

# A new hexactinellid sponge from the Silurian of the Pentland Hills (Scotland) with similarities to extant rossellids

Joseph P. BOTTING<sup>1,2\*</sup>, Yves CANDELA<sup>3</sup>, Vicen CARRIÓ<sup>4</sup> and William R. B. CRIGHTON<sup>4</sup>

<sup>1</sup> Nanjing Institute of Geology and Palaeontology, 39 East Beijing Road, Nanjing 210008, China.  
Email: acutipuerilis@yahoo.co.uk

<sup>2</sup> Department of Natural Sciences, Amgueddfa Cymru – National Museum Wales, Cathays Park, Cardiff CF10 3LP, UK.

<sup>3</sup> National Museum of Scotland, Chambers Street, Edinburgh EH1 1JF, UK.

<sup>4</sup> National Museums Collections Centre, 242 West Granton Road, Edinburgh EH5 1JA, UK.

\*Corresponding author

**ABSTRACT:** The Pentland Hills sponge fauna (Llandovery, Telychian) consists of an unusual, aberrant assemblage, but of low diversity. A new specimen of a unique sponge, *Eoghanospongia carlinslowpensis* gen. et sp. nov., is described from the classic locality of R82. The mushroom-shaped, probably stalked body (peduncle attachment to body not exposed) resembles that of some living rossellids, especially *Caulophacus*. The sponge also shows prominent projecting pentactins and monaxon derivatives – a spicule type diagnostic of the Rossellidae among living taxa, albeit in a robust form not described from extant sponges, including *Caulophacus* or other pedunculate lyssacinoidans. Certain attribution to the Rossellidae is not possible from the single specimen, largely because of weak preservation of the primary spicule skeleton, but no other fossil or modern sponges show any significant similarity to it. Although similarly early relatives of the Rossellidae have recently been described from elsewhere, the new sponge is even more unexpected in being from a shallow-water environment, making the absence of rossellids through the rest of the Palaeozoic much more problematic.



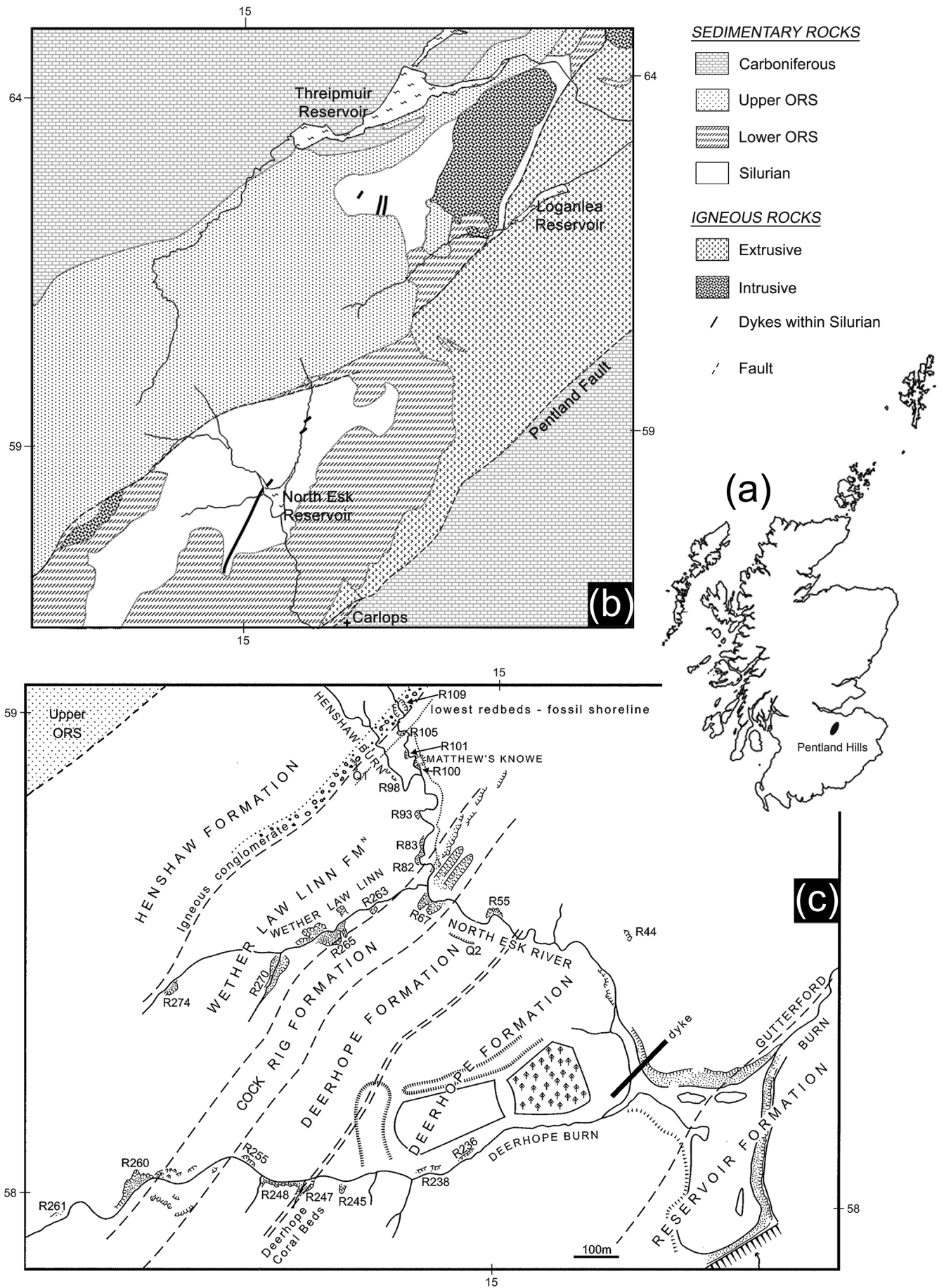
**KEY WORDS:** fossil, North Esk Inlier, Porifera, prostalia, Rossellidae.

