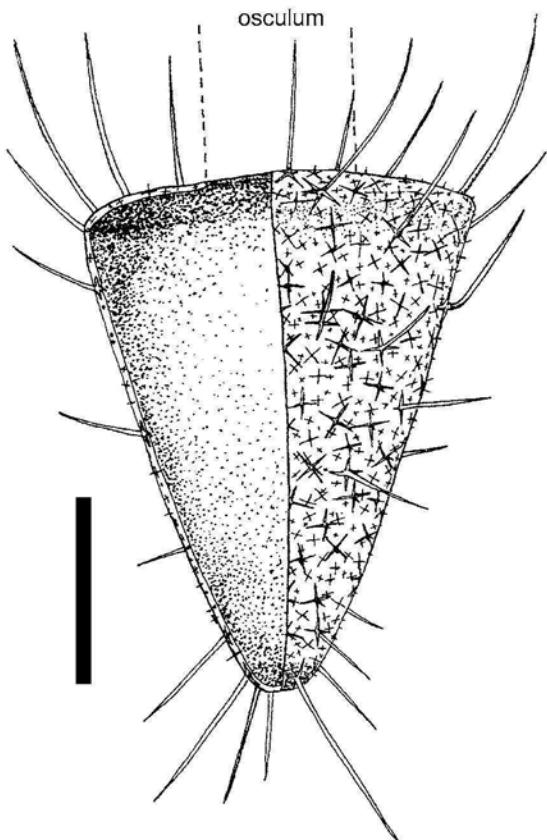


Figure 10 Cut-away reconstruction of adult *Acutipuerilis spinosus* gen. et sp. nov., including position of osculum; scale bar = 5 mm.

at each order, with at least six, probably seven, size orders present in the holotype. The largest size order appears to be slightly hypertrophied, but no complete spicules are visible; however, one suggests a ray length of at least 4.8 mm, and the distal ray is often strongly reduced in these spicules. It is unclear whether it should count as first-order or zero-order, but other characteristics also suggest affinity with the asthenospongiids. Two common modifications of spicules are those with non-orthogonal tangential rays, typically altered to 70–80 and 100–110°, and smooth curvature of all rays in one direction. Each modification can occur in any size order.

REMARKS. The modified spicules are diagnostic at present, although the curved morphotype is similar to the hypertrophied spicules of '*Protospongia*' *spina* Mehl *et al.*, 1993, which differs in possessing a much more regular grid. Details of spicule growth parameters may be useful for distinguishing closely related taxa, should they be discovered. The only species currently described that could be confused with it are *Asthenospongia acantha* and *A. cambria* sp. nov., both of which possess modified zero-order spicules with unpredictable ray orientations and they lack both the regular modifications and the abundant granules seen here.

Family UNCERTAIN

Indeterminate protospongoid sp. A (Fig. 13A)

MATERIAL. SM X.41097; single, near-complete; base damaged.

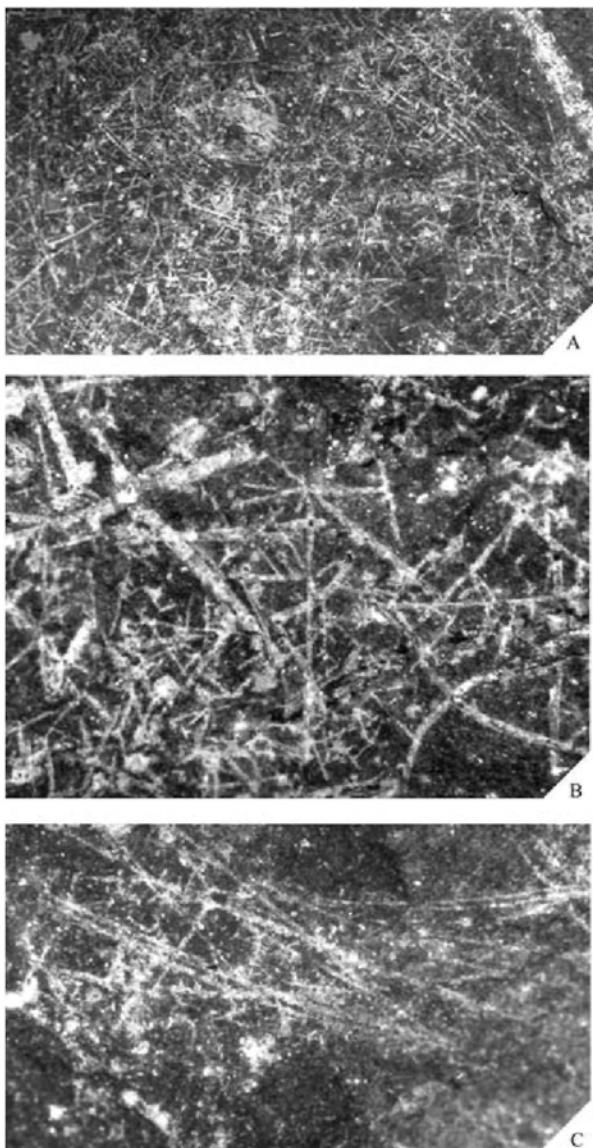


Figure 11 *Granulispongia obscura* gen. et sp. nov. (A) SM X.41087, holotype, overall view, $\times 4$; (B) SM X.41087, detail showing diagnostic spicule morphologies, $\times 30$. (C) SM X.41088, paratype, showing detail of disarticulating oscular margin (?), $\times 20$. All photographs taken under water.

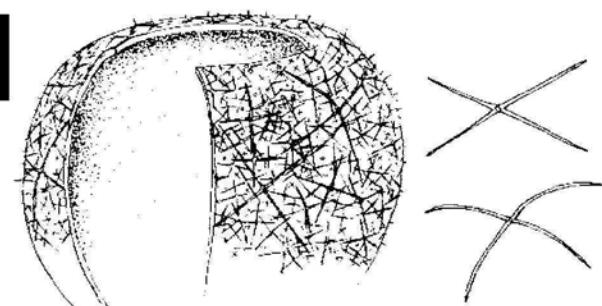


Figure 12 Cut-away reconstruction of *Granulispongia obscura* gen. et sp. nov.; scale bar = 5 mm.

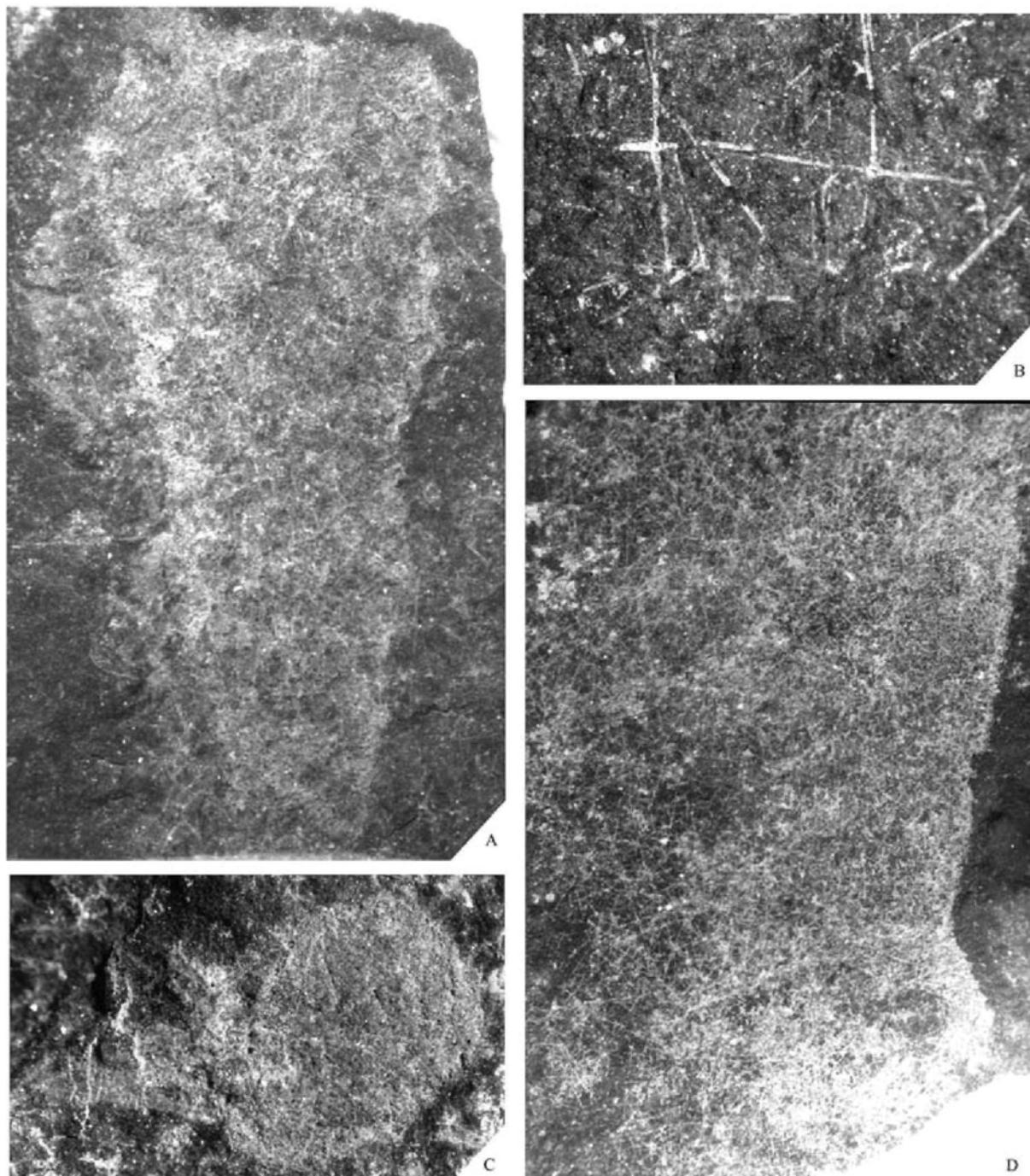


Figure 13 Indeterminate protospongoids, all from locality 2a. (A) SM X.41907, sp. A, $\times 7.5$; (B) SM X.41099, sp. B, $\times 15$; (C) SM X.41186, sp. C, $\times 23$; (D) SM X.41187, sp. D, $\times 5$. Photographs (A), (B) and (D) taken under water.

OCCURRENCE. Locality 2a.

DESCRIPTION. Tall conical sponge preserved as a mass of irregularly distributed spicules, partly hidden by iron oxides that mark soft tissue. Height 18 mm, with maximum width of 8 mm, at apex. Osculum occupies essentially entire upper surface. Base 3 mm wide, rounded, with some scattering of spicules; widening evenly thereafter. At least five orders of spicules present, but no distinct zero-order. Spicules entirely hexactines or simple derivatives. Hexactines have maximum observed ray length of 0.48 mm, corresponding to basal ray

diameter of 0.038 mm. Smaller size orders reduce by a factor of approximately one-third at each order. No visible ornament or modification of rays, which are straight and smoothly tapering.

Arrangement of spicules is unclear over most of sponge body. Regular quadrulung is absent and there is no consistent orientation, but spicules tend to subdivide the irregular spaces rather than clustering randomly. Spicule orientations are extremely variable, but near-45° angles between spicules are very common, suggesting that orientation is not completely irregular. No parietal gaps.

Base preserves no anchorate structure, but may be broken.

REMARKS. The lack of zero-order spicules and simplicity of the hexactines, combined with the single-spicule thickness of the skeletal wall, suggests a position within the *Protospongidae*, but the irregular mesh supports a slightly more derived position. *Heminectere*, for example, preserved a much more regular grid, while those taxa described with a less regular arrangement generally possess more derived features (e.g. spicule morphology and parietal gaps in *Hemidiagoniella caseus* gen. et sp. nov.; thicker wall in *Dilatispongia tumidus* gen. et sp. nov.). The new sponge should be regarded as a derived member of an early lineage of the *Protospongidae*, whose loss of a regular mesh is convergent with that in the rossellimorphs, discussed below.

Indeterminate protospongoid sp. B (Fig. 13B)

MATERIAL. Two small mesh fragments, SM X.41098–9.

