

***Teganium* (Porifera, Hexactinellida) from the Middle Ordovician Castle Bank fauna of Avalonia (Wales, UK)**

Joseph P. Botting, Lucy A. Muir, and Junye Ma

ABSTRACT

The hexactinellid sponges *Teganium* and *Teganiella* are widespread in Ordovician, Devonian and Carboniferous strata in Laurentia, but have not previously been reported outside that palaeocontinent; some other members of the family Teganiidae are also restricted to Laurentia. The genus *Teganiella* in particular is considered to be a Laurentian endemic, with all species specialised for equatorial, shallow-water conditions. However, it is now clear that the diagnostic separation of *Teganiella* from *Teganium* was based on misunderstanding of the latter, and *Teganiella* should be considered a junior synonym. Based on this prior distribution, the discovery of two new species of *Teganium* (*T. avalonensis* sp. nov. and *Teganium* sp.) from the Middle Ordovician (*Didymograptus murchisoni* Biozone) of Castle Bank, Wales, is unexpected. These species are the oldest known and indicate diversification of the genus within a temperate microcontinent, prior to its appearance in Laurentia. The exceptional preservation of the new sponges also reveals detail of a complex body wall, supporting a more derived phylogenetic position within Hexactinellida (possibly affiliated to the Lysacinosida) than previously recognised. The palaeobiogeography may suggest a relatively deep-water origin for the group (as for modern hexactinellids), which then became secondarily specialised for shallow-water environments within a Laurentian diversification.

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INTRODUCTION

The potential usefulness of palaeobiogeographic studies on Palaeozoic sponges is strongly dependent on the groups in question, but where it can be understood, they provide substantial insights into both palaeogeography and the ecology of the groups in question. Such distribution patterns can reveal palaeoceanographic circulation patterns, unsuspected palaeoenvironmental links and simultaneously constrain the ecological requirements of the taxa involved. Reef-building sponges such as lithistids (Carrera and Rigby, 1999) and stromatoporoids (Nestor and Webby, 2013; Jeon et al., 2022) show informative distribution patterns within carbonate facies, but are tied to these conditions, primarily in the equatorial latitudes. Non-lithistid sponges are generally more limited in their potential, because of their low preservation potential and lack of study (Muir et al., 2013). Preservation of the more delicate sponges that lack fused skeletons requires abrupt burial or some other form of exceptional preservation, and this normally occurs in offshore environments influenced by intermittent rapid deposition. In the Cambrian Burgess Shale-type faunas, where sponges are generally diverse and abundant (Rigby and Collins, 2004; Wu et al., 2014; Botting and Peel, 2016; Botting and Muir, 2019) sponge genera were often widely distributed, but the Ordovician communities were much more strongly endemic (Botting and Muir, 2018). Even within a small area with high levels of exceptional sponge preservation such as the Builth Inlier of Wales (Muir and Botting, 2015), the majority of species and even genera are known from single occurrences.

In post-Cambrian offshore sponge faunas, very few genera are known from more than one or two areas, and the majority of these are holdovers from the widely distributed Cambrian lineages (Botting and Muir, 2019). The most widespread Ordovician and Silurian genus in these environments was probably *Cyathophycus*, which is known from several palaeocontinents around the margins of the Iapetus Ocean (Muir et al., 2013). The genus is, however, poorly defined, in that it consists of a very generalised, orthogonal reticulate skeleton with overlap of the skeletal rays. The range of taxa assigned to *Cyathophycus* is very wide (Botting,

2004), including variation in seemingly critical characters such as the existence and nature of an inner skeletal wall. In some species, preservation of fine details such as anomalous (hexagonal) axial canal symmetry suggests a position close to the base of Silicea, and perhaps in the demosponge stem group (Botting and Muir, 2013, 2018). As the various species are found in a variety of palaeoenvironments (with each species being recorded from a single site in many cases), and may be taxonomically disparate, such interpretative limitations also impact the reliability of assessments of palaeobiogeography based on these taxa.

Another complex of Palaeozoic hexactinellid-like taxa with multiple described species is composed of *Teganium* and *Teganiella* (summarised by Finks and Rigby, 2004), which show an environmental shift from offshore to sheltered inshore environments of Laurentia between the Ordovician and Carboniferous. In this study, we describe new material of *Teganiella* from Middle Ordovician strata of Wales, UK. This genus was previously known only from Upper Ordovician to Carboniferous strata of Laurentia; thus, the Welsh material represents a substantial range increase for the taxon. Based on an assessment of the supposed differences between the two genera, we show that they are effectively identical and synonymize them into the senior name, *Teganium*. We demonstrate that the evolution of this genus involved a transition into shallower water through time.

GEOLOGICAL BACKGROUND

Castle Bank is a recently discovered Burgess Shale-type Konservat-Lagerstätte close to Llandrindod, central Wales, within the Ordovician Builth–Llandrindod Inlier (Botting, 2021; Botting and Ma, 2022; Pates et al., 2022; Botting et al., 2023). Precise locality information is housed with the specimens. There are numerous sponge faunas in the inlier, from a range of palaeoenvironments (Muir and Botting, 2015), with Castle Bank representing an intermediate water depth interpreted as being close to storm wave base, on the basis of sedimentology and associated faunas. In particular, the sedimentary succession consists of slowly deposited, laminated graptolitic siltstone interspersed with rapidly deposited event beds that

contain exceptionally preserved fossils (Botting et al., 2023), the combination characteristic of conditions around storm wave base. The fauna is a mixture of shallow-water and (primarily) offshore taxa, with echinoderms in particular being composed only of asterozoans and rare stylophorans that are unique to the site (Botting et al., 2023). The lack of both crinoids (shallow-water) and the typical offshore stylophorans is characteristic of an ecological gap in echinoderm faunas that occur around storm wave base, as described by Botting et al. (2013). Algae are present but rare and transported with the exceptionally preserved fauna. Exact water depth cannot be assessed, but given the palaeoceanic context (a semi-isolated back-arc basin on the margin of the Iapetus Ocean) and proximity to a photic-zone region, is estimated at around 50–100 m.

The age of the site (Figure 1) is constrained by abundant graptolites to the *Didymograptus murchisoni* Biozone, and lithostratigraphically to the Gilwern Volcanic Formation of the Builth Volcanic Group (Schofield et al., 2004). The Castle Bank quarry exposes approximately 10 metres of siltstone and volcanic ash beds, representing a very small part of the formation (which is several hundred metres thick) and a short time interval.

Sponge remains are preserved at multiple levels, but especially within a two-metre interval in the centre of the quarry, where they are usually fully articulated with preserved soft tissue, and co-occur

with other exceptionally preserved taxa. The new species is widely distributed within this interval, and is one of the most abundant sponges in the assemblage. Outside that interval, sponge remains are mostly disarticulated, and the presence of the species cannot be assessed.

MATERIALS AND METHODS

Type and figured specimens are deposited in the Amgueddfa Cymru—National Museum Wales (NMW); comparative material will also be placed in the Nanjing Institute of Geology and Palaeontology, China. Specimens were illustrated primarily using Leica S8APO and M125C (with camera lucida) microscopes (Leica, Wetzlar, Germany), with cross-polarizing ring lights (Leica LED 3000 RL) and a HiChrome MET-AF digital camera (GX Microscopes, Wickhambrook, Suffolk, UK). Some high-magnification images were obtained with a Maozua digital USB microscope. Images were compiled and processed (contrast/brightness) using the OpenOffice software.