The fossil record of sponges is incomplete, complex, and increasingly important for understanding early animal evolution (Botting & Muir 2018). One of the key indicators of our limited state of knowledge in Ordovician and Silurian sponge diversification is the large proportion of highly problematic taxa being described (e.g., Botting & Rhebergen 2011; Botting & Zhang 2013). This implies long phylogenetic gaps between known taxa, which severely hinders a full understanding of how the diversification occurred. In particular, a key point is the difficulty in recognising the last common ancestors of the class-level crown groups. For demosponges this is now becoming clear, but for hexactinellids is still highly problematic, with numerous implications for how to interpret the earliest hexactin-bearing sponge fossils (Botting & Muir 2018). New taxa that may represent early examples of crown-group hexactinellids are, thus, vital to developing our knowledge in this area. This paper adds to the literature by describing a new, surprisingly modern-looking hexactinellid from the lower Silurian rocks of the Pentland Hills, Scotland.

The first geological investigations of the Pentland Hills date to as far back as the early 19th Century, when French expatriate Boué (1820) noted the presence of rocks older than the Old Red Sandstone (ORS). However, he did not record the presence of any fossils at that time, and it was not until 1836 that the first fossils were found by Charles MacLaren (MacLaren 1839). The latter recorded two poorly preserved specimens unidentifiable at the generic level: a cephalopod and a trilobite. The first

fossils from the locality now known as R82 were collected and described by Salter (in Howell & Geikie 1861) during the first mapping of the area by the Geological Survey. Work continued in the North Esk Inlier until the end of the century, culminating with the Geological Survey Memoir by Peach & Horne (1899), a work of lasting quality that played a prominent role in British geology and palaeontology for decades (although the Silurian beds were still regarded there as late Silurian age). Following this, little attention was dedicated to the Pentland Hills, and it was not until Lamont (1947), in which he concludes a late Llandovery age for the North Esk Inlier strata, that decisive works were starting to be published again. From then on, a more steady flux of palaeontological and geological studies were published (see Clarkson *et al.* 2007 for a summary) that contributed to a better understanding of the area.

The sponges constitute a quantitatively minor component of the North Esk Inlier faunas, due largely to the fragility of their skeletons, which results in only localised conditions suitable for their preservation. This is particularly true in shallow-water environments, such as those represented in these deposits, because of elevated turbulence and high silica solubility. There has also been relatively little research on the sponge fauna. The first taxonomic descriptions of sponges from the Pentland Hills were undertaken by Hinde (1883, 1887–1912), who described two species (*Amphispongia oblonga* and *Plectoderma scitulum*) from the Wether Law Linn Formation, and these remained the only studies until Botting (2004, 2007a) reviewed and updated



**Figure 1** (a) Location of the Pentland Hills in Scotland. (b) Geological sketch map showing the three Silurian inliers in relation to the surrounding geology. (c) Geological sketch map of the central part of the North Esk Inlier showing the most important localities (including locality R82), as described by Robertson (1985). Grid reference in margin. Redrawn from Clarkson & Taylor (2007) and Candela & Crighton (2015).

the fauna. In the North Esk inlier, four species of sponges are known from locality R82 [NT 149586] in the Wether Law Linn Formation and one species from a single locality on the Gutterford Burn, which is otherwise unfossiliferous (Botting 2007a). Recent fieldwork has additionally uncovered isolated hexactine spicules from an unidentified taxon at locality R260 (lateral stratigraphic equivalent to R82), along the Deerhope Burn. This assemblage of sponges in the North Esk Inlier is preserved in many cases fully articulated, providing a perspective that is highly unusual due to both the rarity of conditions required for abrupt burial, and the transience of shallow-water siliciclastics (Botting 2007a). The uniqueness of this shallow-water community is reflected in the fact that the majority of the species, and some genera, are only known from their type locality.

The Pentland sponge fauna is not only taxonomically distinct from similar-aged assemblages, but also morphologically distinct. In particular, the hexactine-bearing *Amphispongia oblonga* cannot be related to any other known species, and the distinctive architecture of *Plectoderma* is also difficult to relate to other reticulosans. The uniqueness of this aberrant fauna is reinforced by the discovery of another bizarre new species of sponge, described in the section on Systematic Palaeontology.

The identification and description was by JPB and YC; the specimen was prepared by VC and photographed by WRBC.

## 1. Geological setting

The North Esk Inlier (Fig. 1) is the largest and most westerly of the three Silurian inliers in the Pentland Hills. It forms a 6.8 km<sup>2</sup> elongate area at the head of the North Esk River. Exposure is reasonably good but is often restricted to stream valleys. Within the inlier, the sediments are steeply inclined to vertical, striking in a NE to SW direction, younging to the NW. The Silurian succession is 1500 m thick. The inlier is ringed primarily by a greywacke-conglomerate of early ORS age, but a fault truncates the north-western part of the inlier and throws down Lower Carboniferous sediment of ORS facies (Clarkson & Taylor 2007).

The Wether Law Linn Formation is composed of calcareous mudstones, and is up to 265 m thick. It has been divided by Robertson (1985) into three members, mainly on the basis of their abundant, well-preserved, and varied faunas. Robertson (1985, 1989) and Clarkson & Taylor (2007) provided a description of the lithology. The upper part of the lower member is exposed some 50 m N of the junction of Wether Law Linn with the North Esk River at locality R82 [NT 149586]. This exposure was dug up by Gary Robertson in 1983 and although partially fallen in, excellent fossil specimens may be collected from the scree (Clarkson & Taylor 2007). The base of the exposure is characterised by the *Eoplectodonta penkillensis* Association (Robertson 1989), updated as the *Eoplectodonta–Visbyella* Association by Clarkson & Taylor (2007), although *Visbyella* is very rare and disappears after about 2 m. Some 5 m from the base of this section, a 0.5 m-thick horizon is dominated by the brachiopod *Coolinia pecten*, bivalves (*Palaeoneilo* and *Leptodesma*), the peculiar mollusc *Spirina*, and gastropods such as *Liospira*. This is described as the *Liospira(?) simulans–Synek(?)* Association (Robertson 1989). Through the exposures, molluscs become more important as brachiopods decline, which indicates an upwards trend towards changing or variable salinity. The sediments of the Wether Law Linn Formation are interpreted as being deposited in a lagoonal environment that presumably became more isolated with time.

