An Enigmatic, Possibly Chemosymbiotic, Hexactinellid Sponge from the Early Cambrian of South China

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An enigmatic, possibly chemosymbiotic, hexactinellid sponge from the early Cambrian of South China

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Six specimens of a strongly curved, cylindrical hexactinellid sponge have been recovered from the Tommotian–Atdabanian Hetang Biota of South China, and are described as *Decumbispongia yuani* gen. et sp. nov. The robust, thick-walled sponge shows no evidence of an osculum or basal structures, and the body form is inconsistent with an upright, filter-feeding life position. Interpretations as a detritivore feeding by amoeboid extensions, or as a facultative chemosynthetic symbiosis of sponge and bacteria are considered. The latter interpretation is preferred due to the highly constrained body shape, and the body form is interpreted from this perspective. The species indicates that Cambrian sponges occupied at least some autecological niches that appear to have been vacant since that time.

Key words: Porifera, Hexactinellida, symbiosis, chemosynthesis, Cambrian, China.

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Introduction

The Hetang Biota represents probably the earliest unambiguous fauna of articulated sponges yet known (Yuan et al. 2002; Xiao et al. 2005). The precise age of the fauna is unclear, but correlation with other deposits was discussed at length by Xiao et al. (2005), with the conclusion that the "Stone Coal" unit that houses the sponge fauna was deposited during the late Tommotian or Atdabanian. The fauna includes representatives of several groups, but is dominated by reticulosan hexactinellids (Xiao et al. 2005). Non-sponge elements of the fauna are limited to locally common orthothecid hyoliths, bivalved arthropods, and abundant "algal" remains (mostly referable to *Morania*) (Xiao et al. 2005; JPB, LAM, JPL unpublished data). The previously described sponge fauna consists of eleven species, and is particularly notable for the extremely large size (estimated at around 1 m) of some of the species, leading to well-developed tiering (Yuan et al. 2002). The disparity in size between the largest sponges and small eumetazoans implies a surprisingly advanced separation of different ecologies within this early fauna.

The environment of deposition of the Hetang Formation has been interpreted as a largely anoxic basin with currents bringing some oxygenated water to the benthic community (Zhou and Jiang 2009). This was based on a lack of evidence for transported beds, but further collecting by the authors has revealed substantial lithological variation, with some undulating bedding surfaces and evidence of winnowing and current alignment. At least some of the fauna is therefore likely to have been transported into the environment of deposition, and may have been living in more generally oxygenated conditions. The preservation of intact sponges at numerous horizons suggests that such transport was abrupt, but spiculitic layers imply at least some periods of non-deposition and winnowing. The environment of deposition and the life environment of the sponges are therefore difficult to interpret with certainty, and the fauna was probably ecologically complex. The distribution of many taxa is sporadic (LAM, unpublished data), suggesting a patchy life distribution. Unfortunately the sponge described here is rare, and it is not possible to assess its distribution relative to other species.

An ongoing re-examination of the Hetang Biota, and recent recollection of two sites, has yielded a diverse assemblage of new sponges, which will be described elsewhere. The majority of the sponge fauna is preserved as entirely flattened (collapsed) spicule arrays, with no evidence for soft tissue in any of the material we have seen, except possibly as thin pyritic films in some of the largest specimens (see Xiao

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et al. 2005). Spicules are usually either pyritised or preserved as external moulds, sometimes with partial early replacement by aluminosilicates, or partial secondary void-fill by silica and other minerals. The mineral phases present vary between beds, but there is never massive replacement of the body in three dimensions. Small, thick-walled sponges are present in an unusual, white-weathering bed, but are preserved as voids with partial infill by silica.

Among the new taxa there is a morphologically unusual, problematic species described in this paper. The morphology appears to preclude a normal poriferan mode of life, and the possible interpretations are discussed in detail below. Most specimens are from Hongda Quarry near Lantian (29°55’ N; 118°05’ E), and one further specimen from xidi Brick Pit (29°52’ N; 118°03’ E); more precise locality information is deposited with specimens. An additional specimen was collected by JPL in 2003, from equivalent-aged strata in the Nuititang Formation at Danzhai, Guizhou (26°23’ N; 107°52’ E).

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

Systematic palaeontology

Phylum Porifera

Class Hexactinellida? Schmidt, 1870

Family uncertain

Genus *Decumbispongia* nov.

Etymology: From the Latin *decumbo*, to fall or lie down, referring to the inferred life position. Gender feminine.

Type species: *Decumbispongia yuani* sp. nov., by monotypy; see below.

Diagnosis.—Semi-toroid, cylindrical hexactinellid with rounded proximal and distal ends, one tapering slightly more than the other; dermal spiculation consisting of moderately regular, orthogonal and diagonal hexactines/clinopentactines of several size orders; no osculum or attachment structure.

