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An analysis of vegetational change in the Lower Devonian: new data from the Lochkovian of the Welsh Borderland, U.K.

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Abstract

A recently excavated field near the hamlet of Craswall in Herefordshire, south of Hay-on-Wye, has yielded abundant fossil plants. They are preserved in sandstone and siltstone beds as coalified compressions, for the most part lacking anatomical detail, and as iron-stained impressions. Also present are fish including *Rhinopteraspis crouchi,* which places the exposure in the middle to upper Lochkovian (Lower Devonian), plus prototaxalian nematophytes and *Pachytheca*. The commonest plants, which cover bedding planes, are randomly arranged sterile axes that rarely branch. They are interspersed with *Salopella*, fragmentary strobili of the *Zosterophyllum* cf. *fertile* complex and a number of taxa with more isodiametric sporangia borne terminally on isotomous or anisotomous branching systems. New circumscribed taxa include: *Monnowella bennettii,* a rhyniophytoid, with single sporangia terminating unbranched laterals on a weakly anisotomously branching system; and *Craswallia haegensis*, a possible zosterophyll, comprising

bivalved elliptical sporangia, borne distally on stout unbranched stalks.

Newly found fossils from a second, slightly younger locality at Newton Dingle, Shropshire, include *Zosterophyllum* sp. Together with specimens previously described from the same site, comparisons of *Zosterophyllum* from the two localities are made.

In common with other assemblages in the Anglo-Welsh Basin, the plants described here show more derived architecture and fertile characteristics than are present in older Přídolí (Silurian) representatives. An increase in size and complexity of branching, with concomitant changes in light harvesting, reproductive capacity and spore dispersal efficiency, is noted in taxa from increasingly younger Lochkovian to Pragian strata. These changes are interpreted as responses to increased competition for light and space in early terrestrial ecosystems, which resulted in the local extinction of the rhyniophytes and diversification of the zosterophylls.

1. Introduction

The almost continuous succession of continental rocks from uppermost Silurian through the Lower Devonian in the comparatively small palaeogeographic area that is the Anglo-Welsh Basin, allows reconstruction of terrestrial vegetation and monitoring of any changes as plants diversified and proliferated on land (Edwards

and Richardson, 2004). Nevertheless, detailed analyses remain frustrated by the low numbers of fossiliferous occurrences both stratigraphically and geographically. Particularly significant in this region are assemblages from the Lochkovian, a time interval of about eight million years in the basal Devonian. These assemblages record changes in diversity and disparity involving both tracheophytes (e.g. Lang,1937; Edwards and Richardson, 1974; Fanning et al.,1992; Edwards et al., 1994; Wellman et al., 2000; Habgood et al., 2002; Morris et al., 2011a) and cryptophytes (e.g. Morris et al., 2011b; Edwards et al., 2014) as well as the reconciliation of numerous taxa in the dispersed spore record (Richardson and Lister, 1969; Richardson, 1996) with their producers (e.g. Fanning et al., 1988; Edwards et al., 1989, 1999, 2012a, 2012b; Wellman et al.,1998a; Habgood et al., 2002; Morris et al., 2011b, 2012a, 2012b). Here we report on a further new assemblage at Craswall, Herefordshire, comprising very abundant plant megafossils associated with the heterostracan, *Rhinopteraspis crouchi*, an indicator fossil for the middle to upper Lochkovian. We also describe some recently collected and better preserved material from a younger upper Lochkovian locality on Brown Clee Hill, Shropshire (Ball and Dineley, 1961; Edwards and Richardson, 1974).

2. Locality, geology and material

2.1. *Craswall, Herefordshire*

  The fossils were collected from near the base of a shallow excavation in a field near Craswall, Herefordshire (SO325304: CR, Fig. 1a, b). It is located near the

floor of the Monnow River valley, c. 9.5km south-east of Hay-on-Wye, on the eastern side of Black Hill in the Black Mountains. The plant fossils, together with some fish, occur in strata overlying a conglomeratic fish bed at the base of the exposure. The fish include heterostracans *Rhinopteraspis crouchi* and *Weigeltaspis* sp., osteostracan *Cephalaspis* sp., together with fragmentary acanthodians. The locality was originally discovered, and its importance recognised, by Mr Philip Bennett, a local collector. Its exact stratigraphic position is unknown, but geological mapping by the BGS in the Talgarth area (Sheet 214) indicates that it is part of the St Maughans Formation (Barclay and Wilby, 2003) (Fig. 2), now named the Freshwater West Formation of the Milford Haven Subgroup (Barclay et al. in press). The base of the Senni Formation, marked by one of the 'Ffynnon Limestones' calcrete horizons occurs approximately 250m above on Black Hill.

The presence of *Rhinopteraspis crouchi* indicates that the strata are Lochkovian, in the middle to upper *micrornatus-newportensis* Spore Assemblage Biozone (Richardson and McGregor, 1986), although more precise dating is impossible. Lenses of grey siltstones were collected for palynological investigations, but, after standard bulk HCl-HF maceration, spores were not recovered. Some plant megafossils were also preserved in this matrix, but the majority occur in fine-grained, very micaceous and arenaceous, green to grey or buff-coloured sandstones (c. 125 rock slabs). Some slabs were collected from the basal conglomeratic sandstone beds, which contain gravel-sized clasts composed of mudstone and fish bone (Plate I, 1). Plants are preserved as

coalified compressions, very occasionally as charcoalifications (mostly the nematophytes) and iron stained impressions, the latter dominating on weathered surfaces. They are stratinomically partitioned, mostly occurring along planar or shallow trough cross-laminations (Plate I, 2), but sometimes crosscut laminae. Higher plant axes intermingle with rarer fragments of nematophytes of varying dimensions and further indeterminate thalloid fossils (Plate I, 3). Siltstones contain smaller fragments, a few mesofossils and comminuted debris. A few of the axes show parallel alignment (Plate I, 4), but the majority are a disordered assortment of axes and coalified patches (Plate I, 5) that characterise allochthonous assemblages. The sequences are typical of Lower Old Red Sandstone perennial channel sequences that are well studied from outcrops across the Anglo-Welsh Basin (e.g. Allen, 1964; Allen and Dineley, 1976; Hillier et al., 2007; Morris et al., 2012c).

2.2. *Newton Dingle, Shropshire*

The plant fossils were collected from a stream section known as 'The Gore', in Newton Dingle, 13 kilometres north-east of Ludlow, Shropshire, UK (ND, Fig. 1a), by Emilia Jarochowska. The strata are part of the upper Freshwater West Formation of the Brown Clee Hill area (Ball and Dineley, 1961). A conglomeratic cornstone exposed in the section (locality 74, text fig 1, Edwards and Richardson, 1974) contains fragmentary remains of *Althaspis leachi*? and *Europrotaspis* (Ball and Dineley 1961), which is typical of the *A. leachi* zone of White (1961), and can be correlated with the *breconensis-zavallatus* Spore Assemblage Biozone

(Richardson and McGregor, 1986) of late Lochkovian (Early Devonian) age. Edwards and Richardson (1974) described a plant assemblage from strata just above locality 74 of Ball and Dineley (1961), but the stratigraphic position of the new finds in relation to this is unknown.

Disordered coalified compressions, often with orange iron oxide haloes, occur on, or slightly oblique to, bedding planes in buff-coloured, quartz-rich, very fine-grained sandstones and siltstones. The slightly coarser horizons are also micaceous, with occasional relatively larger, fossil plant fragments (e.g. Plate X, 1) in contrast to the bedding planes of the siltstones that are packed with minutely comminuted plant debris, associated with malachite (e.g. Plate X, 2).

3. Methodology

Following photography of all material, some specimens were developed by removal of quartz grains using tungsten or steel needles. Coalified material was picked off selected specimens, mounted on stubs and coated with gold/palladium followed by scanning electron microscopy (SEM) (FE1 (Philips) XL30 ESEM FEG). Specimens showing some evidence of structure were removed from stubs, treated with Schultze's solution for several hours until amber coloured, washed and mounted in water for light microscopy.

The majority of specimens are housed in the Natural History Museum, London, denoted by the prefix V. Specimens with the prefix CR (Table 1) are housed at the School of Earth and Ocean Sciences, Cardiff University.

4. Megafossil description

4.1. *Craswall*

4.1.1. *Sterile axial fossils* (Plate I)

Descriptions: These are the most abundant fossils in the assemblage, sometimes almost entirely covering a bedding plane (Plate I, 5). Branching is relatively rare and most frequent in narrower axes. The longest fragments are the widest and most conspicuous ones (Plate I, 5, 6). Detailed analyses of widths on selected slabs (Table 1) indicate very little variation in means (x = c. 0.7 mm) on an individual slab, although a few may be dominated by narrower forms (x = 0.5 mm).

The majority of the wider axes are usually straight and parallel-sided (Plate I, 5) or slightly flexuous (<13.5 mm long: Plate I, 6), with rare isotomous branching (Plate I, 7). One specimen is unusual and unique in possessing two closely spaced anisotomies (Plate I, 8). A central, longitudinally aligned line is sometimes present (arrowed in Plate I, 9). Narrower axes of more variable width are more branched, although rarely exceed 2 cm in length. They may show an increase in diameter below a branch point. Branching is variable, sometimes being isotomous (Plate I, 10, 11) with equal lengths of daughter axes above, anisotomous with the wider often overtopping the narrower (Plate I, 12) or combinations of such architecture (Plate I, 13). They never show the development of the pseudomonopodial branching noted in local Pragian and younger tracheophytes. Plate I, 14 shows a unique specimen, where at least eight parallel-aligned axes occur on one side of a single axis. There are three

examples of narrow, crowded, irregularly branching systems (Plate 1, 15, 16, 17). Uncovering of tips is frustrating because the quartz grains are so large that removal of an individual grain distorts the outline of the fossil. However, there are globose expansions of certain axes (arrowed in Plate I, 15) that may be sporangia, although there is no increased thickness of carbon in these regions, as typifies unequivocal sporangia.