The specimen described here was collected from a loose block lying at the bottom of the succession, so its exact stratigraphic provenance is uncertain. However, the associated fauna consist of the reticulosan sponge *Plectoderma scitulum* (Hinde 1883), which is only known from locality R82 (Botting 2007a, b) in the Pentland Hills and, therefore, the loose block is indigenous, and the relatively abundant brachiopods *Eoplectodonta penkillensis* (Reed 1917) and *Coolinia applanata* (Salter *In* M'Coy 1846), and the ostracode *Craspedobolbina (Mitrobeyrichia) impendens* (Haswell 1865). As the brachiopods dominate the associated fauna, this block was almost certainly derived from the adjacent outcrops at the base of the section, possibly from the interval in which *Visbyella* disappears.

## 2. Repository

The specimen described here, consisting of NMS G.2010.38.1 and its counterpart NMS G.2010.38.2, is catalogued and stored at the National Museums Scotland (NMS), Edinburgh.

## 3. Systematic palaeontology

Class Hexactinellida Schmidt, 1870

**Remarks.** The presence of hexactins is itself not restricted to Hexactinellida (Botting & Muir 2018), but the complexity of the body form and architecture suggests a more derived position than the stem-silicean reticulosans. The new sponge has typical hexactinellid-type spicules (including hypodermal pentactins, restricted to a single living family) but its complex architecture resembles only some members of the same family. Although certain assignment to the Rossellidae is not possible with the current material, it appears very likely, and a crown-group hexactinellid position seems to be reliable.

Family Rossellidae? Schulze, 1885  
*Eoghanospongia* gen. nov.

**Derivation of name.** Named after Eoghan Candela, son of the second author, who has helped many times with collecting in the Pentland Hills.

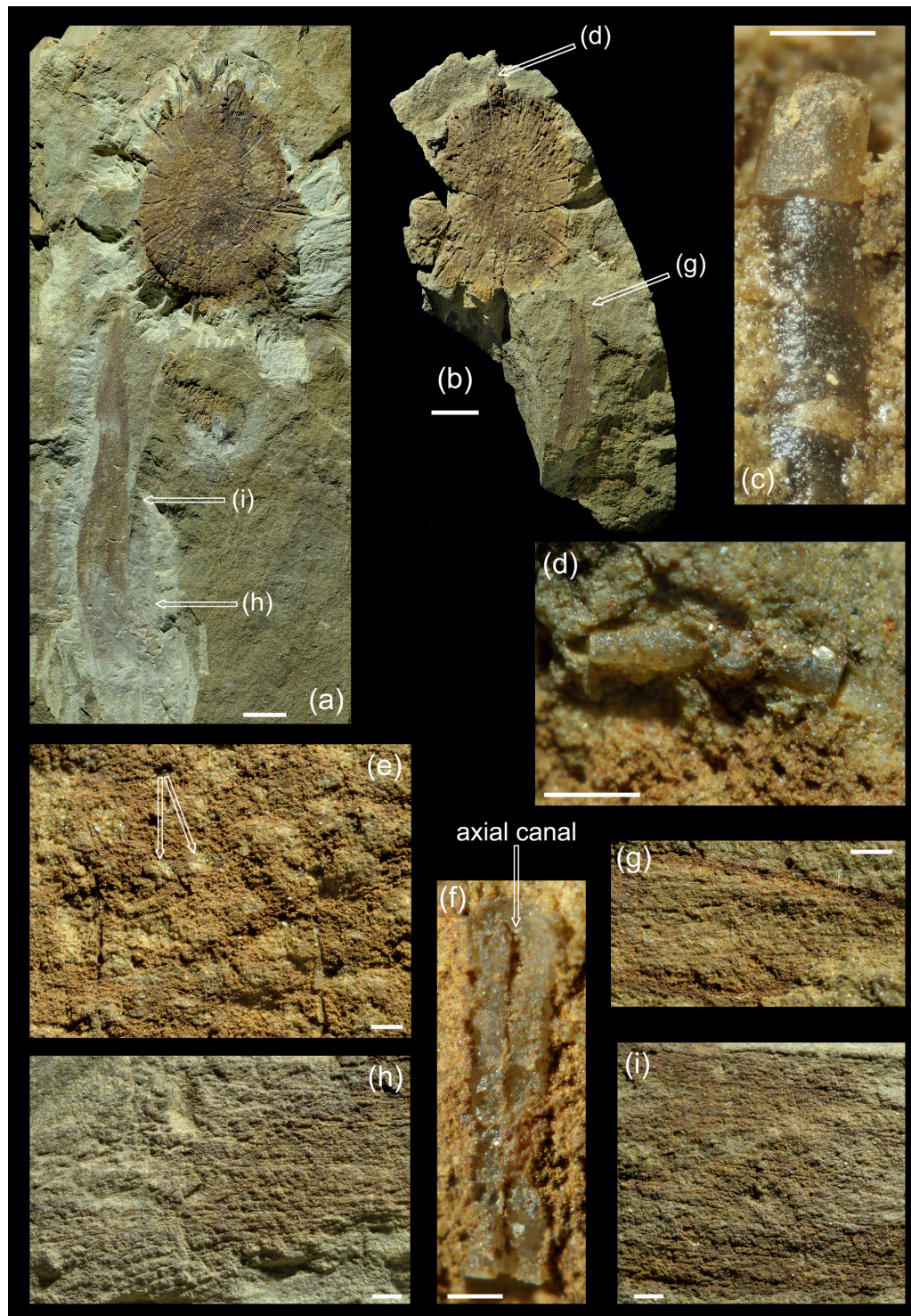
**Type species.** By monotypy; *Eoghanospongia carlinslowpensis* sp. nov., from the Wether Law Linn Formation (Telychian), locality R82 [NT 149586], Pentland Hills, Scotland.

**Diagnosis.** Sponge body in form of large, shallowly convex to undulating ovoid disc with cusped margin deflexed irregularly up or down; array of longitudinal (apparently radial) prostial spicules with greatly enlarged proximal ray, and other rays reduced or absent, the spicule centre extruded beyond the sponge margin; fine spicule mesh of irregular tracts of small, fine hexactines and perhaps abundant fine monaxons, mostly concentric and longitudinal but sometimes oblique; upper surface of sponge with irregular sub-radial and concentric array of small depressions. An associated structure appears to be a long basal peduncle with predominantly fine monaxon spiculation.