DESCRIPTION. Each fragment consists of parts of six grid squares, with some scattered spicules nearby, but SM X.41098 has grid parameters three times larger than that of SM X.41099 and represents a much later growth stage. The spicules are primarily hexactine, with possibly some stauracts; extent of proximal and distal rays unknown. There are at least four spicule orders, perhaps also with zero-order spicules: large, diagonally-orientated and irregularly positioned spicules do not preserve ends of rays. The majority of observed spicules are first- and second-order, with very few of smaller sizes. Length of suspected zero-order spicule rays at least 5.4 mm, with basal ray diameter of 0.12 mm. Maximum observed first-order ray length is 4.3 mm, with basal ray diameter of 0.09 mm. In specimen SM X.41099, basal ray diameter is 0.04 mm for first-order spicules, with ray length at least 1.4 mm. First-order spicule rays overlap extensively in both specimens.

OCCURRENCE. Locality 2a only.

REMARKS. Little discussion can be made of this species, beyond the fact that it differs from all others in the fauna. The large, slender spicules and partial tract development suggest a position on the *Cyathophycus* lineage, supported by the presence of zero-order spicules.

Indeterminate protospongoid sp. C (Fig. 13C)

MATERIAL. SM X.41186; single specimen, very early growth stage.

DESCRIPTION. Globular sponge body of diameter 1.9 mm, showing faint impressions of hexactine-based spicules (probably stauracts) in orthogonal square grid. Grid is poorly preserved over most of the specimen, and each part visible only under specific lighting, but appears at least moderately regular, with consistent orientation over most of the flattened surface. In the centre, grid square size is 0.15 mm, but in places there is sub-division to 0.06 mm. Individual spicules are too small to allow diagnosis of size orders. Basal tuft aligned at 90° to the sponge body, assuming that the converging spicule rays at the top of Fig. 13C represent one pole of the sponge. At least one basalia spicule is hexactine with a hypertrophied ray, 1.4 mm long. Basalia converge distally,

but perhaps resulting from transport. Only four basalia are certainly present, but faint traces suggest the presence of at least two more.

REMARKS. The sponge is presumably a juvenile and the grid is insufficiently developed to allow comparisons with other taxa. The regular grid and sub-spherical morphology recalls *Cyathophycus loydelli* sp. nov., but the basalia are distinct hexactine spicules, as seen in *Hemidiagoniella* gen. nov. and the asthenospongids. In all the latter species, however, the grid is only weakly consistent and it seems unlikely that it represents the juvenile of one of the other species described in this paper. The adult would probably resemble *Protospongia tetraneura* Dawson & Hinde, 1888, although perhaps with a greater number of basalia.

Indeterminate protospongoid sp. D (Fig. 13D)

MATERIAL. SM X.41187.

OCCURRENCE. Locality 2a.

DESCRIPTION. Single, partial specimen showing neither termination and disarticulating on one side. Length of fragment 23 mm and maximum width 15 mm. Irregular but coherent mesh of fine hexactines, some with perpendicular rays reduced, and others with full basal diameter in the distal or proximal ray. It is unclear which surface is visible, since spicules are small and clinopentactines not evident. The mesh consists of locally consistent orientations among some structural spicules, but these are overlain by many smaller spicules in orthogonal, diagonal, or irregular orientations. Positions of spicule centres are not regular, such that first-order grid is difficult to specify over a wide area and, where present, is not sub-divided by second-order spicules in the centres of intervening spaces, but at random positions. First-order squares appear expanded, containing more structural complexity and more spicules than in quadrulated patterns.

Largest (zero-order) spicules with ray length of 2.4 mm and basal ray diameter of 0.07 mm; these are oriented diagonally, and sporadically. First-order spicules with ray length of 1.6 mm and basal diameter 0.04 mm. At least six subsequent size orders, the smallest with ray length 0.1 mm; reduction of ray length by one-third at each order. Ray diameter is constant over most of length. All spicules with straight rays, but rare examples are non-orthogonal, with opposing rays parallel, to angles of 80°. Small granular bodies also present, but not abundant; origin uncertain.

REMARKS. The limited data prevent a full description of this species, which in many respects is very similar to *Granulispongia obscura* gen. et sp. nov. Differences are the relatively small size and slenderness of spicules compared with body size, the absence of the curved spicule morphology and the relative rarity of granules. The grid structure is better preserved in this specimen than in *G. obscura*, but represents a similar grade of organisation. Few other described taxa could be confused with this species, although it is possible that similar fragmentary material is known, but remains undescribed or in open nomenclature. The difficulty with taxa of this type is that they lack any clear distinguishing features and statistical studies are often impossible due to small sample sizes.

Order UNCERTAIN

REMARKS. Overlap between extant and palaeontological taxonomy is negligible among the ‘Rossellimorpha,’ and there are major difficulties with paraphyly. The species below certainly fall within the order Reticulosa, as proposed by Reid (1958) (but regarded by Krautter 2002 as polyphyletic), but in modern terms should be classified among the order Lyssacinosida, as discussed in detail in the section on phylogeny, below. The term ‘Rosselimorpha’ is available for these taxa, but is almost certainly polyphyletic, referring to a structural grade and should not be encouraged. A full revision is required before the biological and palaeontological systems can be reconciled.

Family UNCERTAIN

Genus *HEMIDIAGONIELLA* gen. nov.

TYPE SPECIES. *Hemidiagoniella tenax* gen. et sp. nov.

DIAGNOSIS. Thin-walled protospongiid (single spicule layer) with dense mesh of acanthohexactinal spicules with reduced distal ray, in locally regular sub-quadruloid arrangement, but minimal lateral consistency; orientation of highest-order squares is essentially independent of those three squares away. Several spicule orders present.

ETYMOLOGY. Latin, half-diagonal, referring to the variable orientation of the reticular grid.

OCCURRENCE. Only certainly known from the type locality, except for a single specimen, possibly of *H. tenax*, from locality 1. Isolated spicules closely resembling *Hemidiagoniella* have been recorded in the uppermost *murchisoni* Biozone of Bach-y-Graig stream section, Llandrindod (SO 073 611).

OTHER SPECIES. *H. caseus* gen. et sp. nov.

REMARKS. The skeletal structure of *Hemidiagoniella* represents a previously unrecorded variation on the standard protospongioid arrangement. Most genera related to a *Protospongia*-like form either lose the regularity of the mesh entirely, or develop overlapping spicule rays to form tracts, as in the dictyosponges. In this case, the local regularity is largely retained, but the arrangement of first-order spicules has become irregular. A slight tractose development in *H. caseus* is related to parietal gap development and is generally curved in irregular orientations.

Although isolated acanthohexactines are known from older deposits, this is the earliest example where provenance can be determined. The recognition of surface ornament on *in situ* spicules is often impossible due to weathering of pyritised fossils and low resolution of surface features in external moulds. The recognition of spicular ornament in hexactinellids allows more useful comparisons with disarticulated material and some similarity exists between *Hemidiagoniella* and the indeterminate specimens of Watkins & Coorough (1997) and others, as well as numerous modern lyssakids (e.g. Tabachnik 2002a, b, c).

***Hemidiagoniella tenax* gen. et sp. nov. (Figs 14A–C, 15)**

TYPES. Holotype: SM X.41100; large partial specimen with excellent spicular mould preservation. Paratypes:

SM X.41101–21; partial specimens showing features of morphology or structure.

OTHER MATERIAL. SM X.39426, SM X.41022–41139; numbers refer to slabs—sometimes multiple specimens.

DIAGNOSIS. Large *Hemidiagoniella* in which the spicular mesh is homogeneous, with little or no tract development. Spicule sizes decrease by approximately one-third at each order. Spicules with greatly reduced proximal and distal rays, distal rays apparently only present as small nodes; slight ventral curvature of lateral rays. Overall form based on high cone with flexure point at maximum width, at three-quarters of sponge height, then contraction to around three-quarters of maximum width at apex.

ETYMOLOGY. Latin *tenax*, tough, persistent, referring to the remarkable degree of articulation of most specimens.

OCCURRENCE. Only certainly known from locality 2a, with single possible specimen from locality 1.

DESCRIPTION. Specimens of this species are typically preserved intact and fully articulated, although they dominate in a spiculitic bed (locality 2a) which may represent many disarticulated specimens. Due to large size (greater than 10 cm high; maximum observed width 68 mm), no complete specimens are known, but sufficient fragments to allow reconstruction of entire form. Sponge body is steep conical with rounded base and flexure point at around three-quarters of height, after which diameter contracts slightly. Expansion approximately 20° from axis up to the flexure, narrowing at 10–20° thereafter. Osculum comprises the entire apex.

Skeleton is a dense single-layer mesh of acanthoclinopentactines with a very small distal node representing the sixth ray. Curvature of tangential rays is greatest at the node, straightening and inflexing distally to nearly parallel surface. Local reticulation is regular, with quadruling including almost entirely diagonally-arrayed second-order spicules; subsequent orders may be diagonal or orthogonal relative to local grid. Reticulation irregular on scale greater than two or three first-order squares, deviating to inclined orientations. First-order grid sometimes confused by presence of first-order spicules in diagonal second-order positions, allowing curvature and realignment of primary grid. Five, probably six, size orders present, spicules similar on all scales. Zero-order spicules present in small numbers, typically arranged diagonally.

Maximum observed ray length of first-order spicules is 2.7 mm, but often difficult to assess due to inclination of rays to surface. Corresponding basal ray diameter of 0.08 mm; aspect ratio of spicule rays appears to be constant at 35–40:1 for all size orders.

Several discrete prostalia in the basal region formed by elongating distal ray of hexactines; basalia project subperpendicularly to sponge surface, but limited in length to a few millimetres.

REMARKS. The broad spicule arrangement and morphology are sufficient to distinguish this species from all other fossil genera. Comparison with *H. caseus* is given below.

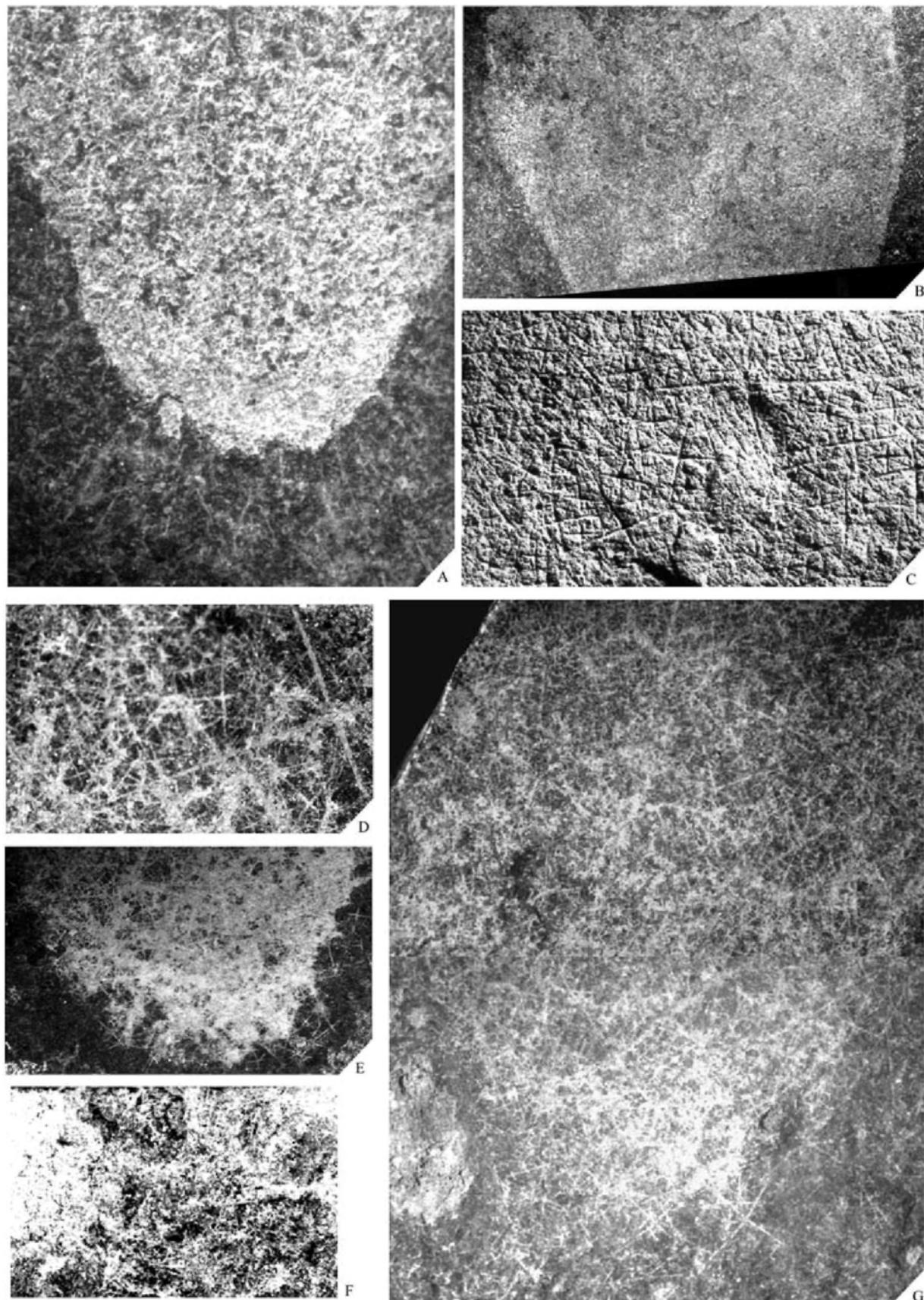


Figure 14 *Hemidiagoniella* gen. nov. (A–C) *H. tenax* gen. et sp. nov. (A) SM X.41101, paratype, showing basalia and proximal morphology, $\times 10$; (B) SM X.41102, paratype, $\times 2.8$; (C) SM X.41100, holotype, showing detail of mesh, $\times 15$. (D)–(G) *H. caseus* gen. et sp. nov. (D) SM X.41140, holotype, detail of upper region, showing spicule arrangement, $\times 5$; (E) SM X.41140, basal region, $\times 2.5$; (F) SM X.41141, paratype, showing parietal gaps; (G) SM X.41188, paratype, near-complete but disarticulating, $\times 5$. All photographs taken under water.