SYSTEMATIC PALAEOLOGY

Phylum PORIFERA Grant, 1836

Class HEXACTINELLIDA Schmidt, 1870

Remarks. Although any sponges with hexactins are traditionally assigned to the Hexactinellida, palaeontological evidence implies that these spicules pre-date the class (Botting and Muir, 2018).

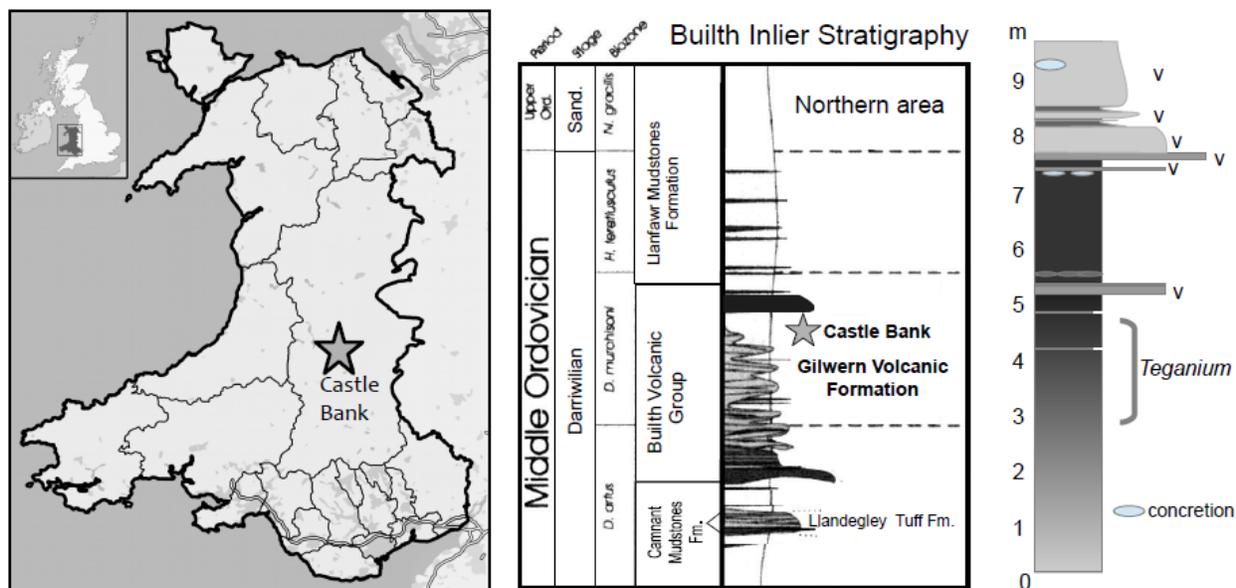


FIGURE 1. Locality map (left) and local stratigraphy of the Castle Bank locality, showing occurrence of *Teganium avalonensis* sp. nov. within the Castle Bank sequence (mainly siltstone, with shading representing colour of sediment; v: volcanic ash layers). Exact locality information is deposited with the specimens.

The majority of early hexactin-bearing taxa have simple, often single-layered skeletons in at least a semi-regular array, and are referred to generally as reticulans; however, this is probably a paraphyletic grouping of early siliceans, at least. As a result, assignment of fossils to the hexactinellid crown or total group can only be confident when based on specific structures of the skeleton, or the existence of known microscleres (almost never preserved in situ). Crown-group lyssacine (lacking a fused skeleton) hexactinellids differ from most reticulans in the complexity of that skeleton, with multiple distinct skeletal layers composed of different spicules in different arrangements. The complex wall structure of *Teganiella* (as seen with additional detail in the new material) supports at least a total-group hexactinellid assignment, and plausibly a crown-group affinity. Specific characters implying a relationship to particular hexactinellid groups are discussed below.

Family TEGANIIDAE de Laubenfels, 1955

Remarks. Finks and Rigby (2004) included the following taxa within the family Teganiidae: *Teganium* Walcott, 1879 (the type genus); *Bulbospongia* Rigby and Mehl, 1994; *Echidnina* Bengtson, 1986; *Rhombodictyon* Whitfield, 1886; *Rufuspongia* Rigby and Mehl, 1994; *Taleolaspongia* Rigby and Mehl, 1994; and *Teganiella* Rigby, 1986. Some of these taxa (*Bulbospongia*, *Rufuspongia* and *Taleolaspongia*) are known only from Devonian strata of Laurentia (Rigby and Mehl, 1994; Finks and Rigby, 2004). *Teganiella*, as stated elsewhere in this manuscript, is previously known from Devonian and Carboniferous rocks of the USA and *Teganium* is an Ordovician genus. *Rhombodictyon* is known from Ordovician strata of Laurentia (Whitfield, 1886; James, 1891; the Devonian stratigraphic range given by Finks and Rigby, 2004, is clearly a typographical error), plus one record from Carboniferous rocks of Poland (Hurcewicz and Czarniecki, 1985). However, we note that *Rhombodictyon* was considered to be an inorganic structure by Ruedemann (1925a). Resolving the affinity of this taxon would require restudy of the type material and is beyond the scope of this study. *Echidnina* consists of tiny (210–300 µm diameter) globular spicular bodies (Bengtson, 1986) and is generally considered to be a radiolarian (e.g., Zhang et al., 2021). Thus, the family is primarily Devonian, with some examples from Ordovician and Carboniferous rocks.

Genus TEGANIUM Rauff, 1894

Diagnosis. (Emended after diagnosis of *Teganiella*, Finks and Rigby, 2004.) Sphaeroidal reticulans with thin wall composed of minute hexactin-based spicules in mostly continuous but irregularly oriented reticulate array, and choanosomal body wall with small, circular internal cavities; circular osculum is in some species lined by dense array of fine marginalia.

Type species. *Cyathophycus subsphaericus* Walcott, 1879, by original designation.

Other species. *Teganiella heathi* Rigby, 1986; *Ti. ovata* Rigby and Mehl, 1994; *Teganium avalonensis* sp. nov.; questionably also *Ti. finksi* Mouro et al., 2019.

Remarks. Separation of *Teganiella* from *Teganium* is highly problematic and is here considered invalid. The structure of the skeleton and soft tissue in the new species is remarkably similar to that described for *Teganium* (Walcott, 1879; Rauff, 1894; Finks and Rigby, 2004), only lacking the presence of abundant prosthelia (Hall and Clarke, 1899). The absence of an osculum was stated by Finks and Rigby (2004) to be a defining feature of the genus *Teganium*. However, the original description of *Cyathophycus subsphaericus* Walcott, 1879 (the type species of *Teganium*), not only states that there is an osculum in many specimens but also gives measurements (9 mm diameter for a 30 mm-diameter sponge). Hall and Clarke (1899) illustrated several specimens that all apparently lack oscules, but the drawings alone are inconclusive. Finks and Rigby (2004) confirmed the non-existence of an osculum based on only the holotype, and it is likely that in this specimen it is concealed by an awkward angle of flattening. In particular, if the holotype is vertically compressed and viewed from below, this could have both obscured the osculum and potentially also given the appearance of abundant lateral prosthelia due to flattening of the radial array of basalialia. The original description of Walcott (1879) makes it clear that the type species possesses an osculum and lacks prominent lateral prosthelia.