Remarks.—The unique form of this sponge differs from all others described, either fossil or Recent. The implications of this morphology are discussed below. The dermal spiculation is similar to that of many reticulosans, and does not suggest any particular phylogenetic affiliation.

Decumbispongia yuani sp. nov.

Fig. 1.

Etymology: After Yuan Xunlai, in appreciation of his discovery and previous work on the Hetang Formation sponges.

Type material: Holotype, NIGP154188, near-complete specimen showing some preservation of spicule impressions on the external mould. Paratypes: two semi-complete specimens (NIGP154189–154190) from the type locality, including one partial specimen with clear spicule impressions, and one partial specimen preserved mostly flattened. A probable juvenile is present on the same slab as the holotype.

Type locality: Hongda Quarry near Lantian, Anhui (29°55’ N; 118°05’ E), South China.

Type horizon: Hetang Formation, early Cambrian (Series 2).

Material.—One semi-complete specimen, NIGP154191, from Xidi Brick Pit excavated in the Hetang Formation of Anhui (29°52’ N; 118°03’ E). One further specimen (NIGP 154192) from the equivalent Niutiang Formation of Guizhou.

Diagnosis.—As for genus.

Description.—Broadly C-shaped sponge with rounded (originally circular) cross-section, in various degrees of compression. The confirmed specimens are consistently curved until they approach half-rings. Largest complete specimen is 52 mm across, with maximum body diameter 14 mm (holotype 47 mm with body diameter 13 mm), although one partial specimen appears be substantially larger (approximately 70 mm, width 22 mm). The only specimen from the Hetang Formation smaller than the holotype is a slightly curved juvenile, 7 mm long and 1.5 mm wide; although it has not been possible to confirm whether it represents the same species, the body proportions are consistent with the other specimens. The Niuitang Formation specimen is slightly more slender, at 8 mm wide and 38 mm across. This very small dataset displays an extremely strong quadratic correlation ($R^2 = 0.995$; Fig. 2) and a slightly less significant linear regression ($R^2 = 0.963$). With the limited dataset it is not possible to judge between these scenarios, particularly given the small uncertainties regarding the diameter of two specimens. However, it is clear that there is a general increase of width with overall size. There also appears to be an increasing curvature with growth stage, from nearly straight juveniles to C-shaped mature adults, but further specimens are necessary to test the validity of this pattern.

Specimens are in most cases preserved at least partially in three dimensions, with a thick weathered mineral deposit obscuring surface detail and implying more substantial early pyritisation (or other mineralisation) than it is seen in other sponges in the deposit. Two specimens show completely three-dimensional preservation, two are largely flattened, and one is effectively flat with a slightly distorted outline. Original cross section appears to have been approximately circular. The cylindrical body is weakly ribbed in some specimens, with six or seven slight constrictions and expansions along the length of the holotype. One termination tapers slightly more than the other, and is also slightly more curved in the available material. By comparison with known hexactinellids, and to maintain some curvature at all growth stages (which may have been important for inferring stability in life position, discussed below), the tapering end is assumed to be proximal. Despite the three-dimensionality, terminations do not show any evidence for an osculum or other apical modification.

Dermal spicules are weakly visible on the surface of the holotype, and are locally well preserved on a small (width 16 mm) fragment (NIGP154191; Fig. 1B), and also on the juvenile. All spicules are hexactine-based, with distal rays reduced to small projections that are most pronounced in the largest spicules, and paratangential rays simple, curved to