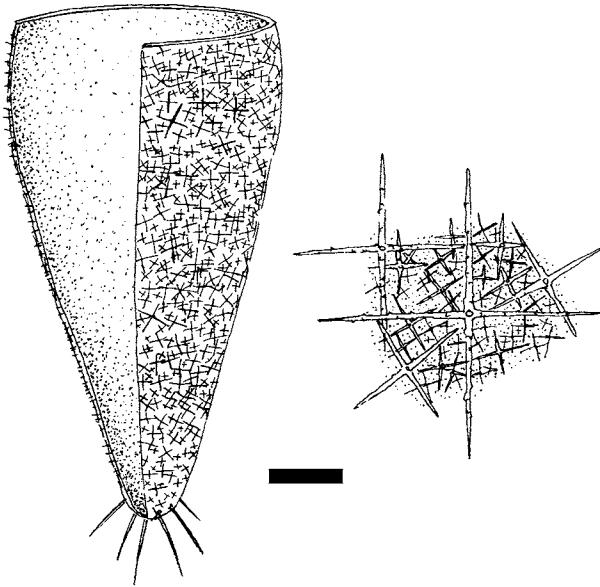


Figure 15 Cut-away reconstruction of *Hemidiagoniella tenax* gen. et sp. nov.; scale bar = 10 mm in overall view and 1 mm in detailed view.

***Hemidiagoniella caseus* gen. et sp. nov. (Figs 13D–G, 16)**

TYPES. Holotype: SM X.41140; complete, but disarticulating at edges. Paratypes: SM X.41141–2, fragments; and SM X.41188, complete but disarticulating.

OTHER MATERIAL. HCM.1998–21/254 (Hereford City Museum); small fragment, lacking diagnostic parietal gaps, but tentatively referred to *H. caseus*.

ETYMOLOGY. Latin *caseus*, cheese, after the inconsistently-sized holes irregularly arranged in the sponge wall. Noun in apposition.

DIAGNOSIS. Broad conical *Hemidiagoniella* with partial meandering tractose development and areas of sparse spicule cover representing parietal gaps. Spicules include large zero-order, thin-rayed acanthohexactines. Hexactines with reduced proximal and distal rays, distal rays reduced more than proximal; lateral rays almost coplanar.

DESCRIPTION. Outline not preserved sharply in rare complete specimens, but broad conical with rounded base. Osculum entire width of sponge, but margin unclear. Width of holotype 45 mm, at height 50 mm.

Skeletal mesh of acanthose hexactines with reduced ray, approximating clinopentactines; proximal ray also reduced, but present. Largely irregular, although with very local ordering within part of one first-order square, often rotated from orthogonal alignment. Structure is perforated by irregular parietal gaps up to 4 mm in width; largest spicule rays cross the gaps and smaller size orders cluster at the margins, further distorting any mesh regularity. Where arrangement is clear, it is based on quadrulung, often with diagonal low orders. There is no coherent first-order grid.

Largest spicules hypertrophied, with maximum observed ray length in the holotype being 10.0 mm and basal diameter 0.25 mm, while the corresponding dimensions for the next largest are 5.3 mm and 1.3 mm. This marked size

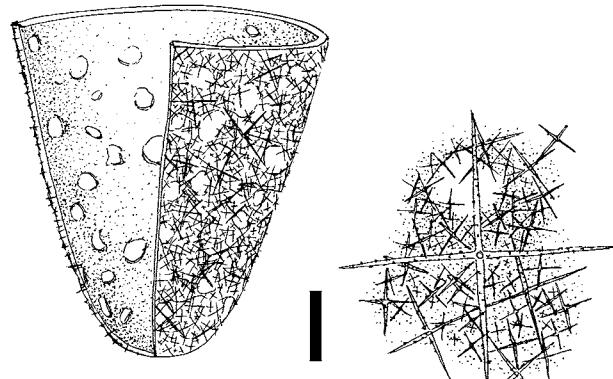


Figure 16 Cut-away reconstruction of *Hemidiagoniella caseus* gen. et sp. nov.; scale bar = 10 mm in overall view and 1 mm in detailed view.

difference and the sporadic placement suggests that these are best interpreted as zero-order spicules. In addition to these, there are at least six further orders in large specimens. Ray length to basal diameter ratio appears to be around 40:1 in all size orders, but is often impossible to measure due to inclined rays.

No prostalia or basalia have been recorded, but this may be due to slight marginal disarticulation in the known specimens.

DISCUSSION. The broad spicule arrangement and morphology are diagnostic of the genus and would be difficult to confuse with other described taxa. *H. caseus* is distinguished from *H. tenax* by the presence of parietal gaps, reduced mesh regularity, and large spicule size relative to body dimensions; and in disarticulated remains by the hypertrophied zero-order spicules.

Genus SOLUSRECTUS gen. nov.

TYPE SPECIES. *Solusrectus rosetta* gen. et sp. nov.

DIAGNOSIS. Thin-walled protospongoid with regular external orthogonal mesh comprising almost exclusively clinopentactines, some with central ornament, in partly quadrulung array. Spicules with reduced proximal rays and distal rays as slight nodes only; slight proximal recurvature of lateral rays, with centre forming boss. Inner layer of sparse oxeas, dominantly aligned parallel to the vertical component of the dermal mesh and normally arranged in pairs.

ETYMOLOGY. Latin, ‘only vertical,’ after the occurrence of monaxons in the subdermal layer.

OCCURRENCE. Known only from the type locality.

REMARKS. This is an extremely interesting genus, in that it shows characteristics of both the protospongids and early dictyospongoids. It resembles *Heminectere minima* gen. et sp. nov. in possessing a part-quadrulung wall of dominantly pentactines, with some ray overlap indicating the beginning of tract development. The weakly-developed inner layer is, however, typical of *Cyathophycus*, as is the size and arrangement of zero-order spicules. These features suggest a

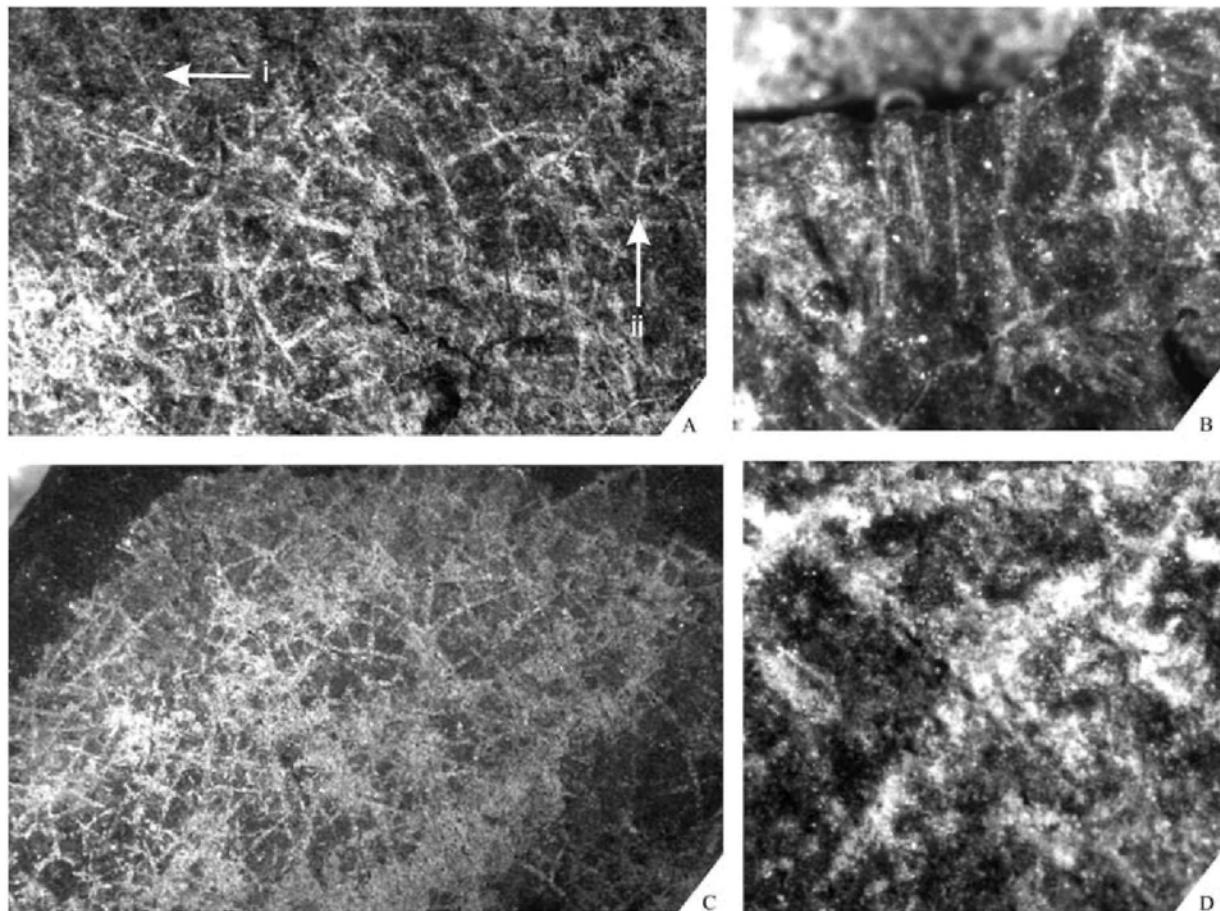


Figure 17 *Solusrectus rosetta* gen. et sp. nov. (A)–(D) SM X.41143, holotype. (A) detail of mesh in apical region, including paired monaxons (i) and apparent pentaradiate (ii), $\times 10$; (B) detail of inner layer, showing several pairs of vertically-aligned monaxons, under water, $\times 20$; (C) part of proximal region of skeleton, showing pyritic film over soft tissue and strong replacement of spicules, under water, $\times 5$; (D) detail of individual rosette clinopentactine from distal region, $\times 40$.

relationship to the early stages of *Cyathophycus* evolution, but the morphologically derived clinopentactines are more complex than the simple hexactines of *Cyathophycus*, suggesting convergent acquisition of either clinopentactines or the inner monaxon layer between lineages (see section on phylogeny, below). The detailed morphology of the clinopentactines is also very close to that described for some supposed brachiospongiids (Webby & Trotter 1993). Morphologically, however, the inner layer is sufficient to classify the genus with the Dictyospongioidea.

Solusrectus differs from *Cyathophycus* in the nature of the monaxial layer and it differs similarly from *Cyathophycella*, while also having a less banded distribution of pentactines. No other bilaminar reticulosans are likely to be confused with *Solusrectus*, if the inner layer is preserved.

***Solusrectus rosetta* gen. et sp. nov. (Figs 17, 18)**

TYPES. Holotype: SM X.41143, near-complete sponge with some disarticulation.

OTHER MATERIAL. SM X.41144–45; fragments probably attributable to *S. rosetta*.

DIAGNOSIS. As for genus.