In their species *Teganiella finksi*, Mouro et al. (2019) noted that although no osculum was visible in the moderately poor material, some specimens have a flattened summit that may indicate its presence and position; this is entirely normal for a laterally compressed reticulans. Given the requirement for at least one exhalant opening in order for the sponge to function, this apparent lack of any terminal aperture is probably due to inconvenient orientation of compression in a globose sponge with a strongly narrowed osculum, to the

extent that it is not clearly visible. It, therefore, appears that *Teganium* and *Teganiella* are identical, and given that the latter is well defined and the former (which would be the senior synonym) is more problematic in (according to some authors only) lacking an osculum, the genera should be considered identical and are here formally synonymized.

An assessment of previously known species of *Teganiella* (here transferred to the senior synonym *Teganium*) was provided by Mouro et al. (2019), who erected the species *Tl. finksi*. The generic definition is revised here, due to some confusion in Finks and Rigby (2004), in which the familial diagnosis contradicts the generic diagnosis in mistakenly requiring the absence of an osculum. The first two named species of *Teganiella* (*Tl. heathi* Rigby, 1986 and *Tl. ovata* Rigby and Mehl, 1994), both show a clear osculum, in at least the latter surrounded by marginalia. The current species is closest to *Tl. ovata*, which differs in some ways from the type species, but is close enough to support congeneric status.

Stratigraphic range. The genus is previously known from Upper Ordovician, Devonian and Carboniferous rocks of the USA (Laurentia); the new species extend this to the Middle Ordovician of Avalonia.

Teganium avalonensis sp. nov.
Figures 2–5

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Name. After the geographic origin, the palaeocontinent Avalonia.

Diagnosis. Oval to rounded quadrate *Teganium* with pronounced, slightly inwardly-directed marginalia surrounding broad osculum, and fine skeleton composed of numerous very small hexactins and derivatives; outer (dermal or hypodermal) layer with a semi-regular reticulation and inner layer with numerous, densely-packed, rounded cavities.

Holotype. NMW.2021.3G.71, large complete specimen with marginalia and basalia, but generally lacking fine skeletal detail.

Paratypes. NMW.2021.3G.72, pair of sponges with well-preserved marginalia but little fine skeletal detail; NMW.2021.3G.73, large complete example; NMW.2021.3G.74, small partial specimen showing oscular margin; NMW.2021.3G.77, the largest complete specimen; NMW.2021.3G.78, three moderate-size specimens; NMW.2021.3G.79, one small and relatively elongate specimen; NMW.2021.3G.80, small complete specimen; NMW.2021.3G.81, cluster of four moderately large

specimens; NMW.2021.3G.82, partial specimen with well-preserved fine detail of body wall.

Description. Sponges are oval, slightly taller than wide, in some cases with somewhat squared outline showing a flattened base (Figure 2C). Specimens up to 14 mm wide and 16 mm tall (excluding marginalia). Osculum of holotype (Figure 2C) 4 mm wide, and proportionally similar in other specimens, being approximately one-third of maximum width; where basal margin is flattened, this covers approximately half of maximum sponge width. In most cases the specimens are preserved in a thick film of carbon and/or iron minerals, but in some specimens, body wall structure is preserved (Figure 3C–F). Wall thickness visible at the lateral margins in several specimens (including holotype, Figure 2C, and in Figure 3C–D), and is irregular but normally up to 0.5 mm thick.

Internal organisation of wall (preserved as denser brown material representing soft tissue; Figure 3C, F) with numerous rounded polygonal to circular cavities or exhalant canals (leading into central atrium) on similar scale to primary skeletal grid (c. 0.1–0.4 mm). In most areas (perhaps excluding base and extreme apex), tissue regions between spaces are narrower than the cavities, with a 0.1 mm-thick wall.

Skeleton faintly preserved due to delicate spiculation, but fine dimpled texture reflecting the primary external grid is visible over surface (Figure 3B); spicules are visible when wet, but specimens are prone to cracking in contact with water. Dimples, representing spaces between spicules, are 0.1–0.2 mm wide and often arranged in sinuous lines resulting from semi-regular spicule grid. Grid is dominantly diagonal, but irregular. Spicules (Figure 3D–E) are simple triaxons, presumed to be hexactins but with gastral and distal rays not confirmed. Ray length typically up to 0.2 mm and extremely fine. The appearance of longer spicules in low-angle light is a result of relief due to locally aligned skeletal grid. Finest spicules appear to be randomly arranged between the larger spicules, including over the spaces within the primary grid, and over cavities preserved in paratype, implying that these occupy an outer layer (probably hypodermal or dermal) overlying internal spaces.

Marginalia (Figures 2A, C–D and 3A) consistently around 2 mm long (even in largest specimen, implying a maximum length reached early), fine (less than 0.1 mm wide), with bases embedded in body wall; they are either diactins or greatly extended vertical rays of hexactins. Rays are straight and inclined inwards at around 45–60°,