Finally Plate 1, 18 shows an axis with H-branching usually thought typical of the basal regions of the genus *Zosterophyllum*, while the small, heavily coalified fragment illustrated in Plate I, 19 shows more condensed branching.

Suggested affinities: The parallel-sided predominantly unbranched axes are attributed to *Salopella* (Edwards and Richardson, 1974). The narrower, more frequently branched axes could have been part of any of the plants of smaller stature with terminal sporangia as described below. Rarer, more irregularly branching examples, with probable terminal sporangia, have dimensions closer to mesofossils (Edwards et al., 2014). Compressions recently described from a lower Lochkovian locality north of the Brecon Beacons (Morris et al., 2011a) fall into this group, and of those illustrated, the specimens described here come under morphotype D, although the terminal expansions are at the higher end of the Welsh sporangial dimensions. Morphotype D included specimens with occasionally curved axes, irregular branching and globose to variably shaped sporangia, although spores have not been isolated. The specimen with H-configuration of axes may derive from the basal regions of a zosterophyll (Walton, 1964) e.g. *Zosterophyllum myretonianum*, although axial widths are smaller than

those in the *Zosterophyllum* strobili in the assemblage.

4.1.2. Fertile specimens

These fall into three broad categories.

1) Smooth axes with terminal short and wide sporangia, some *Cooksonia*, others cooksonioid, others with marginal features.

2) Smooth axes with terminal sporangia that are longer than wide. Subdivisions relate to sporangial dimensions and frequency of branching.

3) Laterally borne sporangia arranged either in strobili or distributed within distal regions.

4.1.2.1. Category 1 – terminal short and wide sporangia

a) Indeterminate cooksonioid: new morphotype (Plate II, 1-3).

Description: The fertile specimen, associated with sterile, usually unbranched axes, a fragmentary nematophyte axis and a possible fish fragment, occurs in a small block of buff-coloured sandstone, much finer grained and less micaceous than the remaining fossiliferous matrix (Plate II, 1). The two fertile stems are unconnected, but their proximity and alignment in an allochthonous deposit strongly suggest that they were part of the same plant. Preserved as impressions, the plants are distinguished from the matrix by their slightly darker colour and presence of a sporadic sprinkling of coalified material which is more consolidated at the sporangial margins (Plate II, 1). Each sporangium terminates an unbranched stem, which widens into the base of the sporangium gradually and

imperceptibly such that sporangial height cannot be measured accurately.
Sporangial outline differs between the two (Fig. 3, type 1a). The right hand one is
fan-shaped (Plate II, 2), the other, which was partially uncovered, elliptical (Plate
II, 3). Such differences in shape are influenced by the relative dimensions of the
subtending stems near the sporangial junctions; dimensions are given in Table 2.
The sporangia are featureless except for a very narrow border comprising a
sporadic coalified strip extending around the free perimeter (Plate II, 2, 3). The
subtending stem on the larger specimen when uncovered appears continuous
with a dichotomously branching one (Plate II, 1, arrow a), but these axes could be
superimposed. Similarly equivocally, a gap extends between the other fertile stem
and a bifurcating one some distance from its base (Plate II, 1, arrow b), although
alignment suggests original continuity.

 Suggested affinities: Specimens broadly conform to the original diagnosis of
Cooksonia by Lang (1937), in that sporangia are short and wide and, although
remaining equivocal, it seems likely that branching was isotomous. It differs in the
presence of the very narrow marginal band, which could be a preservational
feature or a region modified for dehiscence into two valves as, for example, in
Aberlemnia (*Cooksonia*) *caledonica* (Edwards, 1970; Gonez and Gerrienne,
2010). However, compared with sporangial dimensions and borders of the
Scottish material and other fossils originally placed in *C. caledonica* (Edwards,
1970), or specimens that were considered close to that taxon (Edwards, 1979;
Fanning et al., 1992; Morris et al., 2011a), these new sporangia are larger with
relatively narrower marginal bands. Additionally, the positions of sporangial-axial

junctions are not clear in the Craswall specimens and so, combined with the above uncertainties we are reluctant to identify them in terms of existing taxa, and as a new taxon, it lacks sufficient characters for meaningful circumscription at this time.

b) *Monnowella bennettii* **gen**. et **sp. nov**. (Plate II, 4-15).

Description: Apart from *Salopella*, common fertile specimens in the assemblage are small, somewhat elliptical sporangia that terminate 'laterals' produced by overtopping in smooth anisotomously branching stem systems or, more rarely, isotomously branching stems (type 1b, Fig. 3). Most sporangia are attached to stems, although many of these are short (Plate II, 6-8). A few lack a stem (Plate II, 4-5). Stem width ranges between 0.3 and 1.5 mm, with the majority close to the mean (0.6 mm). Stems widen slightly below the sporangia, the junction normally well-defined and straight to slightly curved (e.g. Plate II, 6, 9). Sporangia are only slightly wider than high. The largest one is 2.7 x 2.3 mm, and the smallest 1.5 x 1.1 mm. Isolated sporangia are distinguished by the shallow concave indentation marking the junction (Plate II, 4-5), but are not lobed as in the zosterophylloid forms. A few specimens possess a linear peripheral zone of persistent coalified material (e.g. Plate II, 6, 8), but no well-defined border of any thickness. Although a considerable thickness of coal remains on some sporangia, it yielded neither cellular structure nor spores on SEM examination. A siliceous film is occasionally present. There is no evidence for two valves. However, the proximity of sporangia, where branching is close to the apex, suggests that the sporangia

were not perfectly globular, but ellipsoidal in life.

Branching examples show a variety of architecture, as illustrated in Fig. 3 (type 1b). This may be summarised as being:

a)   strictly isotomous with no overtopping (very rare). In this case, sporangia are borne at the same level;

b)   isotomous, but with overtopping (rare) (e.g. Plate II, 10);

c)   anisotomous with daughter branches of slightly unequal width, but no overtopping (very rare);

d)   anisotomous with small difference in diameter between 'main' and 'lateral' (commonest) stems, although the main stem is never straight and parallel-sided (cf. pseudomonopodial) and the laterals do not branch more than once (e.g. Plate II, 11-14).

'Lateral' systems in these fragments vary in degree of further branching. Some terminate in a single sporangium and, although apparently unbranched, there may be a trace of a further branch point close to the sporangium (e.g. arrowed in Plate II, 14), and thus provide an explanation for the number of sporangia terminating short lengths of stems found in the matrix. Indeed there are some examples of two or three sporangia, each borne by a short stem, alongside each other in the matrix, suggesting that they were once all attached to the same branching systems (Plate II, 15). Other specimens show vertical alignment of sporangia with stems (arrowed in Plate II, 13). However, no lateral system branches more than once. Some laterals may be adaxially curved so that the sporangia are almost held upright (Plate II, 13). The longest fragment (18.5 mm

long), designated the holotype, has three laterals that alternate position, with two on one side bearing single sporangia. The more distal of the laterals also has evidence of a further branch below the fertile one (Plate II, 13, 14). The rare examples of sporangia of identical shape, that lack a border and terminate short lengths of isotomously or slightly anisotomously branching stems, are interpreted as the distal branching system of the plant.

 Suggested affinities: As evidenced by the most complete fragment (Fig. 3, type 1b, 28), the plant was probably small, with sporangia on terminal isotomous branches and singly branched laterals. Such a branching pattern is not seen in *Cooksonia* and its allies, but is broadly similar (although simpler) to that in *Renalia hueberi* from the Emsian Gaspé (Gensel, 1976). The younger taxon has a three dimensional pseudomonopodial architecture and bivalved sporangia with prominent borders, terminating multiple, helically borne, isotomously branching lateral systems, a type of organisation informally described as renalioid by Hao and Xue (2013a). A far simpler plant was described in the lower Lochkovian assemblage in Targrove (Fanning et al., 1992; fig. 16). It possessed a single sporangium with a border, which was attached terminally on an isotomously branching lateral system. Fanning et al. assigned this to *Renalia* sp., as they considered they lacked sufficient information for circumscription of a new species. At the same locality Fanning et al. collected 68 examples of mostly terminal reniform sporangia, two thirds of which possessed a border. Branching was rare, but isotomous. They were uncertain as to whether these specimens should be assigned to *Renalia* or *Cooksonia caledonica* (sic). Sporangia lacking a border

and at the lower end of their size range might well belong to the taxon described here. Further similar specimens were discovered at another lower Lochkovian locality near Brecon (Tredomen Quarry; TM, Fig. 1, 2), and described as cf. *Aberlemnia caledonica* (Morris et al., 2011a, plate V, 4, 5 plate VI, 3, 4). Despite being a similar outline/shape, the Tredomen sporangia do not possess clearly defined borders (Morris et al., 2011b; plate VII, 4, 5). They are thus similar to the new genus at Craswall. Indeed the Tredomen assemblage includes one specimen comprising a stem with distal isotomous branching and a single sporangium, plus a more proximal lateral fertile branch (Morris et al., 2011a, plate VI, 4). It is thus comparable with the overall architecture of the new taxon.