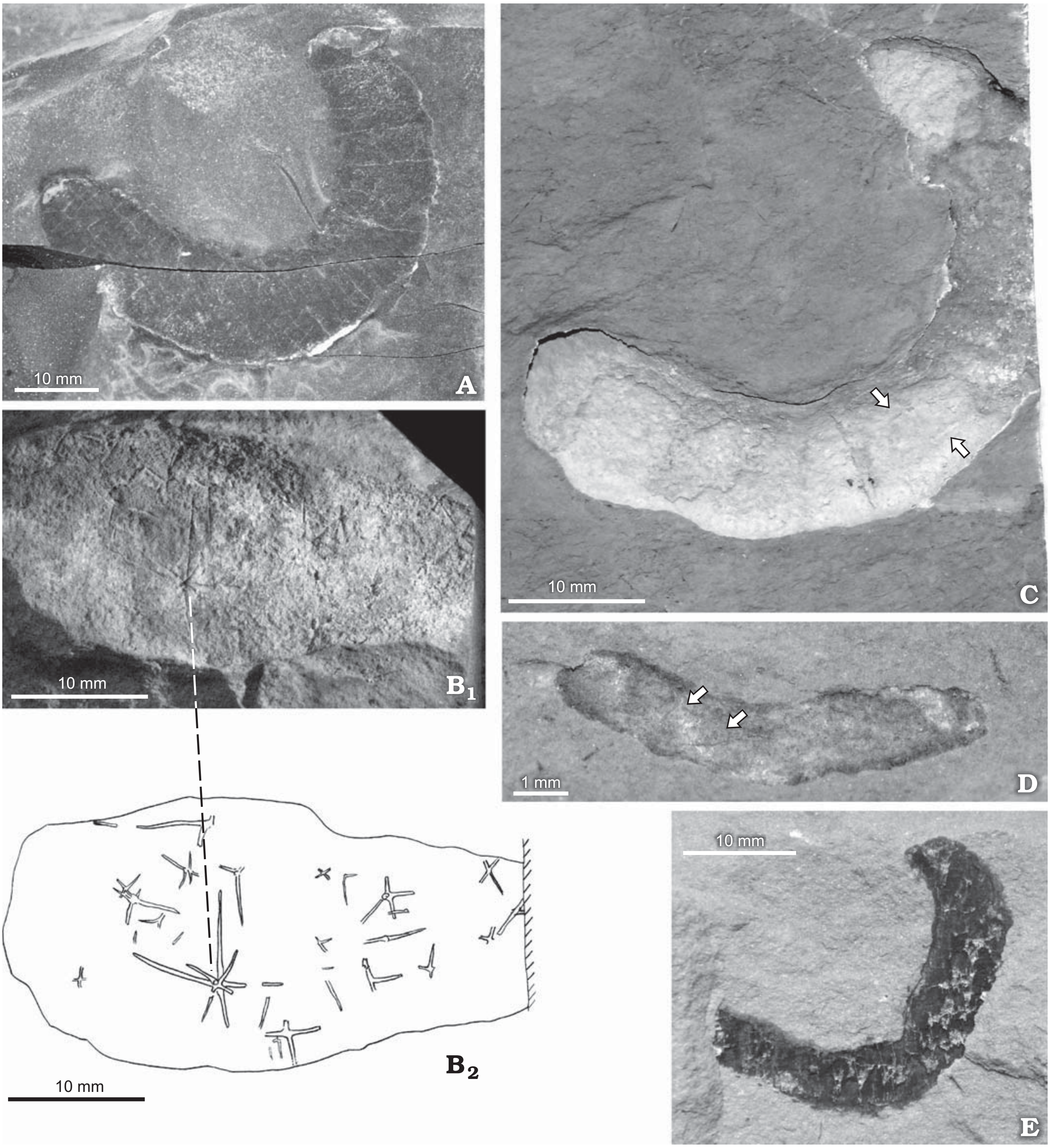

Fig. 1. Hexactinellid-like sponge *Decumbispongia yuani* gen. et sp. nov. from the Hetang Formation near Lantian, Anhui (A–D) and Niutitang Formation at Danzhai, Guizhou (E). **A**. Paratype NIGP154189, a flattened, near-complete specimen preserved as black iron minerals. **B**. Paratype NIGP154190. Fragment with relief showing spicule arrangement preserved at surface, consisting of irregularly clustered, orthogonal and diagonal hexactine-based spicules (B_1). Camera lucida drawing of B_1, clarifying poorly preserved spicule array (dashed line acts as reference for the most prominent spicule) (B_2). **C**. Holotype NIGP154188, near-complete specimen showing annulations, tapering distal(?) end and weakly preserved spicules (arrowed). **D**. Probable juvenile specimen on slab with NIGP154188, showing straighter growth form and well-developed spicules (arrowed). **E**. NIGP154192.

match the surface of the sponge body but not otherwise distorted except for minor deflection. Proximal rays cannot be confirmed with available material. Maximum observed ray length is 6 mm, with basal ray diameter up to 0.3 mm. Spicules are arranged orthogonally or diagonally to the sponge axis, with orthogonal spicules dominant in specimen

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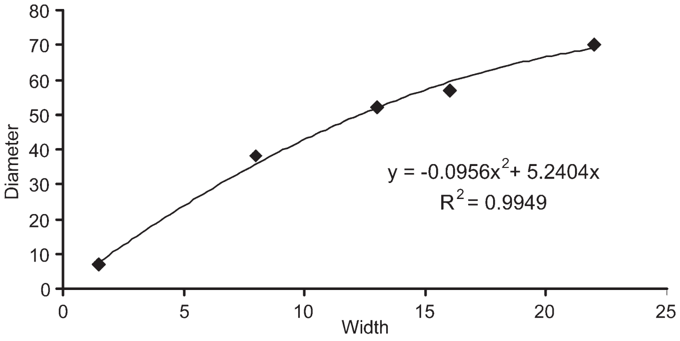

Fig. 2. Plot of maximum sponge diameter (measured across most distant two points on outer surface) versus maximum width (in millimetres) for the available specimens, with intercept set to 0 and a quadratic correlation plotted with regression coefficient $R^2 = 0.997$. Largest two specimens are incomplete, and measurements are approximate; assume errors in d of up to 5 mm for these two only.