*Eoghanospongia carlinslowpensis* sp. nov.  
(Figs 2, 3)

**Derivation of name.** Derived from Carlins Lowp (meaning Witches' Leap), Scots name for the town of Carlops, the closest town to the fossil locality.

**Holotype.** NMS G.2010.38.1 and counterpart NMS G.2010.38.2. Only known specimen.

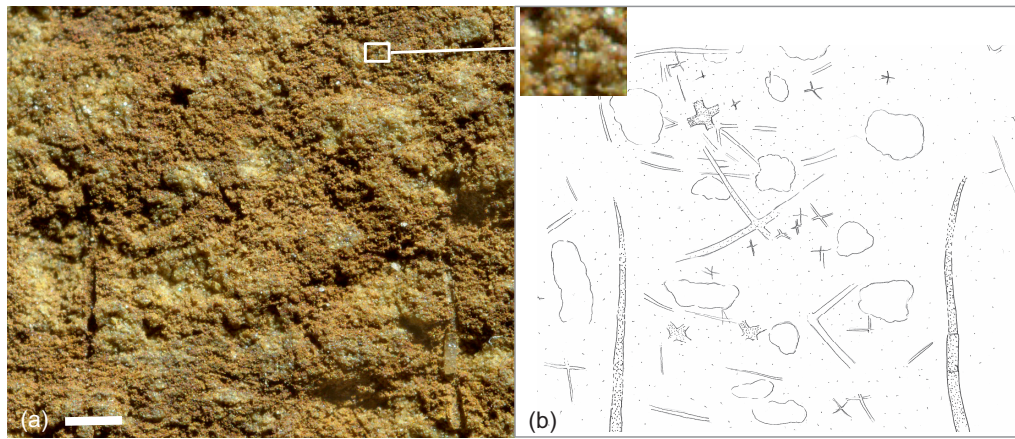


**Figure 2** *Eoghanospongia carlinslowpensis* gen. et sp. nov. (a) NMS G.2010.38.1 (part) and (b) NMS G.2010.38.2 (counterpart), with indications of positions of detail images. (c) Detail of part showing rounded distal termination of large prostalial style. (d) Detail of counterpart showing lateral rays of prostalial pentactin projecting just beyond body wall; position shown by an arrow on image (b). (e) Central part of disc with insertion points of major spicules, and fine spicular skeleton surrounding rounded depressions (presumed exhalent canals, see arrows). (f) Axial canal remnants on longitudinal section of prostalial spicule, shown by vertical arrow. (g) Sub-helical arrangement of fine monaxons in proximal part of stalk/peduncle; position shown by an arrow on image (b). Detail of part showing: (h) diverging fine monaxons in distal part of the stalk (position shown by an arrow on image (a)); (i) transverse spicules (oriented top-bottom) and probable small hexactins in central part of the stalk (position shown by an arrow on image (a)). Scale bars = 10 mm (a, b); 1 mm (e–i); 500  $\mu\text{m}$  (c, d).

**Diagnosis.** As for the genus.

**Locality.** Locality R82 [NT 149586], 50 m N of the junction of the Wether Law Linn and the North Esk River, Pentland Hills, Scotland.

**Description.** Sponge preserved as part and counterpart broken through the thickness of an oxidised (presumed originally pyritised) body wall; spicules normally dissolved, except for largest which retain siliceous composition and occasionally traces of axial canals.



**Figure 3** (a) Detail from Figure 2e, including magnified box showing small hexactin-based spicules, with (b) interpretative drawing to highlight visible spicules. Only the two vertically oriented prosthelia are preserved with recrystallised silica. Largest spicules with greatest relief (dark stippling) include several, with only centre of cross visible, the rest embedded in the matrix. Unstippled areas interpreted as openings of canals. Most spicules are not recognisable, and only the clearest are included. Scale bar = 500  $\mu$ m.

Body consists of a large, slightly convex, ellipsoidal disc (Fig. 2a, b), the major axis measuring 50 mm and the minor axis 40 mm. Margin cusped and irregular, with edge upturned in parts and downturned in others (polarity uncertain, but presumed majority is downturned). Disc with central apex preserved as a low mound; presumed underside not seen. Slight inflexion in the surface of the disc present at nearly half-radius. Outer part of disc with strong inflexion downwards, 3–4 mm high at most, before extending into marginal frill with cusped edge, up to 5 mm wide; marginal frill visible inconsistently due to uneven preservation or development.

Most obvious spicules are large, smooth, longitudinal rays up to 20 mm long and up to 0.75 mm in diameter, extending beyond the periphery of the disc. Some appear to be monaxons with rounded distal terminations (styles) (Fig. 2c), but at least one shows four perpendicular rays (pentactine) (Fig. 2d) that branch from a point beyond the sponge wall margin. Number of primary spicules difficult to assess with confidence due to breakage; we estimate to have been approximately 30, not regularly spaced. Proximal end of these spicules inserted at around 1/3 of the disc radius, with some finer spicules (ray diameter 0.4 mm) inserted more distally. Primary spicule rays parallel to the surface of the disc, including curvature at the marginal inflexion. The distal ends of the coronal spicules extend up to 5 mm beyond the sponge margin in some cases; usually probably less.