Single sporangia terminal on long unbranched 'stalks' are seen in Pragian/Emsian *Danziella artesiana* from France (Edwards, 2006), but are distinct from *Monnowella* because the sporangia are bivalved. By contrast, Basinger et al. (1996) illustrated a Ludlow plant from Bathurst Island described in the legend as a 'cooksonioid-type plant with large globose sporangia terminating short [unbranched] branches' (figure 3A, page 55), but with no additional description in the text. In conclusion, the Craswall specimens merit a new genus on a combination of sporangial morphology and novel vegetative architecture.

Systematic palaeobotany

Plantae *incertae sedis*

Monnowella Morris and Edwards **gen. nov.**

Etymology: From the River Monnow which flows through the valley in which

Craswall is situated.

Diagnosis: Plant with smooth stems; branching isotomous and anisotomous. Single terminal sporangia occur on weakly defined, anisotomously derived, lateral systems which may be unbranched or isotomously branched once. Sporangia are slightly wider than high; junction with stem either flat or slightly concave.

Type species: **Monnowella bennettii** Morris and Edwards **sp. nov.**

Etymology: In recognition of the palaeontological contributions of Philip Bennett.

Diagnosis: As for genus. Plant at least 20 mm high; stem width 0.3 - 1.5 mm (x = 0.6 mm); largest sporangium 2.7 mm wide by 2.3 mm high; smallest sporangium 1.5 by 1.1 mm.

Holotype: V.68562.

Illustrations: Plate II, 13, 14.

Locality: Craswall, south of Hay-on-Wye, Herefordshire, England (Grid Reference SO325304).

Horizon: Freshwater West Formation, Lochkovian, Lower Devonian.

Rhinopteraspis crouchi fish biozone.

c) *Cooksonia hemisphaerica* (Plate III, 1-3)

Descriptions: Three specimens fall into this category (Fig. 3, type 1c). The most complete comprises an almost circular, heavily coalified area that is subtended by a tapering unbranched smooth stem (Plate III, 1). A similarly shaped area is also clearly distinguished from a much shorter stem in Plate III, 2. The remaining

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specimen is represented by a considerable thickness of coal, with no clear delimitation between presumed sporogeneous tissue and the stem (Plate III, 3). Sporangia lack borders. Spores have not been isolated.

Suggested affinities: *Cooksonia hemisphaerica* was described by Lang (1937) as possessing hemispherical sporangia almost as high as wide, with a flat base and junction almost three times wider than the subtending, sometimes bifurcating, stem. The type locality is lower Lochkovian strata at Targrove (TR, Figs. 1, 2), from which Fanning et al. (1992) described a further approximately 80 specimens. Those included here fall into the range in shape encompassed in their figure 1, although we cannot add any anatomical details.

d) Other *Cooksonia* and cooksonioid specimens

There are a number of specimens with short and wide sporangia lacking borders, sometimes terminating isotomously branching axes, which fall into the broad generic definition of *Cooksonia sensu* Lang (1937).

Cooksonia cf. *pertoni* (Plate III, 4-7)

The first of three putative sporangia is elliptical (3.1 by 2.4 mm; subtending stem, 1.4-2.2 mm at sporangial/stem junction) (Plate III, 4, 5; Fig. 3, type 1d, 1). Its orientation relative to the probable branching system is similar to that in *Cooksonia pertoni* as illustrated by Edwards (1979, fig. 13 far right), where the sporangium is tilted and compressed, but unqualified assignation to such a well-described species is impossible. Similar uncertainty holds for a further tilted but

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less well-preserved sporangium (Plate III, 6; Fig. 3, type 1d, 2) and an almost featureless branching specimen characterised by a less regular sporangial area (Plate III, 7).

Cooksonia cf. *cambrensis* (Plate III, 8-12)

Description: A number of sporangia are circular or elliptical in outline and terminate parallel-sided axes (Plate III, 8 - 12; Fig. 3, type 1d, 3-7). They also vary in size (e.g. width x height; 1.5 x 1.3 mm, 2.0 x 1.5 mm). In examples with branching, it is usually isotomous with no overtopping (Plate III, 10). One specimen shows indications of a longitudinally running strand (Plate III, 10, 11).

Suggested affinities: Spherical to elliptical sporangia, terminating axes which do not widen beneath the junction, characterise the Přídolí taxa *Cooksonia cambrensis* forma □ and□, found initially at Freshwater East, Pembrokeshire (Edwards, 1979). They were also recorded from Lochkovian strata at Targrove (Fanning et al., 1992) and Tredomen (Morris et al., 2011a). As is often the case with specimens that lack anatomy and possess a simple morphology, unequivocal assignation to the older Welsh taxa is unwise, hence the term "cf." is employed.

Cooksonioid mesofossils (Plate III, 13-14)

Description: In this group sporangia are very small (less than 1 mm wide), circular to elliptical in outline and very heavily coalified (Fig. 3, type 1d, 8 and 9). Plate III, 13 shows two sporangia, one vertically extended (0.88 x 0.71 mm), and

the other almost globular (0.48 x 0.57 mm), that lie adjacent and parallel to each other, because the stem, 0.4 mm below branching, dichotomises immediately beneath the fertile region. A similar organisation occurs in the specimen illustrated in Plate III, 14, but here one sporangium is globular (4.5 x 4.5 mm) and the other elliptical and tangentially extended (0.40 x 0.46 mm).

Suggested affinities: Such limited information frustrates identification, but in gross morphology the specimens resemble coalified mesofossils assigned to morphotype A by Morris et al. (2011a) in an assemblage from a lower Lochkovian quarry near Brecon (Tredomen, see Figs 1 and 2).

Indeterminate ?cooksonioids (Plate III, 15-17)

Descriptions: A small number of specimens consist of narrow, irregularly branching smooth axes, terminating in swellings that cannot be unequivocally identified as sporangia (Fig. 4; Plate I, 15-17; Plate III, 15-17). In some cases, the latter are globular or elliptical with well-defined outlines but others are more diffuse. These areas lack the increased thickness of coal which usually characterises sporangia and thus are not clearly delimited from axes. In addition they are so small that accidental removal of quartz grains can radically alter their outlines. The most complete is c. 12 mm long (Plate III, 15) preserved in part and counterpart. Where the distal parts were uncovered, some of the terminations are diffuse (Plate III, 15, arrow a). Others have well defined outlines (arrow b). Maximum ?sporangial width is c. 0.8 mm. Most are wider than high. Axial branching is dichotomous, but lacks regularity, both in spacing of branch points

and degree of overtopping. Axial width ranges between 0.1 to 0.5 mm with a decrease in diameter distally. Remaining specimens (Plate III, 16, 17) are more fragmentary and terminal expansions rare (arrows).

  Suggested affinities: Assuming that the fossils represent a sporophytic branching system with terminal short and wide sporangia and possibly vascular tissues, the new material differs from members of the *Cooksonia* complex which are characterised by regularity and symmetry in branching systems. They are intermediate in size between the latter and some of the mesofossil morphotypes (C and D) described by Morris et al. (2011a) from a lower Lochkovian locality near Brecon (Tredomen Figs. 1 and 2). These also lacked anatomical data. Of particular interest is the morphology of younger (Pragian/Emsian) specimens named *Cooksonia* sp. by Schultka (2003). Branching in this German material is mainly isotomous with some overtopping, but the axes are of similar size and terminate in superficially similar sporangia, some with lobed outlines. This material is fascinating in that it shows for the first time the basal regions of a *Cooksonia*-like plant associated with possible *Sciadophyton*, interpreted by some as a gametophyte (Schweitzer, 1983).

e) *'zosterophylloid' sporangia* (Plate IV, 1-9)

  Descriptions: Specimen V.68527 (Plate IV, 1; Fig. 3, type 1e, 1) typifies fertile fragments where an expanding stem intrudes into the base of a sporangium which is considerably wider than high (3.1 mm wide x 1.3 mm minimum/1.6 mm maximum height). There are traces of a border and the presence of a

microcrystalline siliceous layer between two layers of coalified material further indicates a bivalved organisation (arrow in Plate IV, 1). These features are also present in similar, but less well-preserved specimens, in which two, almost superimposed, borders are also seen (arrows in Plate IV, 2, 3). A few isolated sporangia, lacking subtending axes, are of similar gross morphology with basal indentations (Plate IV, 4, 5) and show variation in size, the largest example being 5.3 mm wide and a maximum of 3.4 mm / minimum of 3.1 mm high. These sporangia might be considered as the end of the range of those assigned to type 1e, but their extended lateral lobes (and higher height/width radio) distinguish them from other cooksonioid types.

A single sporangium (Plate IV, 6-8), terminating a possibly branching smooth stem (arrowed in Plate IV, 6), has an almost circular outline (1.8 mm wide x 2.2 mm high) with a prominent border (0.2-0.3 mm wide) showing little change in diameter as it extends around the entire free margin. The surface of the sporangium is granular and a number of striations extend from the almost flat junction with the stalk into the basal third of the presumed valve (Plate IV, 7, 8). Similar features are observed in a second incomplete specimen (Plate IV, 9), but this lacks a border and is approximately 1.7 mm wide and 1.4 mm high. The sporangial stalk is stout (1.5 mm wide) and the junction flat.

Suggested affinities: Such sporangial characteristics are also found in various species of *Zosterophyllum*, although the length of the subtending stem in V.68527 suggests that the sporangium was not part of a strobilus. A zosterophyll strobilus with this type of sporangium is not found in the assemblage. Relative sporangial

dimensions preclude assignment to *Aberlemnia* (*Cooksonia*) *caledonica*.