NIGP154191 and diagonal spicules dominant in the small area of spicules in the holotype. Diagonal spicules are normally oriented at close to 45°, but a few are at apparently random angles to the sponge axis. Spicule rays are often locally adjacent and almost bundled, with in some cases ray centres also clustered, unlike in the standard quadruled array of reticulosans. Arrangement of small spicules is unclear, although traces of them are seen in NIGP154190, dominantly orthogonal to the body axis.

The juvenile specimen on the holotype slab also preserves a few large spicules, with ray length approaching 1 mm; these are oriented both orthogonally and diagonally to the axis, and the longest rays curve substantially in order to follow the sponge surface. In each sponge that preserves spicules they are seen intermittently, and mainly in the central part of the sponge, but they appear to be consistent in arrangement over the preserved regions. There is no indication of modified spicules in the basal or apical regions, and no basalia have been observed.

Remarks.—The preservation of the sponge as three-dimensional bodies, in contrast to all other taxa in the known fauna, implies that it was originally a solid construction rather than a thin wall. This is supported by the extensive (weathered) mineralisation of the interior and lack of osculum. It is not known whether the interior of the sponge was spiculate; the observable spicules are typical of reticulosan wall spicules, but could also constitute a distinct dermal layer. The unusual arrangement of the spicules, particularly the sometimes-overlapping spicule centres and near-bundled rays, would be distinctive even if the sponge consisted only of a thin skeletal wall, preserved entirely flattened.

The first specimens were not originally recognised as sponges due to difficulties in interpreting the preservation. Where the specimens were completely mineralised in three dimensions, the weathered material constituting the interior of the body shows dominantly transverse cracking due to weathering-related volume changes, often infilled by further mineralisation. In the specimen from the Niutitang Formation, a tectonic fabric has resulted in a reticulate crack network whose orientation is independent of the fossil. Both these textures can be superficially similar to spicules, but the massive pyritisation and subsequent oxidation has in most cases destroyed genuine spiculation. The sponge nature of the fossil was recognised only following the discovery of two specimens that had undergone more extreme weathering, leading to removal of the material from the inside of the sponge body, and a mould of the exterior. Even in these cases, spicules are unclear over large areas of the surface, suggesting that massive pyritisation of the soft tissue subsumed surface spiculation into a homogeneous deposit.

An alternative interpretation that must be considered is of a different organism that has agglutinated detrital spicules onto its exterior wall. This, however, is ruled out by the regular curvature of the spicules matching that of the wall, and by the spicule arrangement (Fig. $1B_2$). A dominantly orthogonal array with other spicules positioned at around 45° is typical of reticulosans (e.g., Carrera and Ortega 2009) but difficult to understand for an agglutinating organism in which particles would be expected to be either highly regular in orientation, or disorganised. The sparse distribution is also unlikely for an agglutinated array, whose purpose would presumably be for defence. Finally, the range of spicule sizes present is typical of reticulosan hexactinellids (Botting 2003), but would be highly unusual in an agglutinating organism as the incorporated particles are normally size-selected. There is therefore no doubt that *Decumbispongia yuani* gen. et sp. nov. is a sponge.

Geographic and stratigraphic distribution.—*Decumbispongia yuani* is currently known from black shales of the Hetang and Niutitang formations of Anhui and Guizhou provinces, South China, of early Cambrian (Series 2) age.

Discussion

The aberrant morphology of this species requires a non-standard interpretation of its biology and ecology. In particular, both living posture and feeding mechanism implied by the body form are incompatible with those of normal hexactinellids.

The strongly curved body form seen in all specimens is inconsistent with an erect living position, being inherently unstable. An individual example of such a growth form could be understandable in taxa from rocky shore habitats, as a result of aberrant growth influenced by extremely irregular substrate and strong turbulence, but this is not plausible for multiple specimens in areas of approximately flat, muddy sea floor. Combined with the lack of basalia, it appears untenable for either end to be positioned basally. The only stable orientation for this species was to have been lying flat on the sea floor, a posture that is incompatible with a suspension-feeding poriferan. Not only is the limited local current flow greatly reduced within the benthic boundary layer, the thickness of which is dependent on the flow regime (Bowden 1978; reviewed by Nowell and Jumars 1984), but the pore system is also liable to being clogged by fine particles, especially given the tendency of obstructions in the boundary layer to induce sediment resuspension (Carey 1983). This is true even if the sponge produced large quantities of mucus as some modern taxa do to prevent clogging (Barthel and Gutt 1992). Mucose removal of particles would also be inhibited by the growth form, as gravity cannot significantly clear the deposits, and current flow would have been minimal. The lack of upward growth exacerbates other problems in a muddy environment. In the deep ocean, almost the entire sponge would have been contained within the 1 cm thick viscous sub-layer (Bowden 1978), which would have restricted the effects of turbulence on the local chemistry, maintaining a constant low oxygenation state but limiting oxygen replenishment. There is also a risk of burial of the entire sponge, and even with the sponge lying on the surface, nearly half of the surface area would be unavailable for filter feeding. Areas of modern ocean prone to high suspended particle flux are also difficult for sponges to colonise due to burial and pore clogging (Klitgaard and Tendal 2004); if there was episodic high sediment input in the Hetang Formation, on a timescale of months or years, then such episodes would be particularly problematic for a sponge that did not grow rapidly upwards.