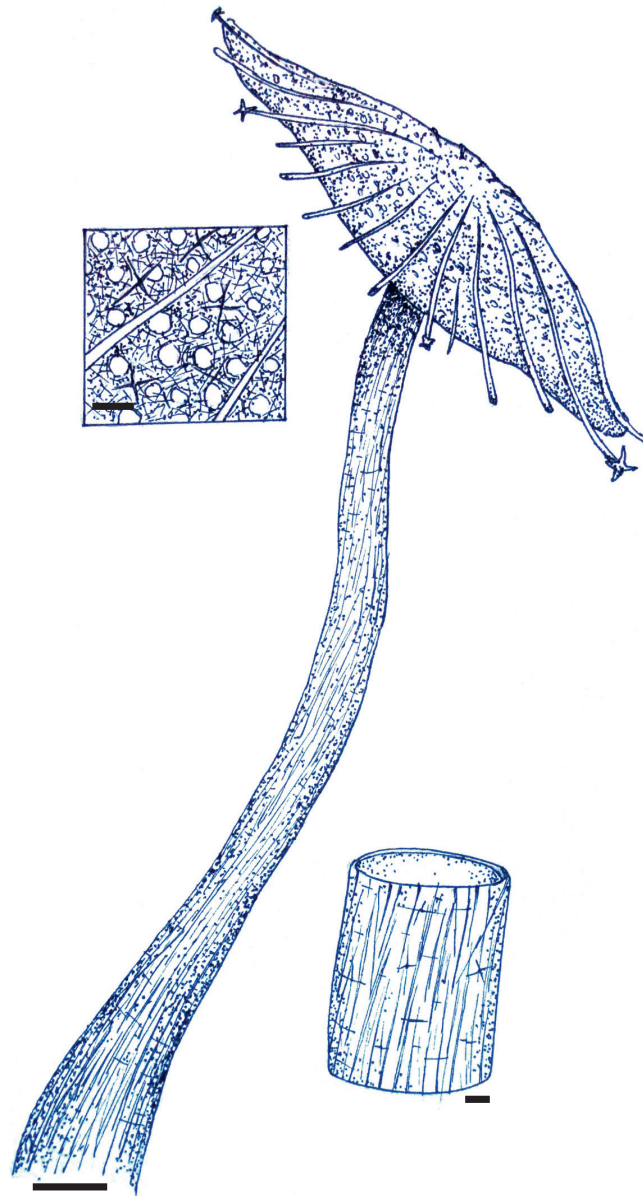
Fine skeleton (Fig. 3) poorly preserved and difficult to characterise, but consists of at least some very fine-rayed hexactines (ray diameter approximately 30  $\mu$ m), and probably abundant fine monaxons. Hexactin-based spicules include numerous sizes, including some with ray length less than 100  $\mu$ m. Fine spicules with irregular longitudinal and concentric tract development locally, but oblique spicules or tracts also present, and overall skeletal organisation is structured around openings to canals on oral surface (Fig. 3). Dense longitudinal monaxon array visible at margins of frill. Any regular skeletal architecture is distorted by the presence of numerous small depressions on the upper surface (often corresponding to similar small mounds on lower surface). Depressions with local radial or concentric alignment, but not consistent. Diameter of depressions up to approximately 1 mm (increasing slightly in average towards outer part), and spacing varies from six in 5 mm centrally, to four in 5 mm in the outer part of the disc.

Central quarter of the disc characterised by densely packed, irregularly arranged depressions only; skeletal structure unclear. Middle part of disc characterised by the insertion points of the major spicules, and clearest fine spicule tract development; depressions locally in concentric arrangement (Figs 2e, 3). Outer section of primary disc with depression arranged radially, constrained by primary spicule rays, often with two rows of depressions between each pair of spicule rays.

Primary spicules typically show a laminar internal structure, although the fine-scale laminae present in extant species of hexactinellid sponges like *Euplectella* (Aizenberg *et al.* 2005) are not preserved. Evidence for an axial canal is preserved in only a few examples (Fig. 2f); the rest are destroyed by recrystallisation.

Associated with the sponge body, curving towards and perhaps attached to the centre of the underside (but unexposed) is either a second unique sponge specimen, or more probably a peduncle or stalk. Exposed length is 80 mm, with implied length exceeding 110 mm, if connected with the sponge body. Spicules are predominantly fine monaxons, 2–2.5 mm long and 15–20  $\mu$ m in diameter, with helical arrangement in narrowest part (Fig. 2g), diverging unevenly distally (Fig. 2h). Some transverse spicules may also be present, but are inconclusive (Fig. 2i). It is not possible to determine whether the spicules are fused, due to the coarse preservation. The margins of the structure are more heavily mineralised than the interior, and spicules extend through the (very thin) sediment thickness rather than being restricted to a planar wall, but do not show the dense internal spiculation of an anchoring root tuft. The spicules are much finer and less densely packed than in the proximal part of *Plectoderma*, which occurs at the same locality. This combination of features demonstrates that the structure is a pedunculate stalk composed of spicules and soft tissue, rather than a dense, purely spiculate basal tuft.

**Remarks.** Uncertainty over whether the stalk-like structure is part of the sponge body hinders the interpretation, but it is unlikely that two unique specimens would co-occur on the same slab in such a way by chance. The preservation of this structure, including the presence of sediment inside it, supports an interpretation as a peduncle or stalk structure that is very different to those known for co-occurring species (Botting 2007a), and implies that it was part of the sponge body and with spicules embedded in soft tissue, rather than a purely spiculate basal root tuft. This interpretation is used for



**Figure 4** Interpretative reconstruction of *Eoghanospongia carlinslowpensis* gen. et sp. nov., including the probable peduncle, the connection of which to the sponge body cannot be confirmed without damaging the holotype. Upper detail views show the structure of the upper (convex) surface, including presumed exhalant canal openings between large prostalia styles/pentactins (smallest spicules only rarely preserved). Lower detail shows hollow peduncle/stalk, with dominantly sub-longitudinal monaxon (diactin) spiculation in thin wall. Scale bars = 10 mm in main image, 1 mm in detail views.

the reconstruction (Fig. 4). The morphology of the sponge body, being flat and without an apical osculum, is also best interpreted as being raised off the sea floor (by analogy with modern hexactinellids such as *Caulophacus* Schulze, 1886). Because of all these factors, assigning this structure to *Eoghanospongia* is highly likely, but cannot be considered categorical from the material available, and cannot be confirmed without significantly damaging the specimen.

Although only a single specimen is yet known, the good preservation characteristic of the Wether Law Linn Formation at locality R82 allows a reasonable characterisation of this new taxon, which is distinct from all previously described sponges in several ways. Classification of the new species into higher groups is challenging because of the unique character combination, and the lack of any similar described forms, and we therefore discuss several known groups as possible candidates for comparison.

Superficially, the morphology of the specimen described here is crudely similar to *Choia* and *Choiaella*, two members of the cosmopolitan (but probably paraphyletic; Botting *et al.*

2013) family Choiidae, the geographic range of which extended from South China, Siberia, and Laurentia (including peri-Laurentian margins) to Gondwana (Finks & Rigby 2004a; Botting 2007a, b; Beresi *et al.* 2010). *Choia* consisted of a flattened, circular to elliptical bowl, with a central disc of longitudinal (apparently radial) monaxons, enhanced by an array of large coronal monaxons radiating from the peripheral part and extending beyond the central disc. *Choiaella*, first discovered from Cambrian rocks in China, was described (Beresi *et al.* 2010) from the Late Ordovician of the Southern Uplands, Scotland, as well as from the locality R82 discussed here (Botting 2007a). *Choiaella* is morphologically similar to *Choia* in possessing a radiating, thatched central disc, but lacks coronal spicules.