As for specimens with striations, there is no evidence that these belong to the same taxon, but the feature is not recorded elsewhere in the assemblage. With thick borders and sporangial striations, the sporangia resemble those of *Sartilmania jabachensis* from the Emsian of Belgium (Fairon-Demaret, 1986), a taxon thought to be an intermediate between rhyniophytes and zosterophylls. However, the sporangia of *Sartilmania* are larger (a minimum of 2.5mm in width) and more oval in shape.

f) *Aberlemnia* sp. (Plate IV, 10-11)

Description: A single specimen (V.68567), overall 12 mm in length, comprises an isotomously branching smooth stem with, initially on splitting the slab, a single sporangium terminating each daughter branch (Plate IV, 10; Fig. 3, type 1f). The sporangia are elliptical in outline and slightly wider than high (2.5 x 2.0 mm; 3.0 x 2.1 mm), each with a distinct but very narrow border (Plate IV, 11). The subtending stems are slender (0.4 and 0.5 mm wide) and increase in width below the sporangium, where the junction is flat or slightly concave. The branching angle is wide (c. 60°). On developing the right hand branch the sporangium and a short length of stem broke away (arrow in Plate IV, 10), revealing a further sporangium and stem beneath. The displaced fragment was examined in the SEM, but showed no anatomical detail.

Suggested affinities: Gonez and Gerrienne (2010) reinvestigated Scottish Lochkovian *Cooksonia caledonica* Edwards following the discovery of new

material in the Lochkovian of the Parana Basin, Brazil and based on the presence of a border indicative of a bivalved sporangium, placed the Scottish plant in a new genus *Aberlemnia.* In basic characters the fragmentary specimen from Craswall conforms to the diagnosis of *Aberlemnia caledonica*, and like the material from both localities, lacks anatomy. However the stems of the Scottish and particularly the Brazilian material are much wider relative to sporangial width and the border more prominent than seen here and so the fragment is considered better left as *Aberlemnia* sp.

4.1.2.2. *Category 2 – Terminal longer than wide sporangia*

a) *Salopella allenii* (Plate V, VI)

The circumscription of *Salopella*, type species *S. allenii*, was based on a single specimen bearing two sporangia and its counterpart from upper Lochkovian strata exposed at Newton Dingle, Clee Hills, Shropshire (Edwards and Richardson, 1974) (Fig. 1, 2 for locality). Since then although a number of species have been added to the genus (Dou and Sun, 1983; Tims and Chambers, 1984; Fanning et al., 1992; Mussa et al., 1996) little has been added to the information on the type. This justifies the inclusion here of the numerous specimens recovered from Craswall, which contribute information on ranges in size, dehiscence mechanism and spores, and which are the largest and most conspicuous fertile specimens at the locality.

Description: Figure 5 shows the range in outlines and sizes (type 2a); dimensions are given in Table 3. Examples illustrated in Plate V, demonstrate the

range in form, with some specimens showing a greater width to height than others. The maximum width is usually at mid height. The narrowest sporangia are almost spear shaped (Plate V, 1-3), the width of the sporangia being only a little greater than the subtending axes. There is some variation in the nature of the sporangial tip, from rounded (Plate V, 5, 6, 8, 11, 13) to almost pointed (Plate V, 1, 4, 7, 9). The latter is particularly evident in a partially three dimensionally preserved specimen (Plate V, 7), the sporogeneous area near its tip being filled with fine-grained sediment producing an isodiametric solid cone. More proximally the specimen is fractured, accompanied by lateral displacement, and the infill is missing. More compressed specimens have rounded apices (e.g. Plate V, 6). In many examples, there is a difference in thickness of coal between the entire sporangium and subtending stem (Plate V, 1). A few show a constriction in the stem just below the sporangium (Plate V, 9), but, unlike in the holotype, evidence of branching in this area is rare. Such an exception is illustrated in Plate V, 10. The surface of a sporangium may be smooth or bear obliquely orientated longitudinal striations (Plate V, 3, 11), presumably reflecting cell orientation in the sporangium wall. Very rare sporangia show outlines of individual cells (Plate V, 12). Splits in the coalified material showing similar orientation suggest that such wall construction may be involved in dehiscence (Plate V, 13, 14).

Subtending stems are long (maximum length = 53 mm), parallel sided and sparsely branched. A longitudinally orientated central strand is a rarity (arrow in Plate V, 9). Branching is usually isotomous to slightly anisotomous (Plate V, 16).

In a few cases, a group of fertile specimens (2+) occur in proximity on a bedding

plane, with similar orientation and similarly sized sporangia at approximately the same level (Plate V, 15, 17). Bearing in mind that this is an allochthonous assemblage involving fluvial transport of plants, it seems highly unlikely that this juxtapositioning is accidental and allows the inference that these fertile axes were proximally attached, although we have no unequivocal information on the organisation in this region. The single sterile specimen in which numerous stems are attached to one side of another (Plate I, 14) may be representative of the latter, although the stems in this case are much narrower than those subtending sporangia.

No further superficial anatomical detail was seen when viewed under the SEM, apart from the traces of cells on the surface of sporangia (as noted above) that appear as folds or striations (arrowed in Plate VI, 1, 2). Where the wall has been removed mechanically, the outlines of very compressed spores are observed, sometimes partially covered by numerous pyrite crystals (Plate VI, 3) or multilobed (i.e. framboidal) granular material (Plate VI, 4-6). Spores have a circular amb, and surfaces may be smooth (Plate VI, 7) or pitted, the latter produced either by pyrite or possibly tapetal residues (Plate VI, 8, 9). Coalified material isolated from sporangia and subjected to prolonged maceration includes over oxidised, pale spores when compared with the still opaque to amber-coloured sporangial wall tissues. They thus appear thin-walled and are heavily folded. Although lacking sculpture, their surfaces are frequently covered by clusters of spherical granules. Convincing trilete marks have not been observed. Average spore diameter is 31 µm.

Suggested affinities: Based on size, overall architecture and spore characters, these new specimens are closer to *S. allenii* than the coeval *S. marcensis* Fanning et al. 1992, which is recorded from a number of localities in the Welsh Borderland (e.g. Targrove, Fanning et al., 1992; North Brown Clee Hill, Edwards et al., 1994; Figs 1, 2). *Salopella marcensis* is based on much smaller plants (maximum recorded height = 6.4 mm) with elongate fusiform sporangia (0.8 – 3.4 mm high and 0.3 – 0.9 wide), that terminate smooth stems with isotomous branching occurring close to or up to 2 mm from the sporangial base. This branching system, illustrated in the silhouettes (Fanning et al., 1992, fig. 35) and smaller dimensions distinguish *S. marcensis* from *S. allenii*. Anatomical details were not preserved. Přídolí compressions from the north-west of China named *S. xinjiangensis* (Dou and Sun, 1983) and the Australian impressions, *S. australis* and *S. caespitosa* (Tims and Chambers, 1984) also lack anatomy. *Salopella australis* from Ludlow and Pragian rocks is readily distinguished from *S. allenii* because the sporogeneous material appears confined to the basal two thirds of the sporangium. Pragian *S. caespitosa,* based on a single specimen, has fusiform sporangia terminating stems that branch up to three times, but usually some distance below the sporangia. Stems are parallel-sided and not that much narrower than the sporangia. Superficially these specimens are morphologically more similar to those in *S. allenii*, but absence of any anatomical features made the authors' decision to erect a new species the sensible one. Whether or not such morphospecies are biologically related is considered very unlikely. As a minimum, spores are essential for assessment of relationships.

b) *Salopella* / *Tortilicaulis* sp. (Plate VII, 1-4)

Descriptions: Two specimens have small fusiform terminal sporangia. The more complete (Plate VII, 1; Fig. 5, type 2b), is 9.5 mm long, and comprises a dichotomously branching stem with a sharp decrease in diameter (0.8 to 0.2 mm) above the branch point. The right hand sporangium (Plate VII, 2), with an intact acuminate tip, is 3.0 mm long and 1.0 mm wide at mid-point. An oblique striation in the coalified material possibly indicates spiralling of cells. The second uncovered sporangium (Plate VII, 3) is 2.5 mm long, incomplete distally and 0.9 mm wide. A further similarly shaped, but somewhat narrower example, is represented by an isolated sporangium, 3.2 mm long and 0.8 mm wide (Plate VII, 4).

Suggested affinities: These specimens resemble *Salopella*, except that in Plate VII, 1 and 2 (V.68563) the sporangial width is considerably greater than the subtending stem, although this is perhaps less completely preserved than the left hand branch. In dimensions it is closest to *S. marcensis* (Fanning et al., 1992). While oblique striations have been recorded in sporangia here assigned to *S. allenii*, they are absent in *S. marcensis*, which sometimes has a vertical cleft. They are however found in *Tortilicaulis*, where the entire sporangium is sometimes twisted (Edwards, 1979; Edwards et al., 1994) When Lochkovian coalified specimens described from Targrove (Fig. 1a) were removed from the matrix, obliquely orientated coalified strands occurred on the rock surface, as well as occasionally on the fossils themselves (Edwards et al., 1994, figs 1, 2). The

specimens described here fall into the size range of these probably middle Lochkovian examples (width = 0.63 – 1.81 mm; length = 1.63 – 7.17 mm). However, in shape (see Fanning et al., 1992, fig. 34) and in the lack of any constrictions or twisting in the subtending axes, the specimens are probably closer to *Salopella marcensis*. Sporangia containing spores are essential for unequivocal identification.

c) Vertically elliptical sporangia (Plate VII, 5-7)

Description: Two specimens belong to this group (Fig. 5, type 2c). The more complete (Plate VII, 5, 6) has two vertically elongate, elliptical sporangia, each 2.0 mm long and 1.4 wide, which terminate isotomously branching axes (axial width 0.3 – 0.5 mm), 11 mm in overall height. Slight expansions in both daughter axes equidistant from the sporangia (arrows in Plate VII, 5) may be bases of two further branches. When tilted, each sporangium shows a shallow groove running along the distal margin delimited by very narrow bevelled edges (arrow in Plate VII, 6), which is suggestive of dehiscence into two equal valves.