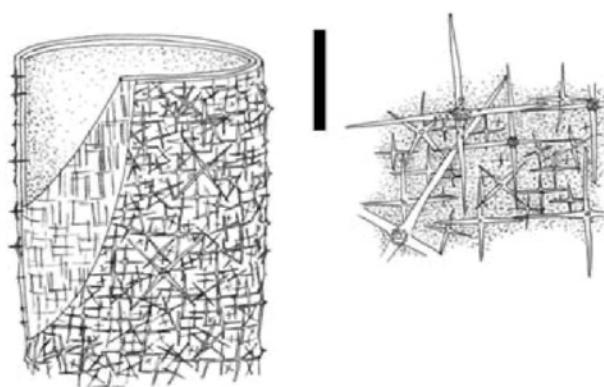


Figure 18 Interpretative cut-away reconstruction of *Solusrectus rosetta* gen. et sp. nov.; scale bar = 10 mm in overall view, 1 mm in detailed view. Regularity of the mesh is slightly enhanced, allowing for the slight disarticulation of the holotype.

ETYMOLOGY. Latin for rosette, after the distinctive ornament on clinopentactine bosses. Noun in apposition.

OCCURRENCE. Locality 2a only.

DESCRIPTION. Overall form of sponge uncertain; the holotype is a partial specimen showing broadly cylindrical form, disarticulating on one side. Width 36 mm and preserved length 65 mm, but probably originally much longer. Skeleton bilaminar, with outer layer of moderately regular, quadrulated clinopentactines. Inner layer of sparse monaxons arranged dominantly vertically, parallel to the outer layer.

Clinopentactines mostly sub-orthogonal, but with frequent spicules at 45° to first-order squares, which are defined by partial ray overlap in the *Cyathophycus* pattern. Subdivision of first-order squares by up to six orders of smaller clinopentactines, in locally regular quadrule arrangement. Clinopentactines with reduced proximal ray and distal ray very reduced or absent. No clear relationship between spicule size and the development of distal ray. Lateral rays initially convex, forming a prominent boss, then inflexed to become parallel to the body wall. In many spicules, the boss is ornamented by a ring of 8–10 small tubercles, arranged in a circle around the distal ray. In some spicules, there appear to be further tubercles over the proximal parts of the lateral rays, but preservation is poor. Rays are generally straight, with occasional spicules showing significant curvature of one or more rays and tapering gradually over their length.

Zero-order spicules are distributed sporadically over the sponge and are invariably oblique (usually close to 45°) to the primary mesh. They appear to be morphologically similar to first-order spicules, but in some cases lack any distal ray or ornament. Due to their size, the boss is raised slightly above the sponge surface, but the rays appear to lie below the lower-order spicules that cross them.

Inner layer poorly developed, comprising fine oxeas in dominantly vertical orientation. Although not clearly seen, the oxeas regularly occur in parallel pairs, even in disarticulated areas; in one region, three sub-vertical pairs and three single oxeas lie sub-vertically and transversely aligned. A few sub-horizontal oxeas are also seen and the layer is presumed to be a partial orthogonal array.

A single, second-order ?pentaradiate is seen (Fig. 17A). This is assumed to be teratomorphic, in the absence of further material.

REMARKS. The precise arrangement of the partially-preserved inner layer must be regarded as tentative, although it is clear that such a layer exists and that it was composed primarily of orthogonal oxeas parallel to the primary mesh. This feature is of great interest in taxonomic and phylogenetic terms, as it seems to represent a simple (and perhaps primitive) variation on the inner spicule layer of *Cyathophycus* and the dictyosponges. This is discussed more fully in the section on phylogeny, below.

The similarity to other sponges is discussed under the genus and there seems to be little chance of confusion in well-preserved material. If the inner layer is not visible, confusion is possible with the other clinopentactine-bearing sponge *Hemidiagoniella tenax* gen. et sp. nov., but the regularity of the dense dermal mesh and extensive spicule ornament of *H. tenax* distinguishes them.

Family ? DICTYOSPONGIIDAE Hall, 1884

REMARKS. *Cyathophycus* was placed in the Hintzespongidae by Finks (1983) and followed by Rigby (1995), Rigby & Mehl (1994) and many subsequent workers (e.g. Krautter

2002), based on the presence of two spicule layers in the body wall. Previous interpretations placed them either in the Protospongiidae (de Laubenfels 1955), or the Dictyospongidae (Hall 1884; Rigby 1986, by implication). The similarity to the Hintzespongidae relates to the inner layer of irregularly-oriented hexactines, which is compared with the monaxon layer of *Cyathophycus*. However, in *Cyathophycus*, the layer is only irregular if parietal gaps are present and it is frequently composed of monaxons, despite the emended diagnosis of Rigby & Mehl (1994), which states that the inner layer consists of irregularly-arranged hexactines or their derivatives, surrounding parietal gaps. However, Rigby (1995) described specimens of *C. reticulatus* Walcott, 1879 (the type species) and *C. pseudoreticulatus* Rigby, 1995 and found no trace of the inner spicule layer in either species. Walcott (1879, 1881) also makes no mention of a secondary layer in *C. reticulatus* and the spicules are referred to as ‘thread-like’ (Walcott 1881: 395), presumably implying monaxons. Dawson & Hinde (1888, 1889) also found no inner layer and the present species possesses an inner layer with no parietal gaps, but a regular cross-hatch of grid-parallel monaxons. In contrast, Rigby & Chatterton (1994) found a possible dermal layer with parietal gaps in their new species, *C. mackeniensis*, although spicules could not be discerned.

The species assigned to *Cyathophycus* so far include a wide diversity of morphologies and structures, the only fully consistent features being the partial bundling of spicule rays in the regular orthogonal grid of the primary layer. The secondary layer is either present or absent and, if present, is dermal or gastralia, consisting of regular or irregular monaxons (or hexactines?), or perhaps no megascleres at all. None of these species are closely similar to *Hintzespongia*, in that the nature of neither spicule layer has been shown to correspond closely to that of the latter. The inner layer of *Cyathophycus* is considered here to be non-homologous with that of *Hintzespongia*, because of the absence of zero-order spicules in the latter and the lack of either dermal quadruling, or a clear description of hexactinal spicules in the inner layer of *Cyathophycus*. The earlier view, that *Cyathophycus* represents a primitive member of the Dictyospongioidea, is preferred. This is also discussed in detail in the section on phylogeny, below. The genus *Cyathophycus* requires revision and clarification.

Genus CYATHOPHYCUS Walcott, 1879

REMARKS. The morphology of *Cyathophycus loydelli* is closer to that of dictyosponges than is that of most other *Cyathophycus* species, in that circular parietal gaps are not developed. Parietal gaps existed in some dictyosponges, but they were formed by vertical and horizontal separation of the tracts, rather than irregular, discrete regions. The morphology of the first true dictyosponge is unknown, but both open conical and sub-globose forms have been described, the conical being much more diverse. *Cyathophycus* was probably close to the ancestral dictyosponge, but the precise significance of the genus is not clear. The earliest dictyospongoids, such as *Quadrolaminiella* and perhaps *Palaeophragmodictya*, differed in some structural characteristics and Mehl (1996), Mehl-Janussen (1999) has argued convincingly for polyphyly. In this case, *Cyathophycus*

would be a natural structural and stratigraphic precursor of the Dictyospongidae (*sensu stricto*). The presence of diagonally-oriented zero-order spicules with reduced distal rays in both *C. loydelli* and *Reticulicymbulum tres* (Botting, in press *a*) supports this interpretation. Pending a revision clarifying the diagnosis of *Cyathophycus*, *C. loydelli* is included within it.

***Cyathophycus loydelli* sp. nov. (Figs 19, 20)**

2003 *Cyathophycus* sp. nov. Botting, p. 42.
In press *b* *Cyathophycus* sp. nov. Botting.

TYPES. Holotype: SM X.39398; showing both skeletal layers, but lacking basalia; locality 2b. Paratypes: SM X.39394–95, SM X.39399–406, SM X.39427; varied specimens, mostly complete, from localities 1, 2a–c.

OTHER MATERIAL. SM X.39407–39425, SM X.39428–51. Specimen numbers refer to slabs, containing in total approximately 200 specimens, often crowded on bedding planes and in all growth stages. Primarily from locality 1, but with additional specimens from all others.

DIAGNOSIS. Sub-spherical *Cyathophycus* lacking parietal gaps, with maximum spicule ray length around 1.2 mm and at least five spicule orders, including zero-order. Root tuft small rope of fine monaxons.

ETYMOLOGY. After D. K. Loydell, who donated the first specimens from the type locality and thus initiated the investigation.

OCCURRENCE. All sponge localities at the Llanfawr Quarries, but not known elsewhere.

DESCRIPTION. Body morphology truncated spheroid with broad osculum occupying two-thirds of total width. Maximum observed diameter 60 mm and minimum recognised 1.7 mm, although smaller specimens could have been overlooked. Detailed description of skeletal dimensions and growth was provided by Botting (2003) and only a summary is required here.

Skeletal mesh comprises eight to 12 first-order squares in compressed equatorial half-circumference at earliest growth stages, with strongly overlapping rays. Second-order spicules also present at early growth stages, sub-dividing the primary grid but relatively inconspicuous. Homogeneous expansion of spicules and grid with size, with appearance of third and fourth-order spicules by a diameter of 4 mm. At around 6 mm, the second-order spicules have enlarged to appear part of the first-order grid, resulting in doubling of the number of squares/circumference. Further expansion leads to an additional increase of around 50%, and a final value of around 30–35 squares/compressed half-circumference. Spicules expand continuously to a maximum ray length of 1.2 mm, which only first-order spicules have been observed to have reached, at a body diameter of around 40 mm. In the described population, very few individuals reached this size, with most being up to 15 mm in diameter.

All dermal spicules are hexactines, smooth with evenly tapering rays and no obvious modification of the distal ray, except for some reduction; it is difficult to establish the length of prostriae due to their orientation in the rock, but basal

distal ray diameter was significantly less than that of lateral rays.

The inner layer is intermittently preserved, since almost all specimens are external moulds with some replacement of the dermal layer, but is visible between the dermal spicules in some specimens. Individual spicules cannot be distinguished due to dense packing, except in slightly disarticulating specimens, where they are oxeate monaxons. Arrangement is in dense orthogonal bands parallel with the dermal grid. The spatial relationship between vertical and horizontal monaxons could not be established. No evidence of parietal gaps has been observed in either layer, although it is possible that they exist in the monaxon layer.

The root tuft is not preserved articulated with any specimen and appears to have been more fragile than the body, although several isolated examples have been recovered from the near-monospecific beds at locality 1, some in close association with body fossils and these are referred to *C. loydelli*. The tuft consists of perhaps 70–100 fine monaxons, each 0.02 mm wide and several millimetres long. Individual spicules do not appear to run the entire tuft length and terminations are oxeate where visible. The tuft width is constant at approximately 1 mm and length at least 10 mm, up to 34 mm observed maximum.

DISCUSSION. No other species of *Cyathophycus* has a sub-spherical form. Several taxa with similar spicule arrangements could potentially be confused with *C. loydelli* in poorly preserved material, such as *Heminectere conica* (Rigby & Harris 1979) and *H. minima* gen. et sp. nov., but these lack the inner monaxon layer and differ markedly in that they possessed only a rudimentary attachment, if any, based on a few pronounced basalia (Rigby & Mehl 1994).

Order LYSSAKIDA Zittel, 1877

Genus *DILATISPONGIA* gen. nov.

TYPE SPECIES. *Dilatispongia tumidus* get. et. sp. nov.

DIAGNOSIS. Moderately thin-walled, but with multiple spicules present within wall thickness; arrangement based on orthogonal quadruling, but poorly preserved beyond very local scale. Dermalia clinopentactines, with short distal boss and further clinopentactines and probably hexactines within wall. Secondary wall component of meandering tracts of similar spicules, producing irregular array of rounded regions with lower spicule density. Tractose bands appear to permeate entire wall thickness. Spicules of several orders, including zero.

ETYMOLOGY. Latin *dilatare*, broad, expanding; referring to the increased wall thickness without the development of separate layers.

OCCURRENCE. Known only from the type locality.