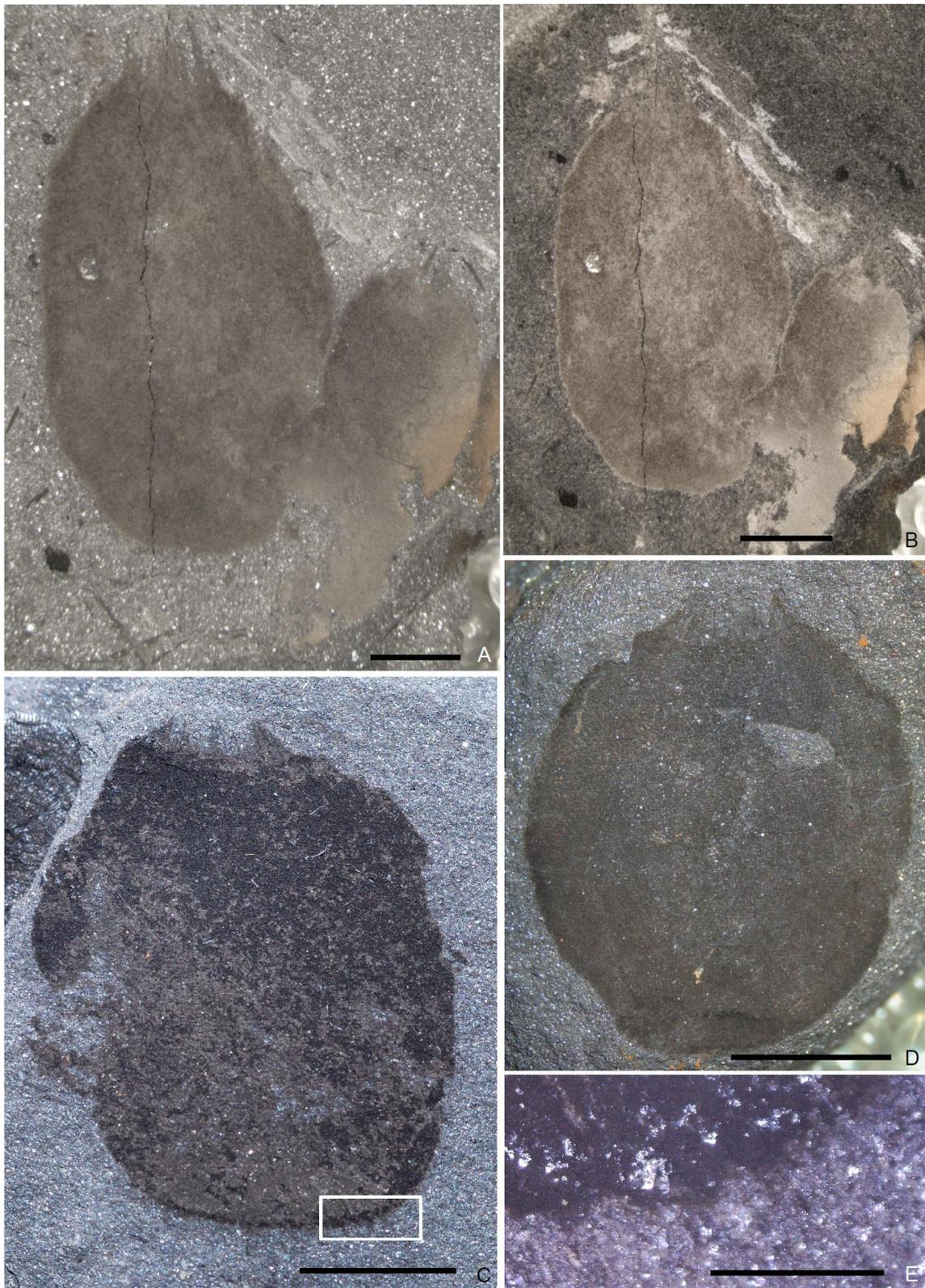


FIGURE 2. *Teganium avalonensis* sp. nov., from the Middle Ordovician Castle Bank Biota, Wales. A–B: paratype slab NMW.2021.3G.72, with pair of sponges in A, plane-polarised light, and B, cross-polarised; C, E, holotype NMW.2021.3G.71: C, overall view, with box indicating area enlarged in E; E, detail of basal region showing projecting basalalia; D, paratype NMW.2021.3G.73, overall view. Scale bars: A–D equal 5 mm; E equals 1 mm.

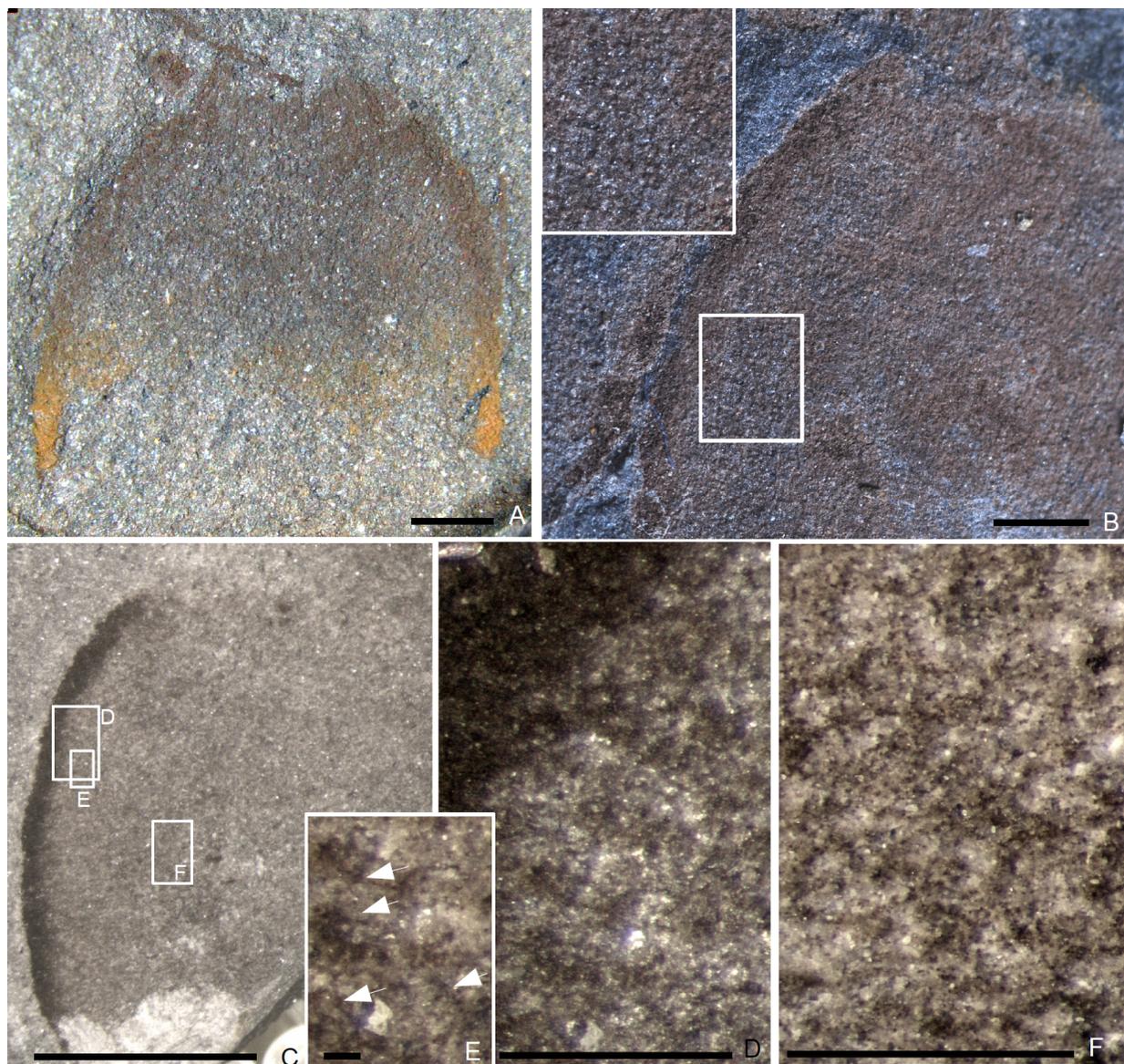


FIGURE 3. *Teganium avalonensis* sp. nov. A, paratype NMW.2021.3G.74; apical part with marginalia, imaged with directed light (from right) to highlight texture of body wall; B, paratype NMW.2021.3G.98, with low-angle light to highlight diagnostic texture of body wall (boxed area enlarged inset); C–F, paratype NMW.2021.3G.82, partial specimen with the boxes in C indicating positions of D, E and F; D, lateral detail to show reticulate skeletal grid (plane-polarised light); E, detail showing scale of minute triaxon spicules within the same area; centres of several spicules arrowed; F, detail of central part of specimen in cross-polarised light (contrast enhanced) to highlight the small circular cavities within choanosomal (internal) layer of body wall. Scale bars: A, B, D, F equal 1 mm; C equals 5 mm; E equals 0.1 mm.

forming a barrier around sides of slightly depressed osculum. No lateral prostalia or even projecting distal rays are visible, although the lateral margin of flattened sponges is slightly rough; the preservation is not detailed enough to demonstrate conclusively whether any of the smaller dermal/hypodermal spicules had any rays projecting.