Specimen V.68556 comprises a single vertically elongate sporangium terminating a smooth stem with the remains of a bifurcation (Plate VII, 7). It is slightly more robust than the first example (axial width 0.4 – 0.6 mm), with a larger sporangium (2.3 x 1.5 mm), although its height is conjectural because there is little distinction between stem and fertile area.

Suggested affinities: There are two genera with vertically elongate elliptical sporangia which terminate smooth axes in the local Lower Devonian. *Tarrantia*

salopensis was described from compressions of isolated sporangia from Lochkovian strata at Targrove (Fanning et al., 1992, Figs 1, 2). Subtending axes are short and unbranched, and in most examples are wide when compared with sporangial width. They lack evidence of any marginal, dehiscence features. By contrast *Uskiella spargens* Shute and Edwards (1989) are similar in relative proportions of sporangia and branching pattern, but the younger, Pragian fossils are much larger and sporangia show clear distinction into two valves with anatomical evidence of a dehiscence feature and a border extending around the margin in compression fossils. *Uskiella reticulata* (Fanning et al., 1992; Targrove, Lochkovian) has similarly sized sporangia with some evidence of marginal dehiscence in two valves, but they possess a superficial reticulate pattern, a feature that might be obliterated during fossilisation. On balance, we feel that the new specimens should be left as cf. *Uskiella*.

d) 'Urn shaped' sporangia (Plate VII, 8-11)

Description: A single specimen (V.68563 & counterpart) had, at first glance, an unusual urn-shaped sporangium (Plate VII, 8, 9; Fig. 3, type 2d), terminating a much branched, dichotomously branching axial system (Plate VII, 10, 11) and a further uncovered sporangium which is almost complete (arrowed in Plate VII, 10, 11). Subtending axes are parallel-sided; the bases of the sporangia are well preserved but are less well-defined distally. Anisotomy is accompanied by overtopping, but two successive daughter branches occur on one side of the 'main'. The overall height is 33 mm, with axial width ranging between 0.1 and 1

28

mm.

Suggested affinities: This specimen differs from Category 1b in shape of the sporangial bases, and overall relative dimensions, the uncovered sporangium being longer than wide, and hence closer to the sporangia described under Category 2c here (cf. *Uskiella*). However, a similar branching pattern has not been recorded in the genus *Uskiella*.

4.1.2.3. *Category 3 – Laterally borne sporangia*

a) *Zosterophyllum* strobili (Plate VIII)

Description: This is based on ten fragments of strobili composed of lateral sporangia and lacking any sterile elements (Fig. 6, type 3a). In two examples, the bases of strobili are preserved (Plate VIII, 1, 2): one of these (V.68564) terminates a branching system of smooth axes (Plate VIII, 1). The occasional presence of a border around the convex margin of the sporangium is a marginal feature suggestive of two valves with distal dehiscence (Plate VIII, 3 - 5). However this feature is not easily demonstrated, even though the semi-compressed sporangia are three dimensionally preserved with rock grains intermingled with coaly material and extend through several millimetres of the sandstones. The strobili contain two vertical files of sporangia which occur on one side of the strobilar axis. This asymmetry results in a number of different appearances on compression. Plate VIII, 6 shows the rows of sporangia, which are both partially folded and completely obscure the strobilar axis. By contrast, in Plate VIII, 7, the two rows are preserved on one side of the strobilar axis, the

other with a continuous straight edge. In a third type (Plate VIII, 8, 9) one row of relatively well preserved sporangia seen in face view contrasts with a second row of poorly preserved tangentially compressed or folded sporangia (arrowed). Finally Plate VIII, 10 shows a small fragment with just a single row of sporangia exposed in face view with some indication of attachments of others represented by small mounds. Further variation relates to whether or not individual sporangia can be distinguished, a particular difficulty where sporangia are crowded and overlap vertically (Plate VIII, 11). In such specimens the attachment sites and details of orientation of individual sporangia are obscured. In face view, i.e. when an entire valve is visible, sporangia are almost always wider than high and symmetrical (elliptical when compressed) (Plate VIII, 7-9, 12). A border is rarely seen and details of the junction of sporangia and stalk are unclear (Plate VIII, 13). However, when folded, a border is sometimes apparent, particularly distally. Such sporangia may have a concave abaxial margin (Plate VIII, 14, 15). Their shape is best seen in basal regions of strobili where sporangia are more widely spaced (Plate VIII, 14, 15). They are obliquely attached on short stalks, which curved distally such that the valves are held upright and may slightly overlap the strobilar axis (Plate VIII, 16, 17).

Suggested affinities: The genus *Zosterophyllum* Penhallow (1982) is characterised morphologically by smooth axes terminating in bractless strobili whose sporangia comprise two equal valves that split around the convex thickened margin. The two rowed arrangement is a variant of the usually helically arranged sporangia and characterised the subgenus

Platyzosterophyllum Croft and Lang (1942). In sporangial morphology and mode of insertion on the strobilar axis, on initial examination, the new material bears close comparison with *Z. fertile* Leclercq from the lowermost Belgian Devonian (Leclercq, 1942). More recently some broadly similar strobili from the Anglo-Welsh Basin have been named *Zosterophyllum* sp. (upper Lochkovian, Welsh Borderland; Edwards and Richardson, 1974) or even *Z.* cf. *fertile* (middle Lochkovian, Gwent, Wellman et al., 2000; and Pragian, Brecon Beacons, Edwards, 1969). Such uncertainty might reflect incomplete knowledge, differences in preservation or biological variation in the *Z. fertile* complex. It is also difficult to place the new material in *Z. fertile* because of the following differences (see also Table 4):

1) Although two rows of sporangia are present, these are not attached on opposite sides of the strobilar axis, but are both displaced to one side. A similar asymmetry is seen in the reconstruction of the *Z.* cf. *fertile* from Gwent (but not emphasised in their description) (Wellman et al., 2000).

2) The collection from Craswall shows variability in the vertical spacing of the sporangia; those near the base may appear to be on one row and staggered. The latter may also result from incomplete preservation.

3) Sporangial stalks are usually obliquely attached to the strobilar axis and curve adaxially so that the sporangium is held upright. Perpendicular attachment of a stalk is rare.

4) In face view the valve is elliptical, but only slightly taller than wide. There are no basal lobes and hence the sporangium in face view could not be described

as reniform.

All the specimens in the *Zosterophyllum fertile* complex have the same dimensions (sporangia etc., Table 4), although some of the new incomplete strobili are even longer than the complete Belgian specimen. The sporangium to stalk orientation rules out the Pragian material (Edwards, 1969), where strobili are short and the sporangia occur in two opposite rows. An asymmetric two rowed appearance of the sporangia has been noted in the single specimen from Gwent (Wellman et al., 2000) and the new material from Newton Dingle described here (section 4.2.3), but in the former, the appearance of the valves in face view and relatively slender stalks rule out close affinity with the strobili described above. On balance we consider the new material sufficiently distinct from *Z. fertile*, and all*,* except the Newton Dingle examples, to merit the erection of a new species, but would require differently preserved material, preferably providing anatomical data, before adequate circumscription becomes possible.

b) *Craswallia haegensis* **gen**. et **sp. nov.** (Plate IX)

Description: A single specimen preserved in part and counterpart comprises at least five smooth stems in parallel alignment with rare lateral sporangia, all at approximately the same level in adjacent stems. Bearing in mind the allochthonous nature of the assemblage, such organisation strongly suggests that only one plant at least 45 mm high is involved (Pl. IX, 1, 2). The stems show very little change in diameter along their lengths, measuring 1.3 to 1.8 mm diameter, and no branching. Sporangial descriptions are based on

reconstructions/information from part and counterpart. Sporangial and axial

dimensions are given in Table 5. The most prominent are elliptical (Plate IX, 3 -

5), but not reniform, with a broad conspicuous border (Plate IX, 6) extending

around the entire free convex margin. This is interpreted as a dehiscence feature

involving two equal valves. Possible further complexity in this feature is

evidenced by a very narrow coalified strip at the limits of a valve. The sporangial

stalk is broad, almost as wide as the subtending stem (Plate IX, 4, 5). It is

probably not curved, but is decurrent (Plate IX, 3 - 5) and then holds the strongly

compressed sporangium at an acute angle to the stem. Its length is difficult to

determine because of superpositioning on the stem. A completely uncovered

sporangium is the smallest and is almost circular in outline (Plate IX, 7). The

subtending axis continues some distance distally and is aligned with, but not

connected to a further stem fragment in the part (Plate IX, 1). However,

uncovering of the axis in the counterpart reveals probable continuity (Plate IX, 2).

The distal fragment (part) bears a sporangium on the same side of the axis as the

proximal one (Plate IX, 1), and separated from it by c. 25 mm. A sporangium

attached to the side of one of the stems is represented by an inclined, almost

linear mass of coal (Plate IX, 3, arrowed), indicating the rigid nature of the

sporangium. *Zosterophyllum* sporangia are usually folded when preserved in this

position.