REMARKS. This new genus is potentially significant in understanding the development of thick-walled hexactinellids. Current ideas essentially follow those of Rigby (1986), who advocated an origin for lyssakid amphidiscosan hexactinellids through the bilaminar Hintzespongioidea. Those without a distinct dermal layer, the Malumispongida (Rigby 1967), were presumed to have arisen by loss of the outer quadruled layer, from where the later variations of dermal and gastral

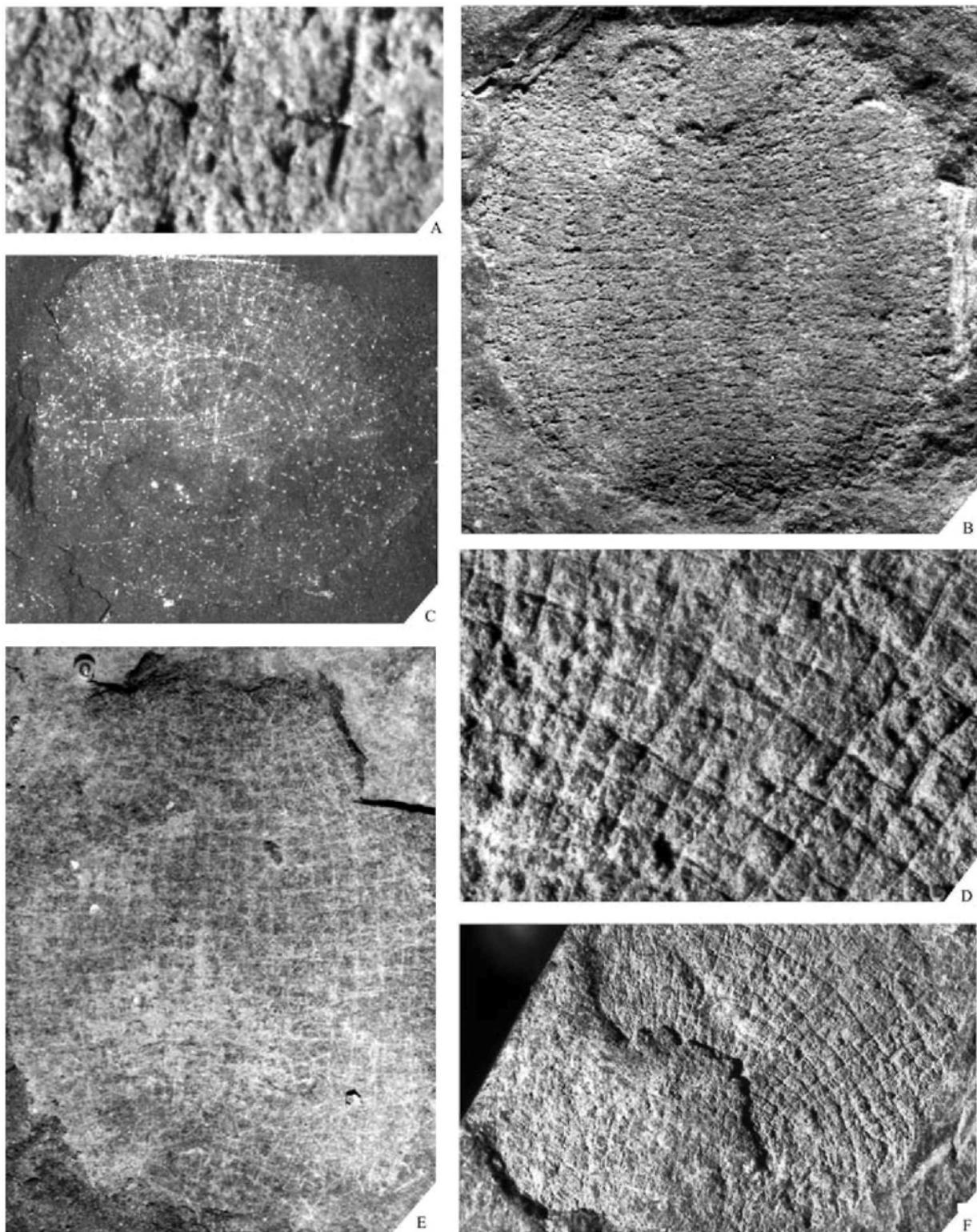


Figure 19 *Cyathophycus loydelli* sp. nov. (A) SM X.39399, paratype, detail showing spicule morphology, $\times 25$; (B) SM X. 39398, holotype, $\times 9$; (C) SM X.39405, paratype in ventral view, under water, $\times 6$; (D) and (F) SM X.39404, paratype. (D) detail showing mesh arrangement, $\times 12$; (F) $\times 6$; (E) SM X. 39402, paratype, $\times 8$.

layers could have been derived. *Dilatispomia* shows an additional or alternative route to the lyssakid condition, which is clearly derived directly from a reticulosan precursor, as shown by the presence of partial quadrules. The presence in the fauna of three other protospongoid species dominated

by clinopentactine dermalia suggests a significant diversification of this lineage, or convergence. Given that there is no indication of more than one hexactine-based spicule layer in the other taxa, it is assumed that the development of specialised spiculation and reduction of quadruling preceded the increase

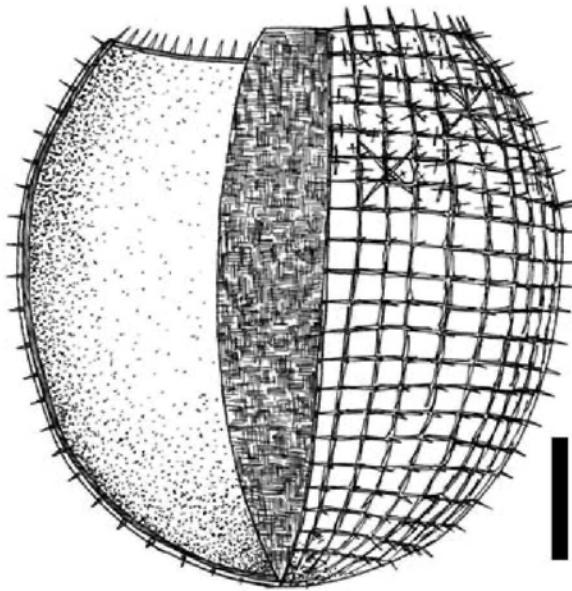


Figure 20 Cut-away reconstruction of *Cyathophycus loydelli* sp. nov.; scale bar = 5 mm. Only the upper right region shows all spicule components; the lower part shows just the primary mesh, for clarity.

in wall thickness. Continuation of the loss of regularity, combined with increasing wall thickness, could have led immediately to such lyssakid groups as the Brachiospongiidae and Malumispongiidae.

Dilatispomia tumidus gen. et sp. nov. (Figs 21, 22)

TYPES. Holotype: SM X.41146. Paratype: SM X.41147; small, poorly preserved fragment, but showing diagnostic features.

OTHER MATERIAL. SM X.41148–9; assignment not absolutely certain, but SM X.41149 has associated fragmentary root tuft.

DIAGNOSIS. As for genus.

ETYMOLOGY. Latin *tumidus*, swollen, after the spicule morphology.

OCCURRENCE. Locality 2a only.

DESCRIPTION. The holotype shows the approximate form to be high conical, expanding upwards at a constant angle of 20° from the axis, to a maximum observed width of 43 mm and height of greater than 68 mm (extrapolated to 80 mm). The base and details of the oscular margin are unknown, although a complex of disarticulating monaxon ropes from the type locality (SM X.41149) shows the base of what is probably this species. An isolated root tuft complex (SM X.41158, below) may represent the structure under ideal preservation. Wall thickness is difficult to judge due to compression, but is greater than a single layer; the compressed thickness is approximately 0.5 mm, having fractured on several levels and it probably represents a live wall thickness of at least 2 mm.

Internal and external fracture surfaces are distinguished by spicule morphology, with boss and reduced distal ray present externally and lateral rays slightly recurved towards proximal ray, internally. Spicules are dominantly clinopentactines; no other morphologies definitely present. Lateral rays typically slightly inflated, with maximum diameter around one-tenth of ray length from base. Rays occur at irregular angles and opposite rays are frequently non-parallel; inter-ray angles vary from 30–150°, although they are usually close to orthogonal. Rays are smooth and usually almost straight except for proximal curvature. Spicules are relatively blunt, with ray aspect ratio of 12–18:1, larger spicules typically having smaller ratios. The largest spicules have a basal ray diameter of up to 0.33 mm and ray length of at least 4 mm. At least four orders of spicules are present, excluding zero-order, which are occasional and distributed largely diagonal to the primary grid. There is no pattern to spicule position within the wall thickness, although the bosses of zero- and first-order spicules are often dermal, with the recurved rays projecting into the wall.

There are two components to spicule arrangement. The entire surface comprises a weak quadrile-based array, often with roughly alternating orthogonal–diagonal orientations at each size reduction. This pattern is only clear for parts of one first-order square, while adjacent regular regions are typically misaligned. Spicules smaller than third-order are rarely present in geometric arrangement. Superimposed on the mesh is a series of meandering tracts, composed of densely-packed spicules of primarily the same type; some regions may also contain monaxons, but none have been confirmed and many are clearly hexactine-based. The tracts contain the majority of small spicules, as well as many larger orders, particularly including those with strongly non-orthogonal rays. Tracts vary between 0.4–1.3 mm wide, except at junctions, where they can be wider. The tracts curve and branch repeatedly, often with small side branches that intersect other tracts. The resulting open spaces are 1–3 mm in diameter, often elongated or otherwise irregular. The tracts appear to occur on the same levels as the mesh spicules, throughout the wall thickness; there is no division into two layers.

REMARKS. *D. tumidus* is among the most distinctive of Palaeozoic hexactinellids described from Britain; no others possess the combination of weak grid and tract development that mimics parietal gaps. The obvious comparison is with *Hintzespongia bilamina* Rigby & Gutschick, 1976, which also possessed a quadrulated grid and tracts/parietal gaps. However, *H. bilamina* consisted of two distinct layers, the spicules were stauracts and perhaps hexacts, rather than clinopentactines, the quadrulated layer was much more regular and the tracts much less dense. In poorly preserved material, the tract development may not be obvious and confusion with taxa possessing large parietal gaps (e.g. *Ratcliffespongia* Rigby, 1969 or *Stephenospongia* Rigby, 1986) is unlikely. Superficially, *Rufuspongia* Rigby & Mehl, 1994, may appear similar, although in this genus there are three distinct layers producing complex apertures, rather than tracts intermingled with a grid and the spicules are primarily diactinal. No other described Palaeozoic sponge has the same structure as *D. tumidus*, although the development of an irregular spicule tract network is common to many extant lyssacinosidans, albeit usually without the pseudo-quadruled mesh.

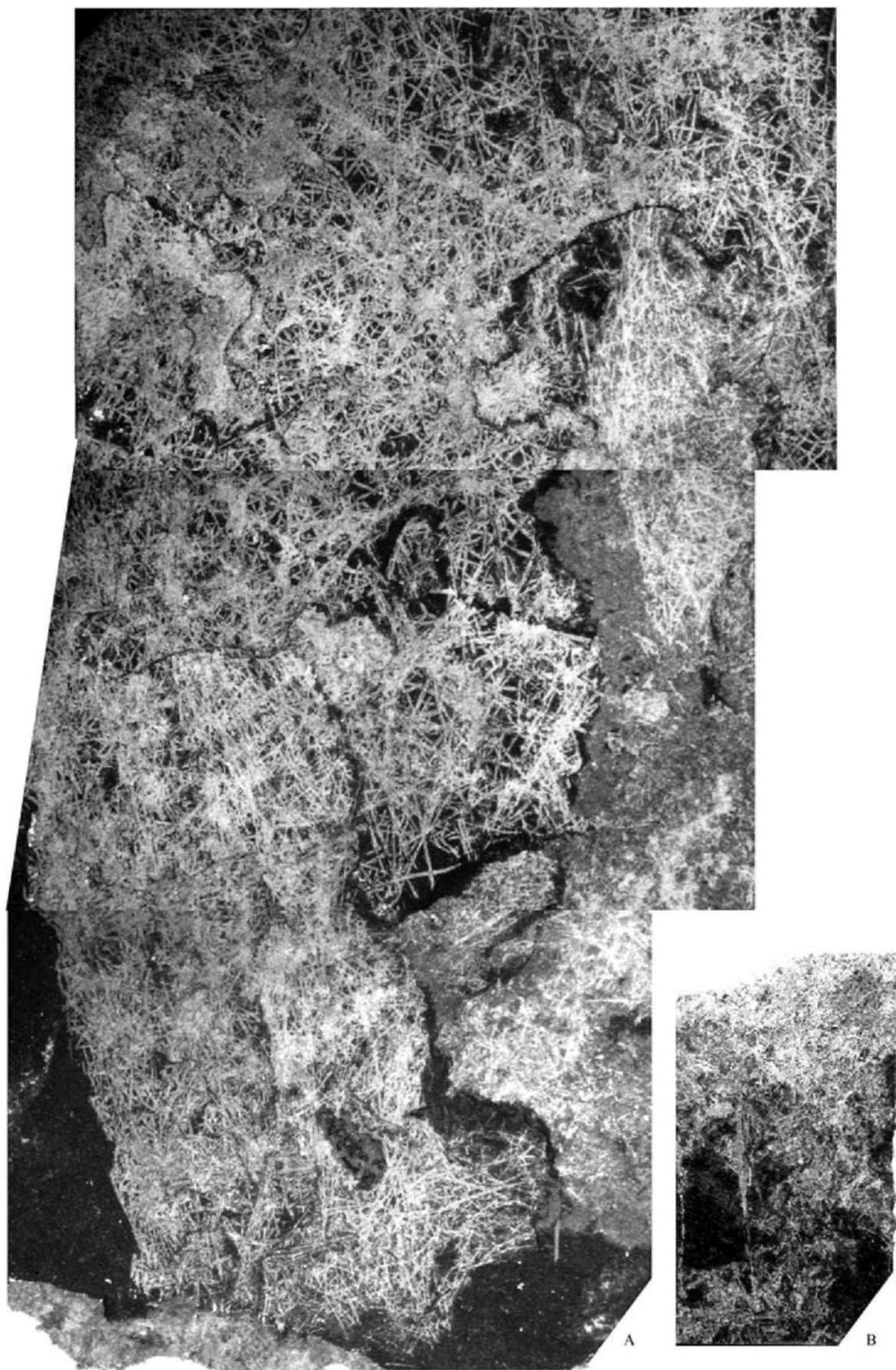


Figure 21 *Dilatispongia tumidus* gen. et sp. nov. (A) SM X.41146, holotype, under water, $\times 4$; (B) SM X.41149, probable *D. tumidus*, showing scattered basal tufts, under water, $\times 6.4$.