Basalia (Figure 2C, E) preserved in holotype as bases of coarse spicules protruding into sediment. Spicules 0.1–0.2 mm wide, extending unknown distance into sediment, and are less well preserved with increasing distance from the sponge body (a documented feature of sponge preservation in, for example, the Anji Biota; see Botting et al., 2020). Basalia appear to have been

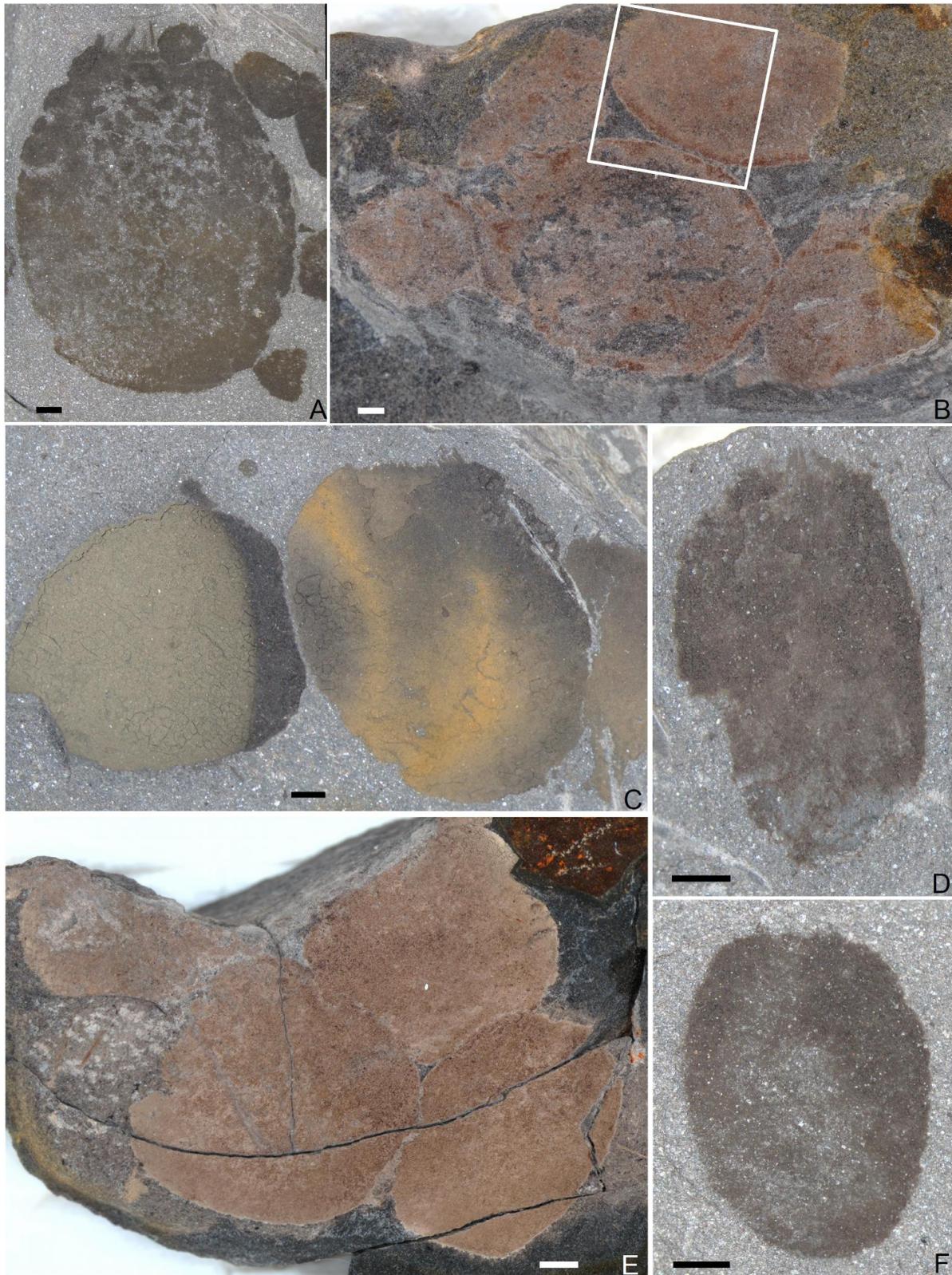


FIGURE 4. Paratypes of *Teganium avalonensis* sp. nov. A, NMW.2021.3G.77; B, NMW.2021.3G.98 in cross-polarised light (boxed area enlarged in Figure 3B); C, NMW.2021.3G.78 with pair of specimens, the right-hand one with marginalia; D, NMW.2021.3G.79; E, NMW.2021.3G.81 with multiple specimens, in cross-polarised light; F, NMW.2021.3G.80. Scale bars equal 1 mm.

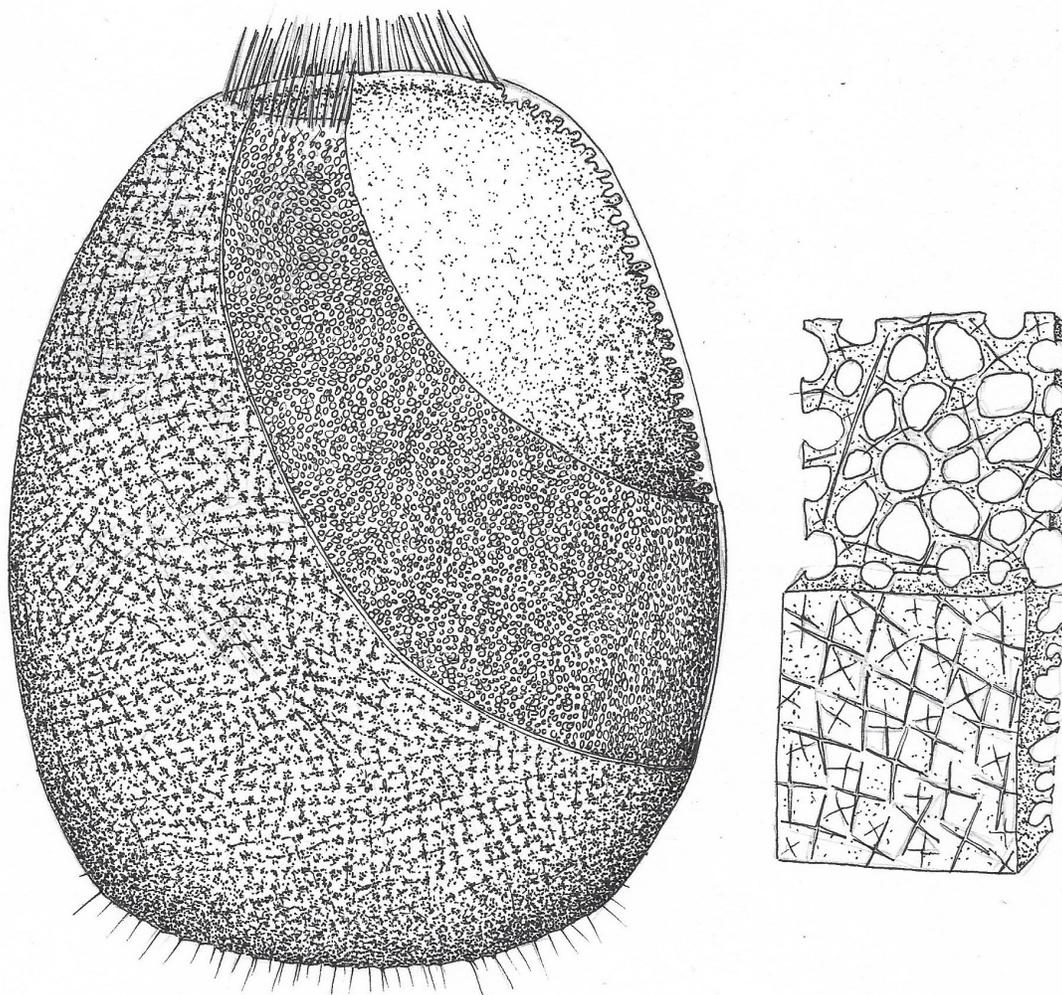


FIGURE 5. Cut-away reconstruction of *Teganium avalonensis* sp. nov., with detail of wall structure on the right; dermal/hypodermal skeleton in lower part, and choanosomal layer with exhalant canals in upper part.

numerous, extending into sediment from the entire basal part, equating approximately to the flattened region of the body.