Suggested affinities: Axes bearing lateral sporangia with marginal dehiscence

into two valves characterise the zosterophyll clade. The absence of a strobilus,

consisting of closely packed, predominantly reniform sporangia, excludes this

new material from the type genus. Comparisons with those taxa in which sporangia occur dispersed along branching stems are not satisfactory, because of the fragmentary nature of the Craswall material and its absence of branching, but there is limited support for a distal fertile region. On such evidence, a new genus is proposed within the zosterophylls.

Systematic Palaeobotany

Subdivision Lycophytina *sensu* Kenrick and Crane, 1997

Class Zosterophyllopsida Hao and Xue, 2013b

Order Zosterophyllales Banks, 1968

Family Zosterophyllaceae Banks, 1968

Craswallia Morris and Edwards **gen. nov.**

Etymology: From Craswall, the nearest hamlet to the locality.

Diagnosis: Plant with smooth stems, with evenly distributed, laterally attached sporangia in the distal regions. Sporangial outline elliptical to circular, constructed of two valves, with broad borders. Sporangia attached at acute angles to the main stem via broad stalks of similar width to the latter.

Type species: ***Craswallia haegensis*** Morris and Edwards **sp. nov.**

Etymology: From Haeg, the Old English name for Hay, the closest town to the locality.

Diagnosis: As for genus. Plant at least 70 mm in height. Distal fertile zone at least 45 mm long. Fertile stems 1.3 – 1.8 mm wide. Largest sporangium 4.9 mm wide x

4.2 mm high, smallest, 2.3 x 2.3 mm. Sporangial border c. 0.2 mm wide, stalks

1.0 – 1.7 mm wide.

Holotype: V.68527.

Illustrations: Plate IX, 1-7.

Locality: Craswall, south of Hay-on-Wye, Herefordshire, England (Grid Reference

SO325304).

Horizon: Freshwater West Formation, Lochkovian, Lower Devonian.

Rhinopteraspis crouchi fish biozone.

General discussion on Craswallia: Particularly interesting is the diameter of the

sporangial stalk that approximates to that of the subtending stems and, together

with its orientation, raises the possibility that the sporangium terminates a short

shoot, produced by unequal dichotomy of the main apex (Niklas and Banks,

1990; Hueber, 1992; Kenrick and Crane, 1997). This is an extreme example of

overtopping, although anatomical evidence to substantiate this is frustratingly

absent. This interpretation conforms to one of the two hypotheses relating to the

development of aggregated sporangia into strobili which were reviewed by Niklas

and Banks (1990). They postulated that the apex of a potentially fertile axis

divided unequally with the larger branch continuing apical growth and the smaller

branch terminating in a sporangium. In this scenario, the sporangial stalk would

be considered homologous to an axis with the potential to be vascularised. The

branching process would be repeated, its timing resulting in either a dense

strobilus or spaced sporangia. In the alternative, initials would be produced on the

sides of a single stem with persistent, dominant apical initials. These lateral

initials would develop into sporangial complexes, with fewer tendencies to be

vascularised (see also Hueber, 1992; Kenrick and Crane, 1997).

4.2. Newton Dingle

4.2.1. Naked sterile axes and axial-like fragments (Plate X, 1-8)

  Found in sandstones, these truncated axes range between 0.3 and 2.0 mm

diameter (x = 1.1 mm; n = 12), the longest being 6.0 mm long. The latter contains

a central longitudinally aligned coalified strand (arrow in Plate X, 3), thought to

represent conducting tissues. A further axis is delineated by two narrow bands of

coal even though most of the superficial material is missing (Plate X, 1). Two

specimens show isotomous branching at angles of 60º and 70º (Plate X, 4, 5).

  The largest specimens in this recent collection are two strap-shaped fragments

with more or less parallel sides measuring 1.7 cm long x 0.6 cm wide and 0.6 cm

long x 1.7 cm wide (Plate X, 6, 7). The surface in specimen V.68576 is

longitudinally striated (Plate X, 8). The curved end of this specimen indicates

erosion during transport and this feature together with the striations suggest

affinity with the *Prototaxites-Nematosketum* complex (Burgess and Edwards,

1988).

4.2.2. Indeterminate fertile material (Plate X, 9-10)

  Amongst coalified patches (probably derived from thalloid terrestrial vegetation)

and sterile axes are occasional fragments with discrete outlines reminiscent of

isolated sporangia, but in absence of spores cannot be unequivocally identified as such. One specimen comprises a hemispherical structure c. 2.4 mm maximum width x c. 2 mm wide (Plate X, 9). It is similar in shape to compressed *Cooksonia hemisphaerica* Lang 1937 (Fanning et al., 1992), except that it is slightly asymmetric. The fragment in Plate X, 10 is interpreted as comprising an elliptical sporangium with possible curved junction with a short length of subtending axis. Such features characterise *Zosterophyllum* and certain *Cooksonia/Aberlemnia* sporangia. Further identification is impossible.

4.2.3. *Zosterophyllum* sp. (Plate X, 11-13; Plate XI)

Descriptions: Two strobili preserved in part and partial counterpart (V.68581) are aligned more or less in parallel (Plate XI, 1, 2; Fig. 6, type 3c, 1), but with some indication of convergence proximally (Plate XI, 3), suggesting that the pair was part of the same plant with branching just below the fertile regions. However, we failed to show organic connection. Dimensions are given in Table 4. The sporangia are variously preserved with c. 20 in each strobilus. They are unusual in that they show marked relief, particularly evident in the 'folded' sporangia where deep indentations/ridges may mark the borders (Plate XI, 5-10). Some granular or layers of vitreous coaly material remain on iron-oxide stained 'impressions' (e.g. Plate XI, 8-10). Staining has also diffused into the matrix, blurring outlines (e.g. Plate XI, 4, 8). Some sporangia are infilled with sediment. Sporangia are inserted in two rows (e.g. Plate XI, 5-7); information from part and counterpart indicates that these are not inserted on opposite sides of the strobilar

axis. Thus on the removal of the axis, a greater proportion of the adaxial valve of the sporangium is exposed, as compared with the half of the abaxial valve seen in the row where sporangia are attached at the edge. The former are thus attached on the surface of the compression. The latter show the stout sporangial stalks which are inserted at an angle of c. 50-90º and then curve adaxially so that the sporangia lie close to the axis (e.g. Plate XI, 8-10). Some show concavity in the distal part of the folded valve. There is very little space between the adaxial surface of the stalk and the basal parts of the valves. Sporangia are poorly preserved in partial face view. The rounded distal margin has some traces of a border but we have no information on the shape of the basal regions. Sporangia are crowded and less well defined in the distal, and probably incomplete, parts of the strobilus (Plate XI, 4). In the basal regions they are more widely spaced, and do not overlap the sporangia above (Plate XI, 5).

The second specimen (V.68582), collected in part only, is less well preserved in the fertile area, but, on uncovering, shows an isotomous dichotomy in the subtending axis, some 2.2 cm below the right hand strobilus (Plate X, 11; Fig. 6, type 3c, 2). The axis on the left is partially missing, but the orientation of the strobilus suggests it was connected. The right hand strobilus contains just one fragmentary sporangium, possibly in face view, attached to the axis below (arrow in Plate X, 12). The left hand one has a row of at least four folded sporangia c. 1.5-2 mm high with marked topography, but lacking definition between sporangium and stalk (Plate X, 13). Layers of vitreous coal demarcate the thickened margins. The abaxial edge is convex just below the sporangial tip.

Suggested affinities: It seems likely that all the strobili belong to the same taxon, but show differences explained by preservation and orientation. The discussion on the affinities of the Craswall specimens (see section 4.1.2.3) is also appropriate here and sporangial orientation and insertion in two rows indicate affinity with the *Zosterophyllum fertile* complex. Here we concentrate on comparisons with the two specimens already described from Newton Dingle (Edwards and Richardson, 1974). They were preserved as coalified specimens with some iron-oxide staining in coarse grey-green, micaceous to arenaceous sandstone and are more compressed than the new material. The more complete specimen had a bifurcation in the base of the fertile region. Sporangia were more widely spaced but similarly orientated, but individual sporangia show greater separation between the stalk and the basal parts of the valves. In one branch of the spike, they are attached on opposite sides of the strobilar axis. The second example was far more fragmentary and the sporangia difficult to distinguish because they overlapped vertically and were arranged in two rows on one side of the axis. It was thus much closer to the new specimens. Edwards and Richardson (1974) left both as *Zosterophyllum* sp. with closest similarities to *Z. fertile*.

5. General discussion

5.1. Grades of organisation in Craswall plants

The incompleteness of specimens prevents adequate taxonomic placement of many of the Craswall taxa. When compared with plant fossil assemblages outside of the Anglo-Welsh Basin, the Craswall plants possess grades of organisation

that are similar or less advanced than taxa from much older deposits elsewhere (e.g. Ludlow deposits of Victoria, Australia, including *Baragwanathia, Salopella australis* and zosterophylls; Tims and Chambers, 1984). Thus the Anglo-Welsh Basin should not be identified as the crucible or cradle of tracheophyte diversification, but that morphological grades apparent in earlier strata elsewhere reflect subsequent migration and vicariance. Unfortunately the latter hypothesis is impossible to test because of the lack of mega- and particularly microfossil data. Nevertheless it is of interest to examine the grades of organisation exemplified by the Welsh Borderland assemblages (Table 6) leading to an analysis of the reasons of any changes through time.