The absence of an obvious osculum, and therefore presumably of a fully developed internal canal system, appears to be unique among hexactinellids, and implies a highly unusual autecology. Modern demosponges often possess one or several small oscula, however, which would not be visible in fossil material, and although this type of exhalent canal system has not been seen in any living or fossil hexactinellid, it is not possible to discount the possibility entirely. Among demosponges with minimal oscular development, some such as *Haliclona compressa* (Ghiold et al. 1994) are derived, dendritic demosponges with a compound growth form and complex (leuconid) internal canal system; in these cases the canal system is fully functional, but a large, discrete osculum is lacking. This is probably only possible in very small or narrow-branched sponges, due to limitations apparently imposed on a functional canal system by the relative areas of inhalant and exhalent surfaces (Reiswig 1975; Sperling et al. 2011). Other non-oscular sponges include fan-shaped haplosclerids in the genus *Cribrochalina* Schmidt, 1870, in which the central cavity and osculum is progressively reduced as the sponges develop the thin upper part (Vosmaer 1882).

Although a variety of Calcarea and demosponges appear to lack an aquiferous system and choanocytes, these appear to be deceptive. In most cases these examples are metamorphic stages of a normal sponge exposed to pathological environmental conditions, resulting in conversion of choanocytes to amoeboid cells, or simply reflect a temporary, stress-related contraction of pores (Bidder 1933). Even if *Decumbispongia* gen. nov. were to fall into one of these categories which are again unknown among hexactinellids, the recumbent growth form is still incompatible with a filter-feeding lifestyle, and thus a standard aquiferous system must have been absent.

The best known sponges that lack an aquiferous system entirely are the secondarily predatory taxa such as *Asbestopluma* (Vacelet and Boury-Esnault 1995) and *Cladorhiza* (Vacelet et al. 1995), in which the suspension-feeding mode of life has been superseded by direct digestion of animals, which in most cases become entangled on lateral appendages or filaments. There are now many known carnivorous sponge species, with a diverse range of morphological specialisations, although virtually all are dependent on rare feeding opportunities (Vacelet 2007). Some have developed symbiotic relationships with methanotrophic bacteria at hydrothermal vent sites (Vacelet et al. 1995), substantially supplementing their nutritional intake from predation (Vacelet et al. 1996). In the carnivorous species of *Chondrocladia* (e.g., Kübler and Barthel 1999; Cristobo et al. 2005), the aquiferous system has been retained, suggesting that the predation strategy is a supplement to the sponge's nutrition, rather than a full replacement of it. It is not possible to establish whether a partly functional aquiferous system was present in the current species, but if it lacked pores entirely then it is difficult to explain the consistent growth form (see discussion below).

One Ordovician–Silurian sponge family that appears to have lacked a discrete osculum was the Hindiidae, a group of small, subspherical lithistids. The global distribution and wide environmental range of *Hindia sphaeroidalis* have led to suggestions of a planktic (Carrera and Rigby 2004) or pseudoplanktic (Carrera 2007) habit. This lifestyle interpretation is supported by the hollow (resorbed) interior of the sponge skeletons, which would have reduced their weight and possibly also acted as a space for trapped gases to aid buoyancy. The absence of an obvious exhalent focus, with the canal system being largely radial, would result from inconsistent orientation of the sponge in relation to ambient currents. However, the early hindiid *Eoscheiella* Carrera, 2007, appears to show evidence for an attachment structure, despite also possessing the spherical symmetry of the family. The aquiferous system of *Hindia* may have consisted of a large number of small-scale inhalant-exhalent canals, paralleling the radial spaces within the skeletal structure. Larger Permian hindiids such as *Scheia* developed some degree of differentiation into larger and smaller diameter canals, and other genera became non-spherical (Finks 1971), perhaps in response to the limited efficiency of such a system. Without knowledge of the internal soft tissues of *Hindia*, however, it is unclear whether this interpretation of the hindiid aquiferous system is correct.