Remarks. A reconstruction of the sponge is shown in Figure 5. The new species differs from all others that have been assigned to the genus in the pronounced marginalia, and in the rather more quadrate shape, but in other respects most closely resembles *Teganium ovata* (Rigby and Mehl, 1994)—including the existence of a similar array of basalia. *Teganium heathi* (Rigby, 1986) appears to show no marginalia (a possible taphonomic artefact) and also possessed coarser body wall spicules, and meridional tracts of spicules or spicule rays that are not present in other species. The species described as *T. finksi* (Mouro et al., 2019) lacks any visible osculum or marginalia and

includes much coarser spicules, in some cases up to 2 mm across.

The dense association of multiple specimens on several slabs is typical of the genus (Rigby and Mehl, 1994) and appears to be a consistent ecological feature. In many (but not all) examples, there is little variation in size in such assemblages at Castle Bank, implying that the sponges were approximately the same age; they may therefore represent a colonisation event, as discussed for other sponges found as similar dense assemblages by Botting (2016) and Botting et al. (2020).

Occurrence. Known only from the Middle Ordovician (*Didymograptus purchisoni* Biozone) of Castle Bank, Llandrindod, UK; Gilwern Volcanic Formation.

Teganium sp.
Figure 6

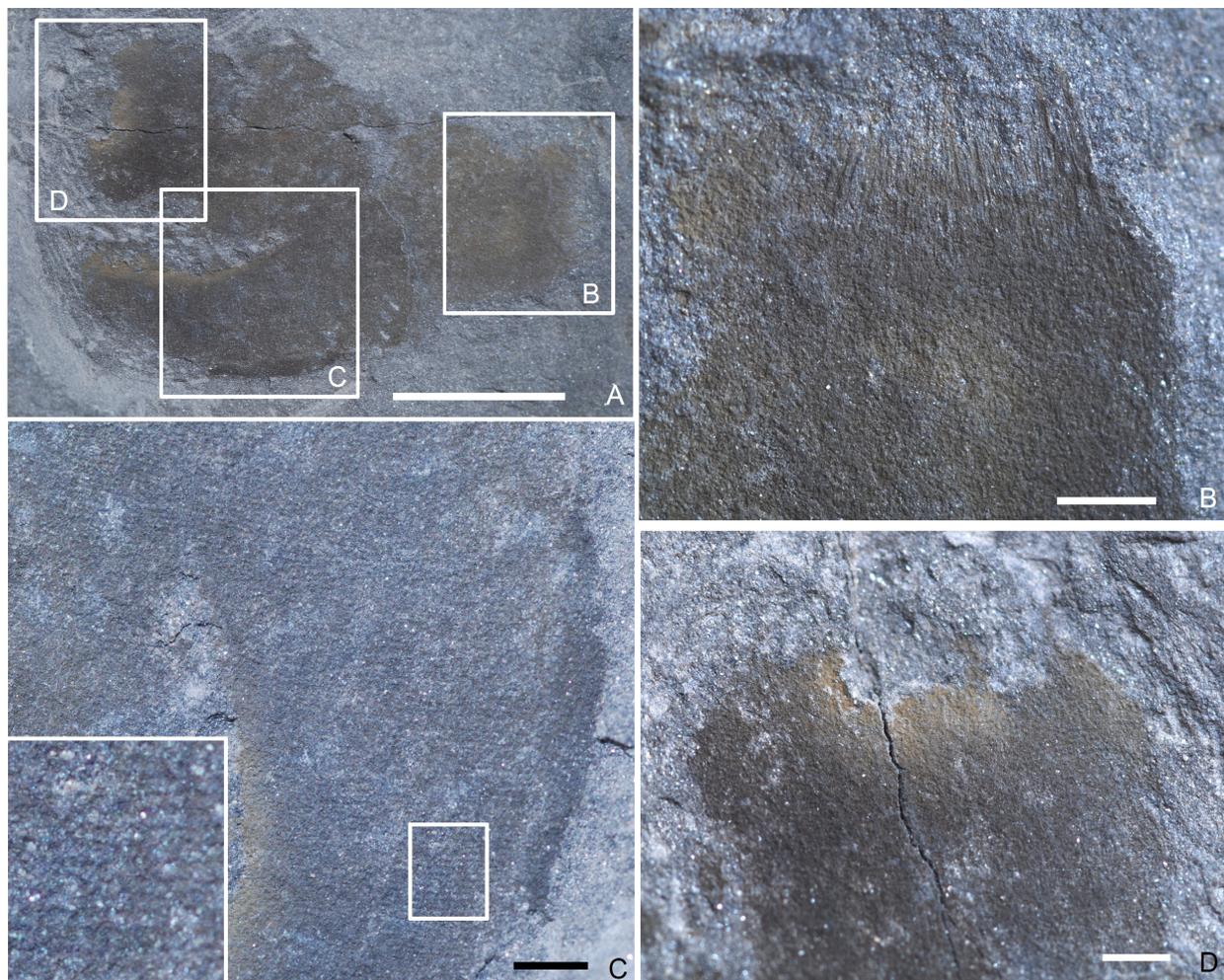


FIGURE 6. *Teganium* sp., from the Middle Ordovician Castle Bank Biota, Wales. A, NMW.2021.3G.76i and ii, overall view, with positions of detail images indicated by boxes (all rotated). B, apex of NMW.2021.3G.76i, apex of sponge showing extensive marginalia; C, detail of body wall showing characteristic texture (boxed area enlarged inset); D, apex of NMW.2021.3G.76ii, with oscular margin and trace of marginalia. Scale bars: A equals 10 mm; B–D equal 1 mm.

Material. NMW.2021.3G.76, two adjacent specimens, partially overlying.

Description. Two specimens, effectively unweathered, adjacent and pointing in opposite directions (Figure 6A); one slightly overlies the other. Information is based primarily on the first (Figure 6B–C), which shows a near-complete outline, especially at the apex; the other has damage to apex and edges, but confirms observations based on the first.

The better-preserved specimen is 24 mm tall, conical and slightly sinuous, with maximum width 7 mm, at or near apex, with upper half of approximately even width. Lower half tapers from 5 mm width at mid-height to rounded point. Second specimen also 7 mm wide at apex, total length approxi-

mately equal to first, but exact base invisible. Apex narrows in uppermost millimetre such that osculum occupies around 80% of full width of sponge, surrounded by dense array of marginalia, 2 mm long (0.02–0.07 mm thick), converging (and sometimes curving) somewhat inwards.

Wall thickness unclear and irregular, but indicated by dark line at edges (representing more massive preservation of soft tissues; Figure 6C), approximately 0.5–1.0 mm thick. Mineralised film over body wall shows irregular mottled patterning (Figure 6B–C) indicating relatively coarse internal cavernosity with cavities typically 0.5–1.0 mm across and separated by bands of more continuous tissue typically 0.5 mm wide. Finer cavities not visible, but may have been present originally.

Skeletal detail not preserved except for reticulation of dermal skeleton, seen in low-angle light and especially clear in mid-height area of better specimen (Figure 6C): a semi-regular grid, roughly longitudinal and transverse, with cell size approximately 0.1 mm or slightly less. Individual body wall spicules not preserved (invisible even when wet). No basalia visible.

Remarks. At present, these two specimens are distinguished from other members of the genus largely by the shape; although internal wall structure also appears to be coarser, it is poorly preserved. It shares the distinctive appearance of the finely reticulate surface with other species, and shares the convergent, dense fringe of marginalia with *T. avalonensis* sp. nov. The unweathered state of the material obscures many of the fine details of the skeleton, which cannot therefore be compared in detail with other species. The same is true for previously described species (Mouro et al., 2019), however, and the key characters are preserved well enough to allow an unambiguous assignment to the genus. The species is left in open nomenclature because the sample size is too small to reject the possibility of an extreme variation of shape within *T. avalonensis* sp. nov.