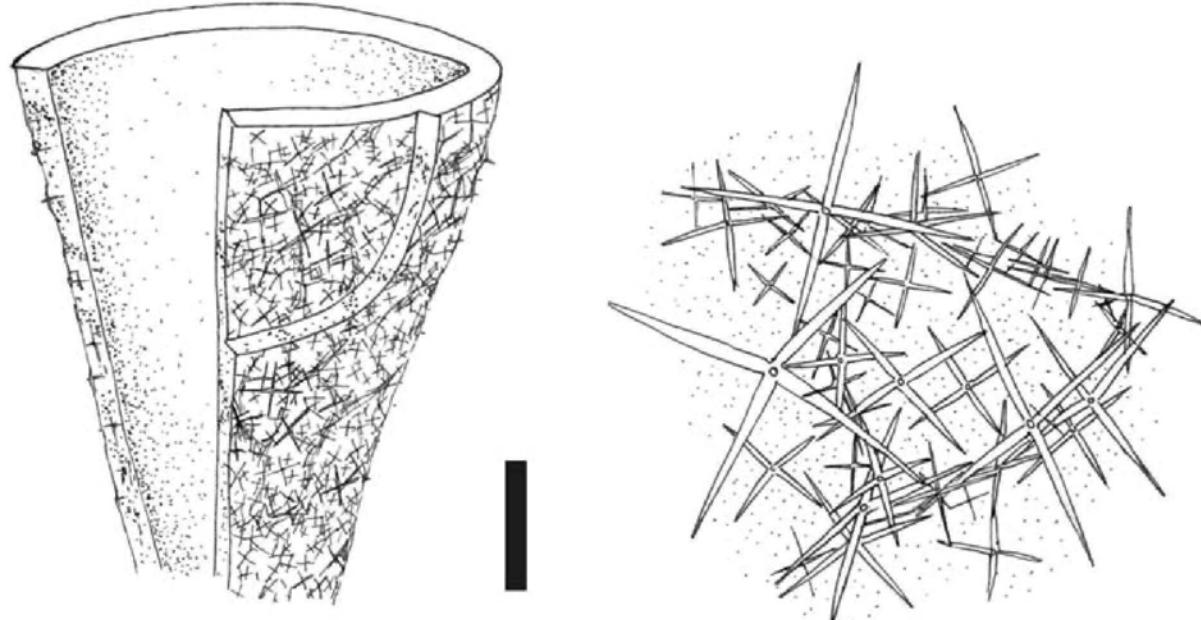


Figure 22 Cut-away reconstruction of *Dilatispongia tumidus* gen. et sp. nov.; scale bar = 10 mm in overall view and 1 mm in detailed view.

ROOT TUFTS

Hexactinellid root tufts are generally treated cursorily in taxonomic studies, since they lack distinctive features and are difficult to assign to known taxa. This is probably true for Recent taxa, which show wide variability and many complex morphologies, often convergent. However, the early Palaeozoic development of root tufts may be of interest in broad-scale phylogenetic and ecological studies and they should be treated in more detail. Of particular importance is their general conservatism, suggesting that differences may be important at a high taxonomic level. This does not exclude the possibility of convergence.

A variety of anchoring structures have been recovered from Llanfawr (Fig. 23), including some preserved in association with the body fossils. The asthenospongiids and *Hemidiagoniella* show a concentration of pronounced prostalia in the basal region. None of the 20 specimens of *Heminectere minuta* show any sign of basalia, although the sponge base is sharply pointed and they were probably directly embedded in the sediment.

Xylochos palindromica possessed a dense cluster of enlarged monaxons, while *Pirania llanfawrensis* shows a radial array of fine projecting spicules in the basal region. *Cyathophycus loydelli*, unusually, preserves the body in generally better condition than the root, but scatterings of monaxons are common around sponge margins and the root was shown, above, to comprise a moderately dense tuft of fine oxeas. The root tufts of *Solusrectus rosetta*, *Granulispongia obscura* and the indeterminate protospongioids are unknown.

Isolated root tufts fall into three groups, with some variation within them: 1, (SM X.41151–41155) fairly dense tufts, as seen in *C. loydelli*; 2, (SM X.41156–41157; U.C.W. (University College of Wales) 19486) divergent splays of monaxons with a common base; 3, (SM X.41158–41160) complex clusters of ropes or splays, which, assuming they are

not clusters of individual root tufts, suggests a broad base. Several examples of what appear to be individual anchoring spicules have also been observed, although these may be isolated prostalia of *Acutipuerilis spinosus*.

The hypothesis that complexity of body morphology broadly parallels complexity of the root tuft in early hexactinellids is consistent with the phylogenetic hypotheses presented below and some trends relevant to phylogenetic reconstructions can be established (Fig. 24). The simplest hexactinellid tufts appear to have been simple modified hexactines as seen in various small protospongiid species, with one ray greatly elongated (e.g. *Protospongia tetraneura* and *P. mononema* Dawson & Hinde, 1889). This is clearly seen in the asthenospongiids, which developed a number of prostalia in the basal region, generally not in contact. It is possible that this represents the ancestral state of root tufts, although other early hexactinellids exist in which no root structures are known (e.g. *H. minuta*); in these cases, it may be secondarily lost, or represent a lineage prior to the evolution of a distinct root structure. *Hemidiagoniella* also possessed spicules of this type. Clusters of basal prostalia were developed in primitive species of *Cyathophycus*, these clusters becoming denser in later species, with the individual spicules becoming diactinal. The type 2, above, may represent an intermediate stage in which spicules are still divergent, but with closely clustered bases. The root tuft of forms allied with *Solusrectus* are anticipated to have been of this type.

Superficially, there is a contradiction in *Dilatispongia*, which shows a cluster of fairly dense tufts, but lacks the derived structural features of bilaminar taxa. This is discussed in the section on phylogeny, below.

Demosponges often lack root structures, but the monaxon cluster of the simple hazelid *Xylochos palindromica* is very similar to type 2 above, suggested to be intermediate stages of the *Cyathophycus* lineage. The dense tuft of very fine monaxons in *Pirania llanfawrensis* may ultimately be derived from this.

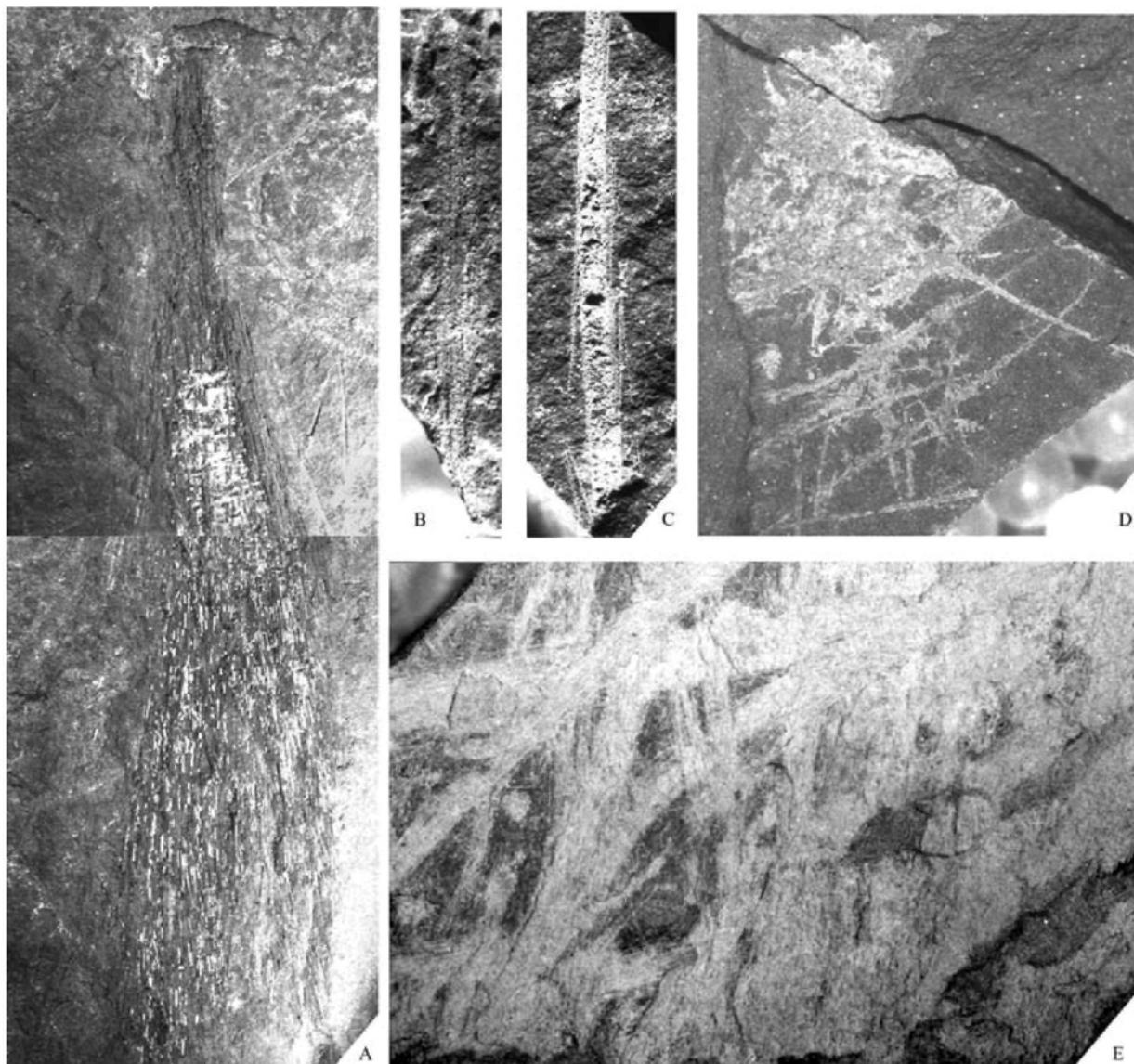


Figure 23 Root tufts. (A) U.C.W. 19486, type 2, \times 3; (B) SM X.41154, type 1, \times 10; (C) SM X.41155, type 1, \times 7; (D) SM X.41160, type 3 with fine tufts, \times 5; (E) SM X. 41158, type 3, \times 4.5. Photographs D and E were taken under water.

PHYLOGENETIC CONSIDERATIONS

Our understanding of early sponge phylogeny is complicated by their relatively poor record. Although there are now a large number of described species from the late Precambrian to the Silurian, most are recorded from very few localities, implying that the record is still extremely incomplete. This is unlikely to be due to ubiquitously strict endemism, based on the moderately wide dispersal of modern taxa. As a result, there are large gaps in the records of many groups, particularly those from high-energy environments (but see Botting in press *a*). Many genera are long-ranging, obscuring stratigraphic indications of relationship. There is also believed to be a high level of convergence at all taxonomic levels, as seen in modern taxa and, in most cases, few characters. Microscleres, essential in modern taxonomy, are rare in the Palaeozoic record, almost exclusively isolated and, thus, of little phylogenetic use despite some dedicated attempts (Reid 1968). However, the record is gradually improving and the

current fauna adds considerably to our knowledge of early hexactinellid and demosponge evolution.