Whilst the lack of an obvious osculum is a striking similarity to *Decumbispongia* gen. nov., the curved body form makes no sense unless it was recumbent and benthic. The possibility that some hindiids may have lived attached to the sea floor, but still retained the spherical body form without a clear osculum suggests that *Decumbispongia* may have been more conventional than it appears. However, the skeletal

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structure of hindiids is particularly suited to a radial aquiferous system, whereas the irregular dermal skeleton of *Decumbispongia* does not suggest any such internal structure, and the recumbent growth remains highly problematic for normal sponge function. For these reasons, we do not feel that the hindiids are instructive in interpreting *Decumbispongia*, although it is possible that some interpretations of the latter could provide an alternative perspective on *Hindia*.

There are some other Palaeozoic sponges with potentially analogous, low growth forms such as the Palaeozoic hexactinellid group Brachiospongiidae (e.g., Beecher 1889), particularly *Brachiospongia tuberculata* (Rigby 1970). In this radially-symmetric species the arms are broadly recumbent, although in at least *B. digitata* the arms are hollow and lead to a central cloaca (see Finks and Rigby 2004), probably with a dorsal osculum, although this does not seem to be preserved. The real similarities are therefore slight, and it is unlikely that the brachiospongiids were ecologically similar to the new species, despite the limiting effects of the growth form on the proportion of the wall surface available for incurrent water flow. The recumbent, spreading growth form may (speculatively) be an adaptation to photosymbiosis as a nutritional supplement in the shallow waters it inhabited, but based on the hollow body form with central cloaca, it appears to have still functioned predominantly as a normal poriferan.

Geologically younger taxa illustrate potential morphological similarities, as for example the Jurassic to Recent pheronematid *Semperella* (Gray 1868). This clavate species is not hollow, and has exhalent canals aligned in grooves along the sides of the sponge; such small osculae are unlikely to be visible in the current material. It is therefore possible that the new species possessed multiple small osculae, although this would be extraordinary for a Cambrian hexactinellid-like sponge, as all known species from this time are essentially globose to vasiform with a terminal osculum. Such an interpretation also does not account for the curved body form, which implies a flat-lying mode of life that would be particularly problematic for a sponge with an array of small excurrent canals, rather than a large (and therefore not easily clogged) apical one.

Based on the above observations and direct implications for mode of life, we do not think it is possible to incorporate the sponge into the normal understanding of poriferan ecology, and like the modern predatory species, an ecologically distinct interpretation is necessary. There are two possible interpretations that we will consider here: detritivory and chemosymbiosis.

Detritivory.—Some modern demosponges are able to adapt to times of food stress by producing exploratory pseudopodia through amoeboid reorganisation of tissues, especially in the basal, attached region (e.g., Bond and Harris 1988). In some cases, such as *Tethya wilhelma*, there is no significant body reorganisation beyond the exploratory pseudopodia, and the sponge appears to move largely through rotation of the entire skeleton (Nickel 2006). The pseudopodia are not used to pull the sponge along the substrate through contraction, but appear to act more as guide or sensory structures, although their role and mechanism are still unclear. Some sponges can change direction instantaneously (Nickel 2006) and it is now widely appreciated that many sponges respond to both physical and chemical stimuli (Jacobs et al. 2007). There is also evidence for complex chemical recognition and selectivity in the uptake and positioning of foreign particles into the skeleton of *Chondrosia reniformis* (Bavestrello et al. 1998).

One possibility is that the new species fed using amoeboid pseudopodia from either suspended or detrital particles. Although typical sponges feed primarily on bacterial-sized particles through the microvilli of their choanocytes (e.g., Reiswig 1971; Riisgård and Larsen 2000), in some cases (Leys and Eerkes-Medrano 2006) particle capture is through pseudopodial extensions of these cells; larger particles (5–50 μm) are often captured by amoebocytes lining the incurrent canal walls (Reiswig 1971). There has also been an increasing appreciation of the role of direct uptake of dissolved organic carbon (e.g., Reiswig 1981; Yahel et al. 2003), but it is not yet clear to what extent symbiotic organisms are responsible for the uptake, and if the sponge itself is responsible, what is the mechanism of uptake. Other studies have also shown that sponge growth rate is independent of the supply of Dissolved Organic Carbon, suggesting a greater dependence on solid particle consumption (Koopmans and Wijffels 2008). It is at least clear that diverse processes operate, and that sponge feeding is not restricted to small particle capture by choanocyte microvilli. We therefore suggest that it is possible for a recumbent sponge to have adapted to feeding through amoeboid pseudopodia, either from the water column above the sponge body, or from particles within the sediment. A similar feeding mechanism is employed by placozoans, and has been suggested as an interpretation of some members of the Ediacaran Biota (Sperling and Vinther 2010); the shared capability for this feeding strategy should not be surprising between early examples of these basal metazoans.