1. Conspicuously rare in the Craswall assemblage is the strict isotomous branching (daughter branches of equal diameter; symmetry bilateral; usually branching synchronous in daughter axes) that characterises early rhyniophytes/ rhyniophytoids such as *Cooksonia*. Instead branching is anisotomous with weak overtopping (i.e. asymmetry but not pseudomonpodial). This may be accompanied by limited isotomous branching in the narrower 'laterals'. Such plants have the capacity for increased vertical growth and, if 'lateral' branching is maintained, increased reproductive capacity via terminal sporangia. Limits on height might be determined by the diameter of the initial sporophytic axis, assuming depletion of the size of the apex at each dichotomy. Such inference is based on observations on *Rhynia gwynne-vaughanii*, where the apical meristem is multicellular (Kidston and Lang, 1920) and on decrease in stem diameter distally in a single compression fossil (Edwards, 1994). This strategy is apparent

in *Monnowella* from Craswall and the Lang specimen from Targrove (Lochkovian) (Fanning et al., 1992). Even earlier, a Ludlow plant from Bathurst Island, Arctic Canada, was illustrated by Basinger et al. (1996) and described in the legend as a 'cooksonioid-type plant with large globose sporangia terminating short [unbranched] branches' (figure 3A, page 55). However it was subsequently described as aff. *Zosterophyllum* sp. B (Kotyk et al., 2002).

2. All the axes recorded in the Craswall assemblage are smooth, as are the specimens from all of the Lochkovian localities in the Welsh Borderland. The first evidence of enations or spines, with potential for increase in photosynthesising surfaces, comes from the Allt Ddu locality in the Brecon Beacons (*Deheubarthia splendens*: Edwards et al., 1989), tentatively assigned to the BZ Spore Assemblage Biozone (Fig. 2). A single specimen of a spiny axis has been recorded in the Přídolí of Pembrokeshire (Edwards, 1979). The first record of lycophytes *sensu stricto* in the Anglo-Welsh Basin are Pragian (*Drepanophycus*), but were present in the Australian Silurian (*Baragwanathia*: Tims, 1980) and the German Lochkovian (*Drepanophycus*: Schweitzer, 1983).

3. A border present around the margin of a small number of terminal sporangia in rhynophytoids and in *Zosterophyllum* species at the locality suggests dehiscence into two valves, as indeed does the longitudinal split in *Salopella*. This trend towards controlled spore liberation is an advancement on the apparently unmodified sporangia characteristic of older rhyniophytes (e.g. *C. pertoni*: Edwards and Fanning, 1985), although lack of anatomy in the majority of the latter make such generalisation premature.

4. Changes in the growth patterns of rhyniophytoids increased light harvesting and reproductive capacity in tandem, but in *Zosterophyllum* the latter is achieved by aggregation of sporangia into strobili on a single stem. The first unequivocal record of the genus in the Welsh Borderland is Wellman et al., (2000), but diversification producing variation in the organisation of sporangia in the strobilus and in sporangial characteristics is already recorded in the Ludlow (Silurian) of Arctic Canada. However production of such sporangia from the apex in terms of organ differentiation is still controversial.

5. The relevance of bilateral symmetry in strobili of certain *Zosterophyllum* species is also intriguing, especially as this type of organisation is also recorded in the earliest record of zosterophylls in the Ludlow of Arctic Canada (Kotyk et al., 2002). Strobili recorded from the Lochkovian of the Anglo-Welsh Basin possess sporangia in two files, while examples from Craswall are typical, in which these rows are not opposite, but displaced to one side of the strobilar axis. The adaptive significance of this is elusive. We have no information on the apices of immature strobili, but it is tempting to conclude that they may have been circinate, as were the vegetative apices of many zosterophylls with scattered sporangia (e.g. *Gosslingia*, *Thrinkophyton*) and even one species of *Zosterophyllum divaricatum* Gensel, 1982. Such a growth habit would have provided some protection, e.g. from desiccation, for developing sporangia. However, isolated circinate tips are very rarely recorded in assemblages and are absent from Craswall, but it could be argued that their preservation potential was low, especially in the presumed absence of the strengthening tissues that occur in the

peripheral zones of the mature stems of most zosterophylls.

In summary in terms of grades of organisation, the vegetation at Craswall exhibits features that would have enhanced light harvesting, reproductive capacity and possible liberation/dispersal efficiency, not found in the earlier Silurian vegetation in the area.

5.2. *Variation in the composition of vegetation in Lochkovian space and time*

Much has been written on the limitations of the fossil record in tracing the history of early land plants, both in terms of the inadequacies of anatomical preservation and the dearth of occurrences (e.g. Edwards, 1990; Edwards and Wellman, 2001). The Lochkovian time interval (~8 million years) contains a number of scattered global records (Gensel and Edwards, 2001), but it is only in the Anglo-Welsh Basin that there is a sequence of assemblages preserved throughout this relatively short time interval, with the new locality at Craswall possibly bridging a gap between the mid MN and BZ Spore Assemblage Biozones. Preservation is variable, ranging from compressions/ impressions, with limited to no anatomical detail as described here, to minute charcoalified fragments with exquisite anatomy that potentially distort the quantitative record. Such is the case for mid MN charcoal assemblages, which reveal much greater diversity and disparity than seen in contemporaneous assemblages in the immediate area. However, comparisons between *in situ* spore studies from charcoal assemblages (and the other localities) and the dispersed spore record elsewhere, suggests that similar vegetation existed, but was not recorded in the megafossil record.

The differences in composition between the diverse Craswall and disparate Newton Dingle assemblages further demonstrate inadequacies in vegetational history based on megafossils alone. Indeed the dispersed spore record indicates that the reduction in crassitate spores, known to derive from *Cooksonia* type rhyniophytes, and assumed extinction of this group, occurred later than the megafossil record in Newton Dingle suggests.

Particularly important is the independent dating and biostratigraphical framework provided by fish and palynology that allow the beginnings of elucidation of changes in vegetation through time. However, the record is distorted by a facies bias (Table 7), the preservation quality and size of plant fragments controlled by the energy of the fluvial depositional environment, with sorting processes affecting the compositions of assemblages.

Nevertheless it has been suggested that, even in the relatively small geographic area encompassed by the Anglo-Welsh Basin, differences in composition of assemblages might reflect differences in the original habitats of the plants, relating perhaps to location (elevation) on the floodplains rather than progressive vegetational change. This hypothesis was addressed in some detail by Wellman et al. (2000) who suggested that small plants with short life cycles and rapid growth might have colonised permanently wet environments subject to disruption by flooding, while taller and thus probably longer-lived plants (zosterophyll communities) would have lived on stable, drier areas, although some flooding must have occurred to facilitate their preservation in fluvial sediments.

Regardless of this limited evidence that local differences in diversity might be

due to environmental / ecological variation, it is clear that throughout the Early Devonian in the Anglo-Welsh Basin, there are changes in species composition that reflect an evolutionary progression, particularly as it relates to the appearance and subsequent diversification of the zosterophylls/lycophytes seen earlier elsewhere. When Edwards and Davies (1990) attributed these changes to increased competition for height and space in an evolutionary context, the global picture was less well known (e.g. Steemans et al., 2010). Thus today the changing composition of the assemblages recorded in the Anglo Welsh Basin might be interpreted as successive invasions of the region by better adapted forms whose dominance and subsequent radiation led to the extinction of more 'primitive' types (the rhyniophytes s. l.). Based on extant vegetation, such invasive species would have possessed combinations of ecological and physiological characters that would have resulted in rapid growth to dominance, increased vegetative reproduction and efficient dispersal (e.g. Beerling, 1995) attributes except for the latter impossible to infer from fossils. Here we would add the gross morphological, anatomical and architectural characters noted above and particularly for *Zosterophyllum,* clonal growth, increased spore production and controlled dispersal.

indispensable for the discovery and description of the new material.

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Table 1. Sterile axes dimensions on slabs.

Slab No.	Range of axial diameter (cm)	Average (cm)	Number
V.68526	0.44-0.98	0.74	9
V.68527	0.10-1.28	0.62	32
V.68528	0.09-1.65	0.63	25
CR006	0.12-2.10	0.51	38
CR013	0.17-3.14	0.94	7
CR017	0.17-2.10	0.77	27
CR021	0.08-1.90	0.63	17
CR032	0.09-1.66	0.63	14
CR038	0.17-2.15	0.88	99
V.68534	0.17-2.00	0.65	30
V.68533	0.12-1.62	0.65	11
V.68531	0.20-2.56	0.91	19
CR046	0.10-1.86	0.83	46
V.68536	0.09-0.96	0.46	16
V.68541	0.15-1.70	0.59	18
V.68547	0.15-2.01	0.68	29

Table 2. Dimensions of Type 1a cooksonioid sporangia (1 & 2) in mm (V.68526).

	Sporangium			Axis		Total height	Sporangium width/ junction width
	Height	Width	Border width	Junction width	Below		
Sporangium 1	c. 3.50	6.00	0.20	?3.10	1.10	1.60	1.94
Sporangium 2	c.3.10	4.10	0.15	?2.00	0.70	6.00	2.05

Table 3. Comparative measurements of *Salopella* specimens.