In contrast, *Eoghanospongia* gen. nov. possesses a radial array of large spicules, with an irregular, sub-concentric fine skeletal mesh rather than a simple radiating thatch of small spicules covering the central disc; furthermore, the coronal spicules are larger and less abundant than in *Choia*. In at least some cases, these spicules are also pentactins, implying

that the projecting styles also originated as pentactins with suppressed rays. Although small hexactins are present within the central disc of some *Choia*-like sponges (Botting *et al.* 2013, p. 9), there is no indication of the coronal spicules being anything other than monaxons in any species. The similarity with choiids is, therefore, entirely superficial.

The new species is characterised, in part, by thin, parallel, concentric monaxon (and hexactine) spicules combined with a radial fabric to form a loosely quadrate mesh. This feature is loosely comparable to the structure of dictyospongioid hexactinellids (Finks & Rigby 2004b), although much less regularly organised, and the robust radial spicules have never previously been described in a dictyospongioid.

Hall & Clarke (1898) described and illustrated numerous reticulate sponges of the family Dictyospongiidae, most of which share a very similar fundamental structure, and differ primarily in body form. Their fine skeletal structure is often poorly preserved, but in overall form, some show a degree of similarity to the new species. For example, the basal area of *Phragmodictya* (a genus restricted to the Carboniferous) is characterised by an oval disc with a 'very fine reticulum' (Hall & Clarke 1898, p. 172, pl. 64, fig. 5). As in all dictyosponges, the reticulum is composed of a strictly radial and concentric spicular grid, the radial striae converging toward the centre of the disc. *Phragmodictya* also lacks the primary radial spicules and the depressions diagnostic of *Eoghanospongia*.

Not only does the fine skeletal architecture of the disc in *Eoghanospongia* lack the regularity of the dictyosponges, it also cannot be easily reconciled with the simple, homogeneously expanding growth pattern of reticulosans generally (Botting 2003). There are also no plausible counterparts in known dictyosponges for the large radial pentactines. Despite the superficial similarity in the fundamental body form and apparent wall structure, the detailed differences refute any assignment relating the new sponge to dictyosponges.

The body form of the new sponge, if the associated stalk region is a part of the sponge, is strikingly similar to the living rossellid hexactinellid *Caulophacus* (Schulze 1886; Tabachnick 2002). In this case, the stalk is essential to raising the flattened, mushroom-shaped-to-convolute discoidal body above the sea floor, and the same could be presumed for the body form described here. *Caulophacus* also has an irregular surface sculpture, with numerous small depressions associated with oscula. However, the skeletal structure of *Caulophacus* consists of a regular, fine grid of hexactins that is quite distinct from the tract development seen here. Although there is no exact counterpart for the large projecting pentactins in *Caulophacus*, such hypodermal pentactine prostaia are indeed limited in modern faunas to the Rossellidae (Tabachnick 2002). Although the origins of the family are believed to be in the Late Palaeozoic based on molecular clock data (Dohrmann *et al.* 2013), a putative stem-group rossellid, *Matteolaspongia hemiglobosa*, also featuring pentactine prostaia, has now been described by the Late Ordovician of China (Botting *et al.* 2018). A rossellid affinity is, therefore, possible, despite the early date and unusual shallow-water environment. The extremely robust prostaia in *Eoghanospongia* differ from all described rossellid examples, but there is a wide variation across the family. The morphology (including multiple exhalent depressions on the upper surface), stalk structure (composed dominantly of monaxons forming a thin wall), and presence of these prostaia all suggest a remarkable similarity to *Caulophacus*, or to related sponges within the rossellid crown group. Without fine detail of the skeletal architecture and spicule morphology (ideally including microscleres), however, this morphology is strongly suggestive but cannot be considered conclusive.

No other described fossil or modern sponges show particular similarity to the new species, and *Eoghanospongia* must, therefore, be left in open taxonomy at this stage, with strong suggestions of a rossellid affinity.

#### 4. Discussion

Interpreting the life position and autecology of uncommon fossils without close living relatives is often problematic. The new genus is described based on only a single specimen, and the proposed interpretation is, therefore, subject to some uncertainty. There are particular difficulties in the interpretation of fossils where the morphology of the sponge differs from the normal vasiform body form with a clear osculum; *Choia*, a Cambro–Ordovician genus that is similar in outline to *Eoghanospongia*, is a textbook example of the problems encountered. Although many specimens have been collected and described since Walcott (1920), it was not until Botting (2007b) that the conventional reconstructed orientation (see Rigby 1986) was inverted. A similar issue exists with the new taxon, in that there are no definitive indications of the life orientation (except for the stalk, if attached), and it could be assumed that the stable orientation (convex upward) represents the life position. However, the functionality of the sponge body plan makes such an orientation very difficult, especially as the direction of flexure of the rim varies around the margin. If the associated stalk is also a part of the sponge, then the orientation is fixed as being convex-upwards, as in the modern *Caulophacus*.

The depressions that may represent oscula or exhalent canal openings are regularly developed over much of the surface of the disc, arranged radially and concentrically. However, the central 20% of the disc does not show any clear geometric pattern. Some of the depressions appear to be locally radially arranged, whereas others are organised in short arcs. If these do represent oscula, then the morphological similarity to the extant *Caulophacus* is reinforced.

The evidence listed above favours the sponge being reconstructed with the convex apex upwards, and a stalked mode of life resembling that of *Caulophacus*. This would be unprecedented in the Palaeozoic, or in shallow-water environments, and indicates a highly derived morphology. Its co-occurrence with other unique sponges such as *Amphispongia* (Botting 2004) indicates that significant evolution of unusual morphologies was occurring in shallow-water environments, as represented by the Pentland Hills deposits. Normally, such environments are hostile to sponge preservation due to dissolution and turbulence, but unusual chemical conditions and rapid burial occasionally yield well-preserved fossils in even the most unlikely environments (see Botting 2005).