This interpretation suffers from several problems, however. It is unclear whether such a slow process as amoeboid pseudopodial development could be sufficient to provide enough food to sustain a sponge, even if the cellular organisation of the pseudopodia could be modified to enable feeding. Also, a highly consistent, constrained morphology is difficult to relate to a sponge in which an amoeboid growth form would be more advantageous, enabling it to cover a wider area relative to its body size. The growth form of *Decumbispongia* also appears to dictate a stable location, whereas mobility should have been useful to a putative detritivorous sponge. This is particularly true given the near-isometric growth (Fig. 2), implying that body form was highly constrained by its function.

Finally, the new species appears to be a hexactinellid, whereas all the taxa with the pseudopodial extensions discussed above are demosponges. The syncytial trabeculum of modern hexactinellids allows nutrients taken at one site on the sponge surface to be transported elsewhere through cytoplasmic streaming (Leys 2003). This could be advantageous

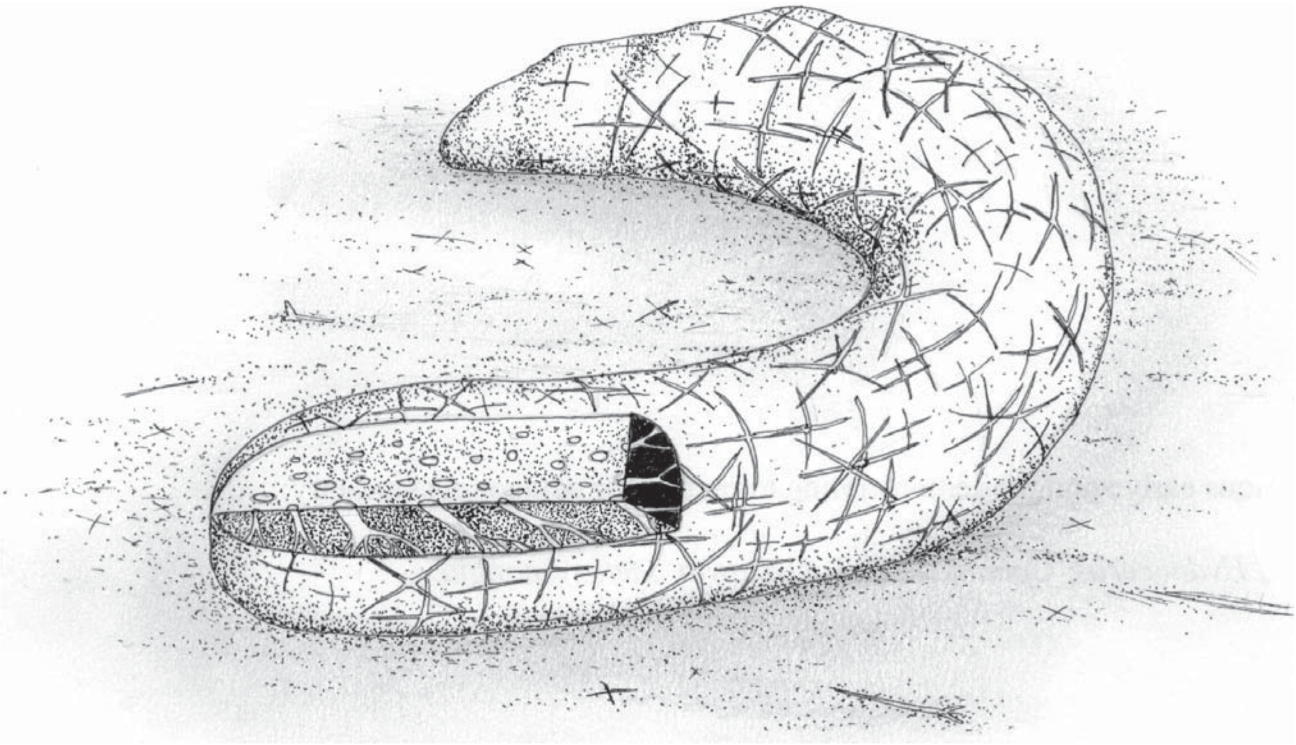

Fig. 3. Interpretative reconstruction of hexactinellid-like sponge *Decumbispongia yuani* gen. et sp. nov. Internal structure is hypothetical and illustrates a possible canal structure allowing ventilation of interior from convex outer surface (see text for discussion), with exhalent canals on concave, inner surface. Internal spiculation, if any, unknown.

if syncytiality was present in the new species and the sponge were reliant on more active particle gathering, but it is unclear whether the feeding processes outlined above could be possible in an early hexactinellid.