Particular problems include the relationship of reticulosan hexactinellids to early demosponges (Botting in press *b*) and the origin of extant hexactinellid groups, such as the hexactinosans. Some primitive living forms, such as the Rossellidae and Euplectellidae, potentially allow some connections with extinct groups, but their histories are very uncertain. Even the origins of extinct Palaeozoic clades such as the Brachiospongidae are still unclear. The fauna described here appears to fill some gaps relating to the origins of the rossellimorphs, brachiospongoids and related groups.

Several structural grades of reticulosan are represented in the fauna. The simplest is that of *Heminectere minima*, involving a single layer of simple stauracts or clinopentactines in regular orthogonal array, with moderately ordered quadruling and partial first-order ray overlap. This type of morphology may be regarded as similar to the most primitive hexactinellids, since Mehl (1991, 1996) has argued that

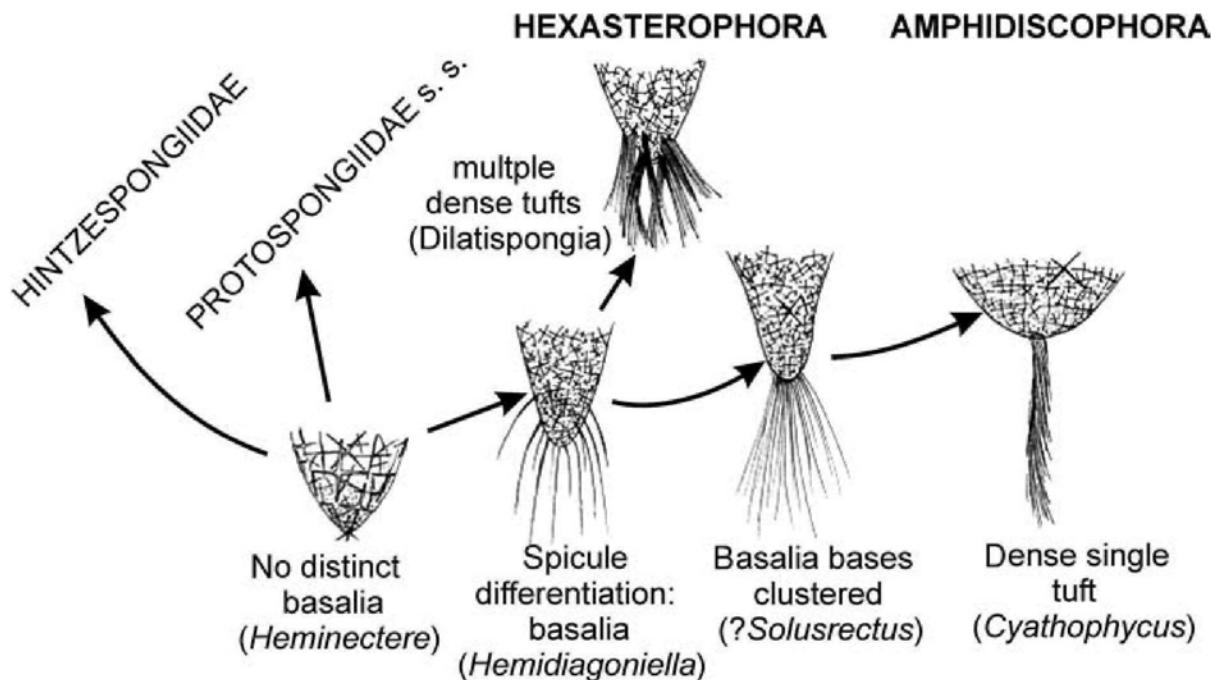


Figure 24 Proposed schematic evolution of hexactinellid root tufts in early Palaeozoic; generic names are used as examples and do not indicate direct relationships. This scheme is an outline and many exceptions are expected, particularly in extant taxa. *s.s.*, *sensu stricto*.

Protospongia itself is derived, while Botting (2003) has shown that the *Protospongia* spicule arrangement could have been derived from a more tractose arrangement by peramorphic growth to large size. Although less regular morphologies are present in the Lower Cambrian (e.g. Steiner *et al.* 1993), later hexactinellids all appear to derive from reticulosans and these other morphologies must be regarded as either early representatives of derived clades, or relatives of extinct stem group taxa from which the protospongoids may have evolved. This view may require modification, but it will be employed as a null hypothesis for the purposes of this paper. *Hemidiagoniella tenax* and *H. caseus* each possessed a single layer of acanthohexactines, with very short distal rays that therefore approximated to clinopentactines and each retains a locally ordered, dominantly orthogonal array. Although it is impossible to state with certainty that they shared a near ancestor with *Heminectere*, the few characters available support a fairly close relationship.

The development of a second spicule layer is critical in early hexactinellid phylogeny and several routes appear to have led to a bilaminar structure. *Mataspongia apaches* (Rigby 1970) developed a dermal monaxon layer, while the otherwise similar *Cyathophycus*–dictyospunge lineage developed a parallel gastral layer and *Hintzespongia*, *Dierespiongia* (Rigby & Gutschick 1976) and allies evolved a second hexactine-based layer. None of the Llanfawr species developed two distinct, hexactine-based layers, but *Solusrectus rosetta* and *Cyathophycus loydelli* possessed a gastral monaxon layer parallel to the external mesh. Of these, *Solusrectus* shows a simpler gastral layer, with sparse distribution of monaxons, typically in vertical pairs, while *Cyathophycus* possessed a dense cross-hatched layer. The dermal layer of *Cyathophycus* was also further from the loose, part-quadrulated array of *Heminectere*, instead showing strong tract development at the first order.

This suggests that *Cyathophycus* represents a more derived part of the reticulosan lineage. However, the dermal spicules of *Cyathophycus* are simple hexactines, in contrast to the derived morphologies of *Heminectere*, *Hemidiagoniella* and *Solusrectus*. This requires either convergent acquisition of clinopentactines, or redevelopment of the distal ray in *Cyathophycus*. However, the acanthose ornament of *Hemidiagoniella* and *Solusrectus* must also have been independently derived, unless the monaxial layer was convergent between *Solusrectus* and *Cyathophycus*, or secondarily lost in *Hemidiagoniella*. Both the latter hypotheses appear unlikely. A preliminary hypothesis is that spicule ornamentation and ray suppression is genetically simpler than the production of a new spicule layer and more likely to be convergently derived. This requires that *Solusrectus* is a sister group of *Cyathophycus* and later forms, with *Hemidiagoniella* being more distant. In this scenario, it seems likely that the clinopentactinal spicules of *Heminectere* represent the ancestral morphology in this lineage. The subsequent modification to ornamented clinopentactines and hexactines appears to have been a recurrent phenomenon and may have been a genetic tendency within the lineage.

The rosette ornament of the clinopentactines in *Solusrectus* is similar to some specimens described by Webby & Trotter (1993) and Acanthocoryna Finks (1960), who referred them to the brachiospongids. The Brachiospongidae are characterised by a loose, irregular skeleton of hexactine-based spicules, comprising a thick wall, with a morphologically distinct spiculation in the dermal layer. This contrasts with the Malumispongidae (Rigby 1967), in which the dermal layer is not distinct. The Brachiospongidae are known primarily from North America, particularly the Ordovician and Silurian. Precursors are uncertain; Rigby (1986) suggested that they derived from the Hintzespongidae by loss of the quadrulated layer, but with no direct evidence. An

alternative scenario is that they evolved via a *Dilatispongia*-type form, from the main protospongoid–dictyospongoid lineage; in this case there is already some thickening of a homogeneous spicule layer. The production of a thick wall represents a novel development in growth pattern, which potentially allowed fused skeletons and radial addition to be utilised (Botting 2003), and is not a trivial transition. Therefore, in the absence of evidence for thickened walls in the Hintzespongioidea, derivation from a *Dilatispongia*-type form is preferred.

The presence of a cluster of root tufts in *Dilatispongia tumidus* is, at first sight, inconsistent with the scheme, because a single dense tuft of this type appears only with *Cyathophycus*. This must be convergent and represents one of two developmental paths from the asthenospongiid condition: (i) concentration of basalia into a single tuft and (ii) development of several tufts corresponding to the positions of individual basalia. Later hexactinellids appear to have largely retained this distinction, with the amphiscophoridan family Hyalonematidae possessing a single, sometimes hypertrophied tuft (Tabachnik & Menshenina 2002), and the Monoraphidae possessing only a single, hypertrophied basal spicule (Tabachnik 2002d); the Pheronematidae generally have a single, but more diffuse tuft. Among the hexasterophoridan Hexactinosa there is more variation, including a variety of cementing attachments to hard substrates, or rigid stalks. The Lyssacinosida (Euplectellidae, Leucopsacidae and Rossellidae) generally possess either isolated basalia or several tufts. The Euplectellidae, in particular, possess basalia that are modified hexactines or their derivatives (Tabachnik 2002a), as seen in *Hemidiagoniella* and the asthenospongidiids. The Leucopsacidae possess a fused basal disc or stalk (Tabachnik 2002b), while the Rossellidae include a variety of forms, including modified hexactine basalia (e.g. *Anoxycalyx* (A.) *ijimai*; Tabachnik 2002c: 1455), and clusters of tufts (e.g. *Anoxycalyx* (*Scolymastra*) *joubini*; Tabachnik 2002c: 1457). The non-lyssacinosidan Hexasterophora also tends towards more plastic morphology than either of the other groups.

Taken straightforwardly, this discussion suggests that the Amphiscophora were derived from the later stages of the *Cyathophycus*–dictyosponge lineage, while the Lyssacinosida evolved from a more primitive stage, perhaps close to *Hemidiagoniella* and *Solusrectus*. Assuming monophyly of the hexasterophoridans, this implies that the Hexactinosa are a later development from this lineage. However, the development of coloniality in those with single tufts would be expected to result in multiple tufts and concentration of several tufts into one is also near-inevitable in taxa with narrow morphologies. Therefore, the number and nature of tufts cannot be taken as an infallible indicator of relationship, particularly in later forms, but is nonetheless an interesting and potentially useful character in primitive hexactinellids.

This scenario is consistent with structural considerations regarding rossellimorph ancestry. The term refers to Recent hexactinellids, particularly lyssacinosidans, that are thin-walled, typically with pronounced dermal clinopentactines or stauracts. The earliest examples ascribed to the Rossellimorpha are the Devonian *Rufuspongiidae* (Rigby & Mehl 1994), but here there are three distinct layers of hexactine-derived spicules. Although they lack the quadruling in one layer of the Hintzespongidae (Rigby & Gutschick 1976), it is possible that they were derived from this lineage, or represent a convergent development.

The Rossellidae *sensu stricto* are defined on hypodermal pentactines that include the development of prostalia and basalia, small dermalia and a chonaosomal skeleton chiefly of monaxons (Tabachnik 2002c). They are similar in many ways to the Euplectellidae, except for the rarity of hexactines or pentactines in the latter (Tabachnik 2002a), and to the Leucopsacidae (Tabachnik 2002b). These comprise the modern understanding of the extant Lyssacinosida and all are united by the loose arrangement of spicules, which are typically acanthose or otherwise modified. These features are also found in *Solusrectus rosetta* and *Hemidiagoniella* spp., which possessed a thin wall of ornamented (acanthose) pentactines, some of which were extended into basalia, as discussed above, smaller size orders of pentactines and hexactines which could be homologous with the rosselid dermalia and, in the case of *S. rosetta*, an inner layer of relatively loosely arranged diactines, possibly representing the ancestral choanosomal skeleton. Although the geometric arrangement of the spicules is more striking in these Ordovician forms, the critical features are all present and these taxa are suggested as representing stem group Rossellidae. The other extant Lyssakida would probably have been derived from this group, since they do not share the dominance of clinopentactines.

The presence or absence of zero-order spicules (*sensu* Botting 2003) also appears to be a useful, although previously overlooked, feature. The poor distinctions between size orders prevent this being useful in modern hexactinellids, but they are normally clearly discernable, if present, in Lower Palaeozoic reticulosans. Zero-order spicules are most prominent in the Asthenospongidae, but also occur in all other members of the *Solusrectus*–*Cyathophycus* lineage, as well as *Dilatispongia*. However, they are certainly not present in the simplest protospongoids, such as *Heminectere* and perhaps not in *Granulispongia*, although this is uncertain – first-order spicules appear slightly hypertrophied, but the regularity of their arrangement is unknown.