The new species further supports previous suggestions that dramatic diversification was occurring among sponges in shallow-water habitats during the Ordovician (Botting 2005; Muir *et al.* 2013), and highlights the limitations of our current knowledge of sponge evolution within these groups. The differences between the new species and any potential ancestors or close relatives, as with *Amphispongia* (see Botting 2004), *Haljalospongia* (Botting & Rhebergen 2011), and others (e.g., Rigby & Webby 1988), implies that we currently have no knowledge of large parts of sponge evolution from this interval, especially regarding the stem group (and perhaps early crown group) of Hexactinellida. If we are correct in interpreting the specimen as a plausible crown-group rossellid allied to *Caulophacus*, or at least crown-group lyssacinoidan, then this builds on other results from China (Botting *et al.* 2018) that exacerbate the problems of the missing record of

sponge diversification, as it implies that many modern groups must have arisen cryptically, and left almost no trace in the fossil record. The presence of a possible derived hexactinellid in a shallow-water, lagoonal setting is in complete contradiction of their modern distribution pattern (deep oceans and caves, both palaeontologically inaccessible), and makes explanation of the missing record even more problematic. Changing environment inhabitation is a common phenomenon within hexactinellid-like sponges generally (Mehl 1996; Mehl-Janussen 1999), but for modern-type hexactinellids, shallow-water colonisation is tied to particular intervals of high sea level, such as the Jurassic and Cretaceous periods.

## 5. Conclusions

A new fossil sponge, *Eoghanospongia carlinslowpensis* gen. et sp. nov., is described from the Telychian (early Silurian) of the Pentland Hills, Scotland. It has a morphology unique in the fossil record, and among living taxa most closely resembles that seen in rossellid hexactinellid *Caulophacus*. However, there are significant differences that preclude a close relationship to known taxa, and the only fossil record of *Caulophacus* is from spicules in Tertiary radiolarite deposits from New Zealand (Hinde & Holmes 1892). Although a long and cryptic deep-sea history of such a genus is possible, we prefer to consider the new fossil to represent an early rossellid that may have evolved a similar morphology convergently. The implications of the new species include further support for the contention that the family Rossellidae has an extremely deep history, and reiteration of the incompleteness of some aspects of the sponge fossil record. The most surprising aspect is the presence of what is now a deep-water (abyssal) sponge in a shallow-water lagoon. This may be an ecological analogue of the recent discovery of living hexactinellids in shallow-water caves in the Mediterranean (Vacelet 1996), a habitat that mimics the dark and quiet-water environment of the deep oceans.

## 6. Acknowledgements

JPB thanks the National Museums Scotland for support through a Visiting Research Fellowship. YC thanks Lyall Anderson for helping with Scots vocabulary. The manuscript was improved by constructive comments from two anonymous referees.