Chemosymbiosis.—Sponges contain a wide range of microbial endosymbionts, and probably parasitic and commensal taxa, although the nature of many of these symbioses are still poorly understood (Webster and Blackall 2009 and references therein). The concept of a sponge being largely composed of bacteria has led to the occasionally-used term "bacteriosponge" to refer to the compound organism (e.g., Reiswig 1981). Individual sponge species have a highly specific complement of bacterial taxa within their tissues, which are passed on through reproduction and are sufficiently constrained to allow phylogenetic reconstructions based on the associated bacteria (Erpenbeck et al. 2002; Steger et al. 2008). In some taxa, the associated microbiota is extremely diverse, and also includes some groups distributed around the choanocyte chambers, suggesting some degree of symbiosis in food gathering (Webster et al. 2001). In the tetractinellid *Geodia barretti*, internal sulphate-reducing bacteria (especially *Desulfovibrio*) facilitate a sequence of sulphate reduction within the sponge tissues in response to oxic-anoxic cycles that relate to pumping of water through the aquiferous system (Hoffmann 2003). It is unclear to what extent the sponge relies on the nutrition from this process, however.

The unusual features of the new sponge could be understood as having evolved through a high degree of chemosymbiosis with internal bacteria. The recumbent growth and lack of an osculum could relate to a reduced aquiferous system, with small-scale pores leading to a polarised network of fine internal canals. A species dependent on endosymbionts would utilise Dissolved Organic Carbon more than large particles, and would not require as efficient a filtration system. Without knowing what bacterial groups were involved, it is not possible to assess the chemical conditions under which the "bacteriosponge" would thrive best, but in a dysaerobic habitat, an erect sponge would experience significantly different redox conditions over its height, which could be problematic for the symbionts. As discussed by Hoffmann (2003), endosymbiotic bacterial reduction in *Geodia* relies on subtle oxic-anoxic changes within the sponge tissues. Pumping was reported to be always very slow, and the osculae of *T. barretti* are unobtrusive, and clustered in depressions on the sponge surface. Occupying a low tier adjacent to the sediment may have allowed *Decumbispongia* to regulate its internal redox conditions more easily, and the loss of a preservable osculum is consistent with the need for only slow water movement, in order not to excessively alter the redox balance within the sponge tissues. The C-shaped body form would provide stability, whereas a recumbent, cylindrical body would be prone to rolling in currents. The strict control of orientation provided by the body form also suggests polarisation of a canal system in order to maintain efficient circulation. The most stable orientation would be for the outer surface of the curved body to face into the ambient water flow direction.

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Reconstruction of possible internal structure is difficult, but interpretations are constrained by functional morphology. The consistent body proportions revealed by the limited material available (Fig. 2) suggests that functionality was strongly dependent on the morphology of the sponge. The increase of width with overall size of the sponge makes it unlikely that purely diffusive processes were involved in circulating nutrients to the interior, as these would be benefitted by a more constant diameter at different growth stages. The sponge interior therefore must have been ventilated directly by canals. The stable current orientation discussed above exposes a larger surface area to the incurrent flow side, and a smaller area to the excurrent surface, leading to high velocity for the exhalent flow. Such a condition has been described as being critical to poriferan function (Reiswig 1975). The most efficient use of bacterial symbionts would be to maximise surface area of the internal canals, but this may be further constrained by requisite oxygenation within the tissues. If the endosymbionts were sulphate-reducing (as suggested by the massive pyritisation of specimens), maintaining internal dysoxia or local anoxia may have required local diffusion of nutrients away from canals across membranes and through short distances of internal tissues that acted as buffers, so that the symbiotic communities are not exposed to fluctuating or elevated redox. We therefore suggest that a regularly spaced canal system was necessary for the symbiotic function of the organism (Fig. 3). The apparent pattern of increased curvature with growth stage is also potentially significant: it may be a mechanism for reducing the exhalent-inhalent pore area ratio for larger sizes, and therefore increasing water flow as the sponge becomes larger.

In summary, all the features observed are consistent with the life orientation being recumbent, and the inner arc surface facing downstream. This strict control of orientation through the unique morphology, combined with the evidence for absence of a fully developed aquiferous system, and the low-oxygen environment, are strongly suggestive of a mode of life dependent on reliable chemical conditions within the sponge tissues. Slow circulation of water through the interior, as in modern chemosymbiotic sponges with controlled internal redox, would also limit clogging of the pores—potentially a major problem in a sponge with recumbent growth form inhabiting this environment. We therefore consider it likely that the new fossil represents a facultatively chemosynthetic sponge-bacteria symbiosis.

Conclusions

Decumbispongia yuani gen. et sp. nov. represents a novel growth form and structure for early hexactinellids. Although it is not possible to interpret the significance of its aberrant features with certainty, at least two potential explanations for the abnormalities can be postulated. One of these, involving detritivory combined with suspension feeding by amoeboid pseudopodia, is highly speculative and difficult to reconcile with the growth form. The recumbent morphology, the lack of an osculum, and its widespread presence in dysoxic to anoxic, organic-rich black shales of South China, suggest instead a chemosynthetic feeding strategy reliant on endosymbiotic bacteria. This would be an extreme utilisation of a food source that appears to be widely used to a lesser degree among modern taxa, and shows that Early Cambrian sponge autecology was more diverse than has been previously understood.

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