DISCUSSION

Phylogenetic Affinity

Morphologically simple hexactin-bearing sponges are difficult to classify in relation to the hexactinellid crown or total group, due to poor knowledge of the sequence of character acquisition in hexactinellid (and deeper silicean) evolution, and limited information in the preserved fossils. The morphological information preserved in the new species clarifies some aspects of the skeleton of *Teganium*, together with the complexity of the body wall and internal cavity and canal organisation. These features allow a comparison with similarly aged fossil taxa that have a better-constrained phylogenetic position, as well as potentially allowing direct comparisons with modern taxa.

Extant Hexactinellida are a highly derived group, which itself includes some even more derived characteristics. In several lineages, fused choanosomal skeletons appear to have evolved independently (Dohrmann et al., 2017), and these lineages have in many cases reduced other features of their construction. Allowing for such secondary reduction, comparison of the extant unfused or partly-fused taxa in the Lyssacinosa and the Amphidiscophora show that a complex

skeletal wall is shared across the class (Dohrmann et al., 2017). In particular, there are multiple skeletal layers (Leys et al., 2007) that were probably present in the last common ancestor (LCA) of extant hexactinellids: dermalia (on the outer surface), hypodermalia (within the surface 'skin' layer), choanosomalia and usually gastral/atrialia (marking the inner margin of the body wall). These layers normally show clearly distinct spicule morphologies and distinct arrangements of those spicules (e.g., Leys et al., 2007). The choanosomal layer shows the most complex architecture, as it houses the choanocyte chambers (that are too small to fossilize commonly), which lead into exhalant canals that feed into the internal cavity of the sponge, prior to water being expelled through the osculum. These canals are reasonably large (e.g., Reiswig and Mehl, 1991) and easily fossilizable as gaps in the skeleton or soft tissues. Such canals and chambers also seem to be a universal feature of modern hexactinellids (except where secondarily lost), and were probably present in their LCA.

In contrast, many of the hexactin-bearing reticulosan sponges described from the Palaeozoic fossil record show a much simpler construction, and there are multiple lines of evidence indicating that hexactins pre-date the Hexactinellida and are likely plesiomorphic, being present even in the LCA of Porifera (Botting and Muir, 2018). The simplest reticulosans, such as *Diagoniella* and allies, show only a single layer of spicules, which may possibly be homologous with the hypodermalia of hexactinellids (although this is yet to be properly assessed). In any case, multiple skeletal layers are not developed, and neither is obvious cavernosity or canals within the body wall; it is likely that at least some of these sponges were asconoid in construction (Rigby, 1978), with the choanosomal surface covering the interior of the body wall, rather than being in specialised chambers. These sponges, without any complex architecture to the body wall, are almost certainly deeply nested within Porifera, prior to the crown group of Silicea (Botting and Muir, 2018). One early, hexactin-bearing sponge with calcite spicules that does not fall into modern crown-group classes indicates that choanocyte chambers developed reasonably early in sponge evolution, at least in one lineage (Nadhira et al., 2019).

The separation of hexactinellids from demosponges (together forming Silicea) appears to be most closely seen in more derived reticulosans such as *Cyathophycus* (Botting and Muir, 2013, 2018). An inner skeletal layer of smaller spicules in

a separate arrangement had also developed, including visible internal cavities or canals within the thin body wall, showing that the basic structure of a differentiated wall had evolved by this point. Primitive characteristics were still present, however, in the thin wall, the regular and simple morphology of the spicules forming the primary skeletal layer, and their simple organisation into a square grid aligned to the body axes and with semi-regular quadruling. Furthermore, the spicule construction was shown to be anomalous (Botting and Muir, 2013), with thick organic layers within the silica; this is a primitive trait that was also found in Cambrian hexactins by Tang et al. (2019).

Based on these key points, the development of a full suite of skeletal layers, including increased modification of spicules and loss of simple regularity in the primary grid, combined with thickening of the body wall (in many taxa) and increased complexity of the internal canal architecture, must all have developed within the stem group of Hexactinellida. These features are recognisable in well-preserved fossils. The evolution of the two main groups of microscleres (amphidiscs and hexasters) must also have occurred either within the stem group, or independently within the two subclasses of the crown group, but these spicules are rarely preserved as fossils.

In *Teganium*, the presence of a dermal or hypodermal skeleton that overlies small internal cavities surrounded by a very fine hexactin-based choanosomal skeleton is a relatively derived feature, although superficially similar to *Cyathophycus* (Botting and Muir, 2013). *Teganium* differs from *Cyathophycus*, however, in the irregularity of the primary skeleton, which is not tied to the sponge axis, and does not show quadruling; this is much more similar to the dermal surface structure seen in many extant hexactinellids (e.g., *Chonelasma*; Shen et al., 2022). Among known Palaeozoic fossils, *Teganium* is in some ways similar to the Hirnantian stem-group rossellids *Matteolaspongia* Botting, Zhang and Muir, 2018 and *Shouzhispongia* Botting, Janussen, Zhang and Muir, 2020; the latter also possessed similarly minute spicules. Unlike those rossellids, there are no pentactine prosthelia in *Teganium*, but the presence of marginalia is similar, and numerous long basalialia are also common among the Rossellidae and related families (Tabachnick, 2002). There are still uncertainties and limitations on our understanding of *Teganium*'s morphology, however, due to the minute size of the spicules. At this stage, a relatively derived position within the stem group or crown

group of Hexactinellida is the most plausible interpretation, but the similarities to early rossellids may be convergent, and result from the limitations imposed by possession of such small spicules. Recognition of a relatively derived position for *Teganium* within hexactinellid evolution is useful, but a more detailed assignment will depend on better understanding of character evolution around the base of the hexactinellid crown group. It should also be noted that *Teganiella* was assigned by Mehl (1996) to her 'Rossellimorpha': a loosely-defined grouping of relatively complex, loose-spiculed sponges that may include taxa related to the Rossellidae, or may be dominated by earlier-branching forms, generating a similar ambiguity to our assessment here.

Palaeobiogeography

The fossil record of sponges with loose spicules is known to be extremely incomplete (Pisera, 2004, 2006; Muir et al., 2013), and much of the known record is based on a small number of faunas with some degree of exceptional preservation. Where multiple Ordovician faunas are known in a small area such as the Builth Inlier, there tends to be little taxonomic overlap, implying a very high total diversity, but localised occurrence of each taxon (Muir and Botting, 2015). This ecological disparity is a feature of Ordovician faunas, but not Cambrian assemblages (Botting and Muir, 2019), and cannot be due to the lack of Burgess Shale-type faunas; many sponge faunas are known from Ordovician rocks, with or without soft tissue preservation. Genera and species that occur in multiple Ordovician sites and regions can therefore be assumed to have been very common and widespread, even though the full extent of their geographical and stratigraphic ranges cannot be assessed with confidence. As these species are the most likely to be informative for palaeobiogeographic patterns, significant range extensions are of great interest, especially if they are accompanied by unexpected discrepancies in palaeoenvironment. This is the case here, with a range extension to a second palaeocontinent, an older age, and confirmation of the deeper-water environment indicated by the type species.