## 7. References

- Aizenberg, J., Weaver, J. C., Thanawala, M. S., Sundar, V. C., Morse, D. E. & Fratzl, P. 2005. Skeleton of *Euplectella* sp.: structural hierarchy from the nanoscale to the macroscale. *Science* **309**, 275–78.
- Beresi, M. S., Botting, J. P. & Clarkson, E. N. K. 2010. A new demosponge, *Choiella scotica*, from the Caradoc (Ordovician) of Wallace's Cast, Southern Uplands. *Scottish Journal of Geology* **46**, 77–83.
- Botting, J. P. 2003. Growth patterns of Lower Palaeozoic sponges. *Lethaia* **36**, 41–52.
- Botting, J. P. 2004. A revision of the hexactinellid sponge *Amphispongia oblonga* Salter, 1861: not a dasycladacean alga. *Scottish Journal of Geology* **40**, 115–18.
- Botting, J. P. 2005. Exceptionally-preserved Middle Ordovician sponges from the Llandeugly Rocks Lagerstätte, Wales. *Palaeontology* **48**, 577–617.
- Botting, J. P. 2007a. Algae, receptaculitids and sponges. In Clarkson, E. N. K., Harper, D. A. T., Taylor, C. M. & Anderson, L. I. (eds) *Silurian fossils of the Pentland Hills, Scotland*. Field Guide to Fossils 11, 36–49. London: The Palaeontological Association.
- Botting, J. P. 2007b. 'Cambrian' demosponges in the Ordovician of Morocco: insights into the early evolutionary history of sponges. *Geobios* **40**, 737–48.
- Botting, J. P., Muir, L. A. & Lin, J.-P. 2013. Relationships of the Cambrian Protomonaxonida (Porifera). *Palaeontologia Electronica*. <https://doi.org/10.26879/339>.
- Botting, J. P., Zhang, Y. & Muir, L. A. 2018. A candidate stem-group rossellid (Porifera, Hexactinellida) from the latest Ordovician Anji Biota, China. *Bulletin of Geosciences* **93**, 275–85.
- Botting, J. P. & Muir, L. A. 2013. Spicule structure and affinities of the Late Ordovician hexactinellid-like sponge *Cyathophycus loydelli* from the Llanfawr Mudstones Lagerstätte, Wales. *Lethaia* **46**, 454–69.
- Botting, J. P. & Muir, L. A. 2018. Early sponge evolution: a review and phylogenetic framework. *Palaeoworld* **27**, 1–29.
- Botting, J. P. & Rhebergen, F. 2011. A remarkable new Middle Sandbian (Ordovician) hexactinellid sponge in Baltic erratics. *Scripta Geologica* **143**, 1–14.
- Boué, A. 1820. *Essai géologique sur l'Ecosse*. Paris: Courcier. 519 pp.
- Candela, Y. & Crighton, R. B. 2015. Revision of *Plumulites ruskini* Lamont, and new data from the Silurian of the Pentland Hills, Scotland. *Scottish Journal of Geology* **51**, 31–42.
- Clarkson, E. N. K., Harper, D. A. T., Taylor, C. M. & Anderson, L. I. 2007. *Silurian fossils of the Pentland Hills, Scotland*. Field Guide to Fossils 11. London: The Palaeontological Association. 218 pp.
- Clarkson, E. N. K. & Taylor, C. M. 2007. Silurian rocks and fossils in the Pentland Hills. In Clarkson, E. N. K., Harper, D. A. T., Taylor, C. M. & Anderson, L. I. (eds) *Silurian fossils of the Pentland Hills, Scotland*. Field Guide to Fossils 11, 8–29. London: The Palaeontological Association.
- Dohrmann, M., Vargas, S., Janussen, D., Collins, A. G. & Wörheide, G. 2013. Molecular paleobiology of early-branching animals: integrating DNA and fossils elucidates the evolutionary history of hexactinellid sponges. *Paleobiology* **39**, 95–108.
- Finks, R. M. & Rigby, J. K. 2004a. Paleozoic demosponges. In Kaesler, R. L. (ed.) *Treatise on invertebrate paleontology. Part E, Porifera (revised)* **3**, 9–173. Boulder, CO & Lawrence, KA: Geological Society of America and Paleontological Institute.
- Finks, R. M. & Rigby, J. K. 2004b. Paleozoic hexactinellid sponges. In Kaesler, R. L. (ed.) *Treatise on invertebrate paleontology. Part E, Porifera (revised)* **3**, 319–448. Boulder, CO & Lawrence, KA: Geological Society of America and Paleontological Institute.
- Hall, J. & Clarke, J. M. 1898. *A memoir on the palaeozoic reticulate sponges constituting the family dictyospongidae*. New York & Albany, NY: Wynkoop Hallenbeck Crawford Co.. 350 pp. +70 pls.
- Haswell, G. C. 1865. *On the Silurian formation in the Pentland Hills*. Edinburgh: Wilson P. Nimmo. 47 pp.
- Hinde, G. J. 1883. *Catalogue of fossil sponges in the geological department of the British Museum (Natural History), with description of new and little-known species*. London: British Museum (Natural History). 248 pp. + 38 pls.
- Hinde, G. J. 1887–1912. A monograph of British fossil sponges. *Monograph of the Palaeontological Society* (1) 1887: **40**(190), 1–92, pls 1–8; (2) 1888: **41**(194), 93–188, pl. 9; (3) 1893: **47**(222), 189–254, pls 10–19; (4) 1912: **65**(322), 255–64.
- Hinde, G. J. & Holmes, W. M. 1892. On the sponge remains in the Lower Tertiary strata near Oamaru, Otago, New Zealand. *Journal of the Linnean Society (London), Zoology* **24**, 177–262.
- Howell, H. H. & Geikie, A. 1861. *The geology of the neighbourhood of Edinburgh*. Memoirs of the Geological Survey of Great Britain. Edinburgh: HMSO. 137 pp.
- Lamont, A. 1947. Gala-Tarannon beds in the Pentland Hills, near Edinburgh. *Geological Magazine* **84**, 193–208.
- MacLaren, C. 1839. *A sketch of the geology of Fife and the Lothians, including detailed descriptions of Arthur's Seat and the Pentland Hills*. Edinburgh: A. & C. Black. 235 pp.
- M'Coy, F. 1846. *A synopsis of the Silurian fossils of Ireland collected from the several districts by Richard Griffith F.G.S.* Dublin: Privately published. 72 pp + 5 pls.
- Mehl, D. 1996. Phylogenie und Evolutionsökologie der Hexactinellida (Porifera) im Paläozoikum. *Geologische Paläontologische Mitteilungen der Universität Innsbruck, Sonderband* **4**, 1–55.
- Mehl-Janussen, D. 1999. Die frühe evolution der Porifera. *Münchner Geowissenschaftliche Abhandlungen, Reihe A* **37**, 1–72.
- Muir, L. A., Botting, J. P., Carrera, M. & Beresi, M. 2013. Palaeobiogeography of Cambrian – Silurian Porifera. In Harper, D. A. T. & Servais, T. (eds) *Early palaeozoic palaeobiogeography and palaeogeography*, 127–44. London: Geological Society, Memoirs 38.
- Peach, B. N. & Horne, J. 1899. The Silurian rocks of Britain, 1: Scotland. *Memoir of the Geological Survey, UK*, xviii. 749 pp.



- Reed, F. R. C. 1917. The Ordovician and Silurian Brachiopoda of the Girvan District. *Transactions of the Royal Society of Edinburgh* **51**, 795–998, pls 1–24.
- Rigby, J. K. 1986. Sponges of the Burgess Shale (Middle Cambrian) British Columbia. *Palaeontographica Canadiana Monograph* **2**, 1–105.
- Rigby, J. K. & Webby, B. D. 1988. Late Ordovician sponges from the Malongulli Formation of central New South Wales, Australia. *Palaeontographica Americana* **56**, 1–147.
- Robertson, G. 1985. Palaeoenvironmental interpretation of the Silurian rocks of the Pentland Hills. Unpublished PhD Thesis, University of Edinburgh, Scotland.
- Robertson, G. 1989. A palaeoenvironmental interpretation of the Silurian rocks of the Pentland Hills, near Edinburgh, Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences* **80**, 127–41.
- Schmidt, O. 1870. *Grundzüge einer spongien-fauna des atlantischen gebietes*. Leipzig: Wilhelm Engelmann, iii–iv, 1–88, pls 1–6.
- Schulze, F. E. 1885. The Hexactinellida. Reports of the Scientific Research of the Voyage of H.M.S. ‘Challenger’, 1873–1876. Narrative **1**, 437–51.
- Schulze, F. E. 1886. Über den Bau und das System der Hexactinelliden. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin (Physikalisch-Mathematisch Classe)*. 97 pp.
- Tabachnick, K. R. 2002. Family rossellidae schulze, 1885. In Hooper, J. N. A. & Van Soest R. W. M. (eds) *Systema Porifera: a guide to the classification of sponges*, 1141–505. New York: Kluwer Academic/Plenum Publishers.
- Vacelet, J. 1996. Deep-sea sponges in a Mediterranean cave. In Uiblein, F., Ott, J. & Stachowitsch, M. (eds) Deep-sea and extreme shallow-water habitats: affinities and adaptations. *Bio-systematics and Ecology Series* **11**, 299–312.
- Walcott, C. D. 1920. Cambrian geology and palaeontology. IV: middle Cambrian Spongiae. *Smithsonian Miscellaneous Collections* **67**, 261–364.

---

MS received 2 October 2018. Accepted for publication 1 February 2019