Among other described taxa, zero-order spicules are absent from *Protospongia hicksi* (e.g. Rigby 1966), *Diagoniella* spp. and *Hintzespongia bilamina* Rigby & Gutschick, 1976, but present in *Protospongia spina* Mehl *et al.*, 1993 and in the structurally complex, bilaminar *Dierespongia palla* Rigby & Gutschick, 1976. They also appear to be absent from the Lower Cambrian Sansha sponges (Steiner *et al.* 1993), although there is too little regularity in the skeletal mesh to allow certain recognition, and from later dictyosponge-like forms such as *Ammonella* (Keupp & Mehl 1995). The trilaminar *Rufuspongia* Rigby & Mehl, 1994, which has been described as the earliest known rosselid (Mehl-Janussen 1999), is composed dominantly of diactines and the attachment structure is unknown. There do not appear to be zero-order spicules, but these could be disguised by the complex, irregular arrangement and reduced spicule rays. I am uncertain whether this is a genuine rosselid, or a member of an independent lineage, perhaps related to *Hintzespongia*.

Although the position of many groups is still largely obscure, comments can be made on the status of some. The coarse network of dermal and gastral spicules in the pelicospongiid *Larispongia magdalena* Carrera, 1998, is structurally very similar to the dense regions of the mesh of *D. tumidus* and the group is probably a closely related lineage. The presence of probable zero-order spicules, especially in the basal region, is consistent with derivation from a group with

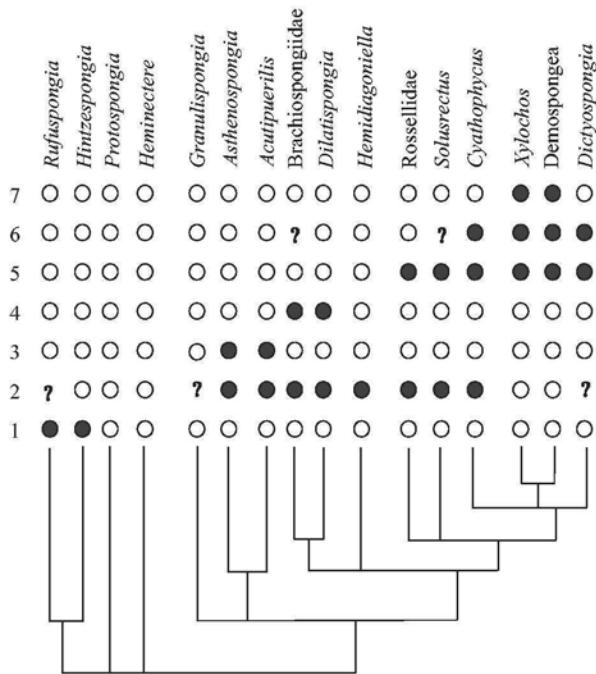


Figure 25 Proposed phylogeny of early hexactinellids, based on the present fauna. Listed characters represent critical structural innovations; 1, second hexactine-based layer; 2, zero-order spicules; 3, hypertrophication of zero-order spicules as prostalia; 4, thickening of single-layer wall; 5, inner monaxon layer; 6, discrete root tuft developed; 7, loss of outer hexactine-based layer. For full discussion of the occurrence of these features, see the text.

enlarged, separate basalia. *Wongaspongia* Rigby & Webby, 1988, also shows evidence of enlarged and irregularly orientated spicules within the endosomal skeleton, but has a bilaminar wall, both layers hexactinal. The structure of the inner wall is again similar to *D. tumidus*, with a combination of sinuous tracts and very weak reticulation, suggesting that this lineage diversified significantly during the Ordovician, including the development of additional spicule layers. There is little similarity of these layers to the bilaminar wall of *Hintzespongia* Rigby & Gutschick, 1976, which lacks zero-order spicules, implying that multiple hexactinal layers have been convergently acquired.

Although the relationships suggested here (Fig. 25, discussed below) are only an outline hypothesis and will doubtless be subject to major revision, they are supported by apparently consistent structural features and are based on important new material. They differ from previous interpretations in attributing significance to attachment structure and presence of zero-order spicules as much as to traditional characters, such as spicule ray overlap, which may be unreliable (Botting 2003). A bilaminar wall appears to have evolved several times in different forms, and the evolutionary emphasis has been shifted away from the Hintzespongidae to the *Cyathophycus* lineage, which is shown to be much more diverse than previously recognised.

According to this scheme, the ancestral hexactinellid would have possessed simple hexactine-based spicules, possibly pentactines, in multiple but similar size orders, and would have lacked a discrete attachment structure. The skeletal arrangement would have been regular and unilam-

inar and either tractose or quadrulored, or some combination of the two. Several of the small protospongiid species, such as *H. conica*, approach this condition, although none fulfil it entirely. Major emergent clades from this group are the *Diagoniella* lineage (possibly a sister group to other hexactinellids), the Hintzespongidae and the Dictyospongioidea. The latter was derived through intermediary stages that apparently gave rise to the Rossellidae and, perhaps, the Brachiospongioidea and thus includes the common ancestor of extant hexactinellids.

There are significant differences between this phylogenetic interpretation and those published previously. Reid (1958) argued for a fundamental separation of Amphidiscophora and Hexasterophora, but this requires extensive ghost ranges and has little direct evidence beyond the modern mutual exclusion of microscle types. He erected the Reticulosa as an independent lineage perhaps derived from the Hexasterophora during the Precambrian and including the majority of Palaeozoic hexactinellids.

Rigby (1986) proposed the Hintzespongidae as being close to the ancestral state for thick-walled taxa such as the Brachiospongidae and regarded the *Cyathophycus*-dictyosponge lineage as an evolutionary dead end. This has been reversed in the present scheme, on the basis that a bilaminar wall of two thin layers is a separate development to a single thick wall. This view is augmented by the similarity of *Dilatispomia* gen. nov. to the thinner-walled brachiospongoids and the absence of zero-order spicules in *Hintzespongia*.

The more detailed hypothesis of Mehl (1996), modified by Mehl-Janussen (1999), is also contradicted in several points. Most critically, the brachiospongids are there regarded as stem group amphidiscophorans and the dictyospongoids as hexasterophorans, but the reverse is proposed herein. Mehl-Janussen derived the 'Rossellimorpha' from the Brachiospongidae, via the Malumispongidae, but distinguished this group from the extant Rossellidae and allies, which were regarded as Mesozoic derivatives of the Hexactinosans. The split between the amphidiscophorans and hexasterophorans was interpreted as a Precambrian event, with the Sansha fauna (Steiner *et al.* 1993) yielding our closest approximations to the ancestral state of hexactinellids. Krautter (2003) essentially followed Mehl's scenario, advocating a Precambrian separation of the extant subclasses and regarding the taxon Reticulosa as polyphyletic, due to the inclusion of hexaster- and amphidisc-bearing forms.

Mehl's (1996) scheme emphasises stratigraphic occurrence and the occurrence of oxyhexasters in *Griphodictya epiphany* Hall & Clark, 1898. In contrast, stratigraphic occurrence is not regarded as critical herein, due to the incompleteness of the record and relatively conservative morphologies through long intervals. The presence of oxyhexasters is regarded as of ambiguous significance. Kling & Reif (1969) described the co-occurrence of paraclavules (closely related to amphidiscs) and microhexactines with terminal branches from their *Itararella gracilis*, with a hexaster that they regarded as foreign. It is not, however, clear that these microhexactines differ significantly from their simple hexaster and co-occurrence of the two microscle morphotypes is a less contrived interpretation. Since true amphidiscs are also known from the Carboniferous and microhexactines almost identical to the hexaster of Kling & Reif (1969), occur in some modern amphidiscophorans (e.g. *Hyalonema*

(*Cycliconema*) *apertum apertum*; Tabachnik & Menshenina, 2003), the mutual exclusion of microscleres taxa appears not to be absolute. Given the rarity of early fossil microscleres, it is likely that some reticulosan groups possessed both types and the subclass division of modern hexactinellids originated during the Palaeozoic; this was also the conclusion of Finks (1970) and Bergquist (1978). The phylogeny proposed here emphasises instead the wall structure, details of spicule ordering, spicule specialisation and root tufts, based largely on information not previously available.

PALAEOECOLOGY

The Llanfawr fauna is unusual in preserving several associations within a short sequence, showing variations in community structure. By far the most abundant and ubiquitous species is *Cyathophycus loydelli*, with the associated *Xylochos palindromica* also widespread. Most other taxa are rare and usually occur at only one locality.

Three associations can be recognised:

1. Near-monospecific assemblage of *Cyathophycus loydelli*, with rare specimens of other taxa, including *Xylochos palindromica*, *Pirania llanfawrensis* and *Granulispomia obscura*. Locality 1; associated fauna is diverse, trilobite-diplogaptid dominated. Perhaps locality 3, but fauna is too limited for discussion.
2. Near-bispecific assemblage of *Cyathophycus loydelli* and *Xylochos palindromica*, with rare additional hexactinellids. Locality 2b; associated fauna of molluscs, dendroid and uniserial graptolites and chitinozoans, plus rare soft tissue preservation of possible arthropod and problematica. Locality 2c; associated fauna of trilobites, brachiopods and diplogaptids, with rare other taxa.
3. Diverse assemblage of almost all taxa, with *Hemidiagoniella tenax* and *Hemicnetera minima* most abundant; includes a sub-assemblage dominated by *H. tenax* and *Xylochos palindromica*. Locality 2a; diverse associated fauna of trilobites, graptolites, brachiopods, conulariids and others.

It is difficult to recognise the environmental differences that may have led to these ecological variations. The only strikingly different associated fauna is that of locality 2b, where a dark mudstone yields abundant chitinozoan masses and frequent dendroids and molluscs, but in which trilobites are very rare. This is also the most unusual sponge preservation in the quarries, with limited pyritisation and showing a dark stain over the region of soft tissue. This suggests a less reducing (sulphidic) environment, but also exclusion of bioturbators and aerobic bacteria. The unusual, diverse fauna is more characteristic of quiet shallow marine settings (e.g. Loduca & Brett 1997) and may represent fluctuating physical or chemical conditions on tidal or seasonal timescales. It is, however, unclear which parameters could have been fluctuating in a relatively deep-water setting, unless it was the influence of seasonal current variations within the restricted Welsh Basin. The entire 10 cm bed is sedimentologically homogeneous, but interpretation as a single event bed is excluded by the internal planes showing chitinozoan masses. The interpretation of this horizon remains enigmatic.

It is clear, however, that sponges were not strongly affected by these changes, since the same assemblage oc-

curs here as in locality 2c, which represents a normal shelf fauna. The main structural difference between *Cyathophycus loydelli* and *Xylochos palindromica* and the remainder of the fauna, is the integrity of their skeletons and resistance to disarticulation. Locality 1, in particular, records cross-bedding in spongiferous horizons, indicating rapid sedimentation above normal levels. There is no obvious obrution deposit at locality 2a, except perhaps for the *Hemidiagoniella tenax*-dominated bed, a species which also retained unusual skeletal cohesion. Throughout the rest of locality 2a, most sponges are at least partly disarticulated and spiculites occur at some points. However, the taphonomy and non-poriferan fauna is almost identical to that of locality 1, indicating that chemical conditions were similar. The only apparent difference between the sites is turbulence and this may therefore have been the main factor dictating sponge distribution within the sequence. It is possible that the apparent rarity of other taxa in locality 1 is due to their complete disarticulation, but this seems unlikely because of the obrution horizons. The high abundance of *C. loydelli*, with crowded bedding planes, is also consistent with high ecological dominance.

Bodzioch (1994) discussed attachment structures in relation to environmental turbulence in Cretaceous hexactinellids, concluding that fused basophytous structures were found in sponges occupying the most turbulent conditions, followed by basal tufts and stalks. A similar dependence of distribution on attachment structure was reported by Mehl *et al.* (1993), with discussion of modern hexactinellid distributions in relation to topography-enhanced currents. Fused basal structures had not developed in this group by the Middle Ordovician and in the Llanfawr faunas, strength of the body wall appears to have been a more critical parameter. The development of meandering tracts in the large *Dilatispomia tumidus* also suggests a strength benefit, since parietal gaps were not fully developed. Occupation of more turbulent environmental niches could therefore represent the main impetus for the convergent development of thick, rigid or otherwise strengthened walls in essentially every group of sponge during the Lower Palaeozoic. This implies a broad onshore migration during sponge evolution, in contrast to the classical onshore-offshore trend characteristic of most metazoan groups during the Phanerozoic.

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