Previous records of taxa assigned to *Teganiella* have been limited to relatively shallow environments from the Devonian and Carboniferous of Laurentia, across several modern US states (Figure 7). *Teganium heathi* is from the Bashkirian (Carboniferous) of Montana (Rigby, 1986); the other Carboniferous occurrence is from the upper

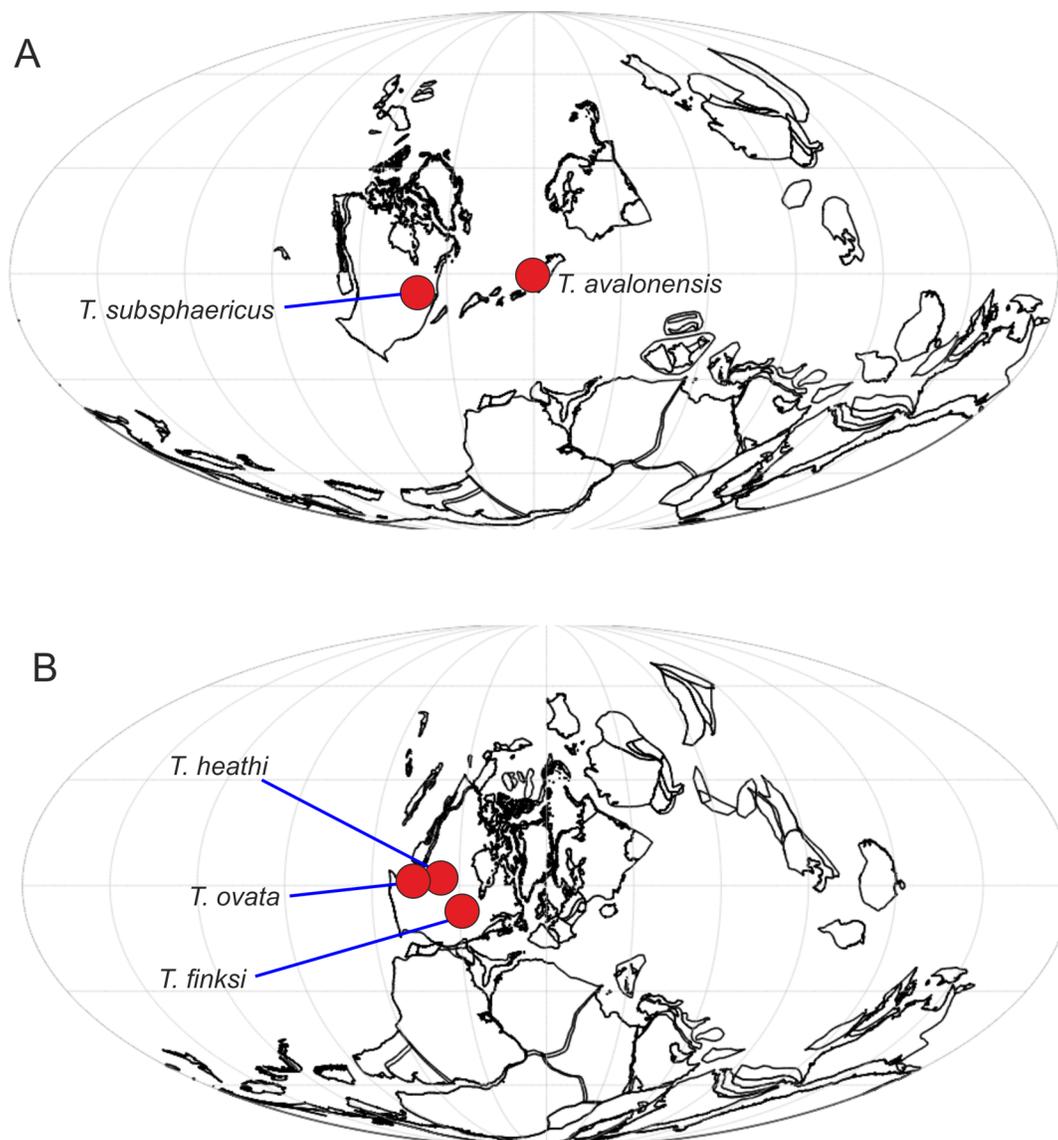


FIGURE 7. Palaeogeographic distributions of species of *Teganium* (all species in B originally assigned to *Teganiella*). A, Ordovician (Sandbian, 458 Ma). B, Carboniferous (Visean, 340 Ma). Map constructed using GPlates (Müller et al. 2018) using data from Torsvik & Cocks (2016). Does not include unconfirmed taxa listed by Ruedemann (1925b, 1934, 1942).

Moscovian of Indiana (Mouro et al., 2019). There has been one report of the genus (*T. ovata*) from the Middle Devonian of Nevada (Rigby and Mehl, 1994). Earlier members of the genus have been assigned to *Teganium*, originally described from the Upper Ordovician Utica Shale of New York State (Walcott, 1879). Other species of *Teganium* were named by Ruedemann (*T. macrosclera* Ruedemann, 1925b; *T. rauffi* Ruedemann, 1925b; *T. minutum* Ruedemann, 1934; and *T. merino* Ruedemann, 1942) from the Utica Shale and other Ordovician units in New York State. Ruedemann also named a Silurian species of *Teganium*, *T.*

claviforme Ruedemann, 1934, from Silurian strata of Klakes Bay, Alaska. Unfortunately, it is not possible to confirm the assignment of any of the material of Ruedemann (1925b, 1934, 1942) to *Teganium* on the basis of his illustrations or descriptions, and so all of these records must be regarded as doubtful pending restudy of the type specimens of each species. To summarise, the only certain record of a species previously assigned to *Teganium* is the type species from the Utica Shale of New York State; most of the other records (which are doubtful) are also from Ordovician strata of the same state. This distribution, including the new species

in offshore sediments of Avalonia, suggests an origin of the genus and family in deeper waters (either mid to deep shelf, or below), perhaps within the Iapetus Ocean region, before the lineage became specialised for inhabiting sheltered, shallow-water facies in Laurentia. The morphology is not particularly useful in interpreting such habitat preferences, but the small size, subspherical shape and very small spicules form a distinctive combination. The small size of spicules may be an adaptation to the limitation of dissolved silica in shallow environments, which is known to impact spicule form in modern taxa (Maldonado, 1999; Shetye et al., 2014), but no clear inferences can be made.

Given the number of occurrences of the *Teganium* complex in Laurentia (and now Avalonia), it is surprising that no records are known from other palaeocontinents, at least of the earlier, offshore representatives. The only similarly widely distributed genus of Ordovician and later reticulosan is *Cyathophycus*, which is known widely from the Iapetus region, across a range of palaeolatitudes (Muir et al., 2013). However, these records are often taxonomically uncertain outside of the Laurentia–Avalonia area (Muir et al., 2013), enhancing the similarity to the distribution of *Teganium*.

CONCLUSIONS

A new species of *Teganium* (which is here synonymized with *Teganiella*) from the Castle Bank Biota is the oldest known, the second from offshore environments, and the first from outside Laurentia; a second, unnamed species demonstrates diversi-

fication at this time. This discovery suggests that this successful later-Palaeozoic group of sponges originated in deeper-water environments, probably within the Iapetus region, before becoming specialised for sheltered inshore environments in Laurentia. New information on the detailed morphology of *Teganium* from Castle Bank (including fine-scale cavernosity and at least two skeletal layers) supports a hexactinellid affinity for the group, either in the later part of the stem group or possibly within the total-group of Lyssacosida. However, in the absence of clear links to known hexactinellid taxa, no further detail of the specific classification is possible at this stage.

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