Salopella (n)	Max. length of specimen (mm)	Axes			Sporangia			Spores +/1 trilete
		Width (mm)	Branching x	±	Height (mm)	Width (mm)	Av. H/W	
S. allenii								
type (1)	24	1.1 - 2.0	1x	+	9.0	2.0	4.5	-
this paper(24)	54	0.3 – 2.2	1x	+	4.4 - 10.6	0.9 – 3.2	3.8	
Targrove (1)	22.7	1.3 - 2.6	-	-	15.8	4.6	3.4	-
S. caespitosa (1)	85	1.2	>3x	+	4.5	1.7	2.6	-
S. australis (20+)	145	0.9 - 2.4	>2x	+	6.5 - 14.0	1.3 - 2.0	5.6	-
S. marcensis (37)	6.4	0.1 - 0.5	3x	+	0.8 - 3.4	0.3 - 0.9	2.9	-
S. xinjiangensis	?	0.3 - 1.0	1x	+	3.5	<1.5	2.3	-

Table 4. *Zosterophyllum* measurements; dimensions of fragments of strobili of *Zosterophyllum* sp.

| Specimen No. | Total length (mm) | Overall width (mm) | No. sporangia | Sporangial arrangement (1-3)[a] | Strobilus axis width (mm) | Sporangium (mm) | | | | | | | Notes |
| | | | | | | Height | Width | | Border +/- | Stalk | | Angle of insertion[o] | |
							face	folded		Height	Width		
Craswall specimens													
V.68529	18.3	>2.5	>12	1	<1.6	c. 2.2		1.2	+	-	-	-	Sporangia widely spaced
V.68560	22.0	2.5	>7	1	1.5	2.5	2.2	-	-	0.8	1.3		
V.68561	30.0	3.0	-	1	2.0	1.7	~2.0	-	0.13				
V.68564	50.0+[b]	2.8[c]	>4	1	c.1.3	2.0-2.5	>1.5	0.7 - 1.5	?	c. 0.75	-		Base of strobilus
V.68549	52	3.5	>20	2	3.5	2.1 - 2.6	2.3 - 2.6	(1.1)	-	0.8 - 1.0	0.7 - 0.9		
V.68567	20	3.5	>7	3	c.1.5	2	2.7			1.4	0.9		
V.68557	10.0	2.5	c. 4	3	1.2	2.2	2.5		0.15				
V.68557	17.0	3.7	c. 12	2	-	-	-	-	-	-	-	-	Crowded, detail obscured
V.68553	27	~2.5	c. 2	?2	1.1	-	2.2	1.6 - 1.7	3	-	-	-	
V.68545	13	~1.8	3(+2)	3	-	[from photo]	1.6 - 2.0			1.5	0.5	64°	
Newton Dingle specimens													
V.68581	55	1.5	c. 20	1	c. 1.0	1.5 – 2.5	-	0.4 – 0.7	+	0.6 – 1.0	0.8 – 1.4	c. 50 - 90°	
V.68582	13	2.1	c. 5	3	c. 1.0	1.5 – 2.0	2.1	0.9 – 1.2	+	-	-	-	

[a] For sporangial arrangements: 1= two files of sporangia, both folded; 2 = two files of sporangia, one preserved in face (valve) view, the other folded; 3 = one file of sporangia, preserved to one side of the strobilar axis, all more or less folded.
[b] Total length of V.68564 includes subtending axis plus fertile region (9mm).
[c] Within strobilus.

Axes 1-6	Fertile stem width (mm)	Sporangia		Stalk		Sporangial Border (mm)	Distance apart of sporangia (mm)
		Height (mm)	Width (mm)	Height (mm)	Width (mm)		
A1 Sp. 1	1.2 – 1.5	4.2	4.9	0.6 [a]	1.3	0.25	-
A2 Sp. 1	1.3 – 1.7	3.0	3.0[a]	2.2	1.0 [a]	-	11.5
A2 Sp. 2		2.8	2.85	1.5	1.4	-	
A3 Sp. 1	1.7	3.0	4.1	1.7	1.5	0.2	-
A4 Sp. 1	1.4 – 1.6	3.1 [a]	2.8	1.7	1.6	-	22.5
A4 Sp. 2		2.0	2.8 [a]	1.0	1.4	-	
A5 Sp. 1	1.6	2.0	2.6	-	1.5	-	11.5
A5 Sp. 2[b]							
A6 Sp. 1	1.4 – 1.5	2.3	2.3	-	1.0	0.2	10.0
A6 Sp. 2		2.4	2.5	-	1.6	-	

Table 5. Measurements for *Craswallia haegensis* gen *et* sp. *nov*. (V.68527).

[a] Estimated/ approximate.

[b] no measurement possible because sporangium preserved end on.

Species	lower MN		middle MN		upper MN		BZ	
	TM[1]	TR[2]	NBCH[3]	BT[4]	CR[5]	ND[6]	AD[7]	MBQ[8]
Cooksonia pertoni		x	x		x (cf.)			
Cooksonia cambrensis	x (cf.)	x			x (cf.)			
Cooksonia hemisphaerica	x	x	x	x	x	? x		
cf. *Aberlemnia* (*Cooksonia*) *caledonica*	x	x			x	? x		
Tarrantia salopensis	x	x	x	x				
Salopella allenii	x	x			x	x		
Salopella marcensis	x	x	x (cf.)		?x			
Tortilicaulis offaeus	x (cf.)		x		?x			
Tortilicaulis transwalliensis		x		x				
Uskiella reticulata		x			?x			
Cooksonia banksii			x					
Culullitheca richardsonii			x					
Fusiformitheca fanningiae			x					
Grisellatheca salopensis			x					
cf. *Horneophyton* sp.			x					
Resilitheca salopensis			x					
Sporathylacium salopense			x					
cf. *Sporogonites*			x					
Pertonella sp.			x					
Paracooksonia spp.			x					
Lenticulatheca spp.			x					
Partitatheca spp.			x					
Ficoiditheca aenigma			x					
Zosterophyllum cf. *fertile*				x	x		x	x
Monnowella bennettii					x			
Craswallia haegensis					x			
Zosterophyllum sp.						x		
Deheubarthia splendens							x	x
Gosslingia breconensis							x	
Uskiella spargens							x	
Dawsonites sp.								x
Zosterophyllum llanoveranum								x

Table 6. Lochkovian megafossils from the Anglo-Welsh Basin. Compiled from the following references: [1]Tredomen Quarry: Morris et al. 2011a. [2]Targrove: Lang, 1937; Edwards and Fanning, 1985; Fanning et al. 1988, 1992; Morris 2009. [3]North Brown Clee Hill: Fanning et al. 1988; Edwards et al. 1994; Edwards et al. 1995a, b; Edwards 1996; Wellman et al. 1998a; Edwards et al. 1999; Edwards and Richardson 2000; Edwards et al. 2001; Habgood et al. 2002; Morris et al. 2011b; Morris et al. 2012a; Edwards et al. 2012a; Edwards et al. 2014. [4]Brynglas Tunnels, Newport: Wellman et al. 2000. [5]Craswall Quarry: this paper. [6]Newton Dingle: Edwards and Richardson 1974; this paper. [7]Allt Ddu: Kenrick 1988; Edwards et al. 1989. [8]Mascle Bridge Quarry: Kenrick 1988; Edwards et al. 1989; Wellman et al. 1998b. MN = *micrornatus – newportensis* Spore Assemblage Biozone; BZ = *breconensis - zavallatus* Spore Assemblage Biozone.

Locality	Geographical area	Stratigraphic unit		Biozone/Age	Taphofacies
Tredomen Quarry	Brecon Beacons	Milford Haven Subgroup	Freshwater West Formation	lower MN Biozone; early Lochkovian	Compressions in distal fluviatile channel siltstones and sandstones[1]
Targrove	Clee Hills, Shropshire				Compressions in distal fluviatile channel and crevasse splay siltstones and sandstones[2, 3]
North Brown Clee Hill	Clee Hills, Shropshire			middle MN Biozone; middle Lochkovian	Charcoal in distal fluviatile siltstones[4]
Brynglas Tunnels	South Wales				Compressions in distal fluviatile siltstones[5]
Cwm Mill	Black Mountains			?middle MN Biozone; middle Lochkovian	Compressions in distal fluviatile siltstones[6]
Craswall	Black Mountains			?middle-upper MN Biozone, middle-upper Lochkovian	Compressions in medial fluviatile siltstones and sandstones[7]
Newton Dingle	Clee Hills, Shropshire			?upper MN to BZ Biozone, late Lochkovian	Compressions in medial fluviatile sandstones[8]
Allt Ddu	Beacon Beacons	Cosheston Subgroup	Senni Formation	BZ Biozone, late Lochkovian	Compressions in medial fluviatile siltstones and sandstones[9]
Mascle Bridge Quarry	Pembrokeshire		Llanstadwell Formation		Compressions and permineralisations in medial fluviatile silty sandstones[10]

Table 7. Lochkovian assemblages from the Anglo-Welsh Basin. [1]Morris et al. 2011a; [2]Fanning et al. 1992; [3]Morris, 2009; [4]Edwards et al. 1994; [5]Wellman et al. 2000; [6]Kenrick, 1988; [7]this paper; [8]Edwards and Richardson, 1974; [9, 10]Edwards et al. 1989.

Figure 1. A) Map of South Wales and the Welsh Borderland illustrating the Lower

Old Red Sandstone (Přídolí to Lower Devonian) outcrops, with Lochkovian

palaeobotanical localities marked. TM = Tredomen Quarry; TR = Targrove;

NBCH = North Brown Clee Hill; BT = Brynglas Tunnels, Newport; CM = Cwm Mill;

ND = Newton Dingle; CR = Craswall; AD = Allt Ddu; MBQ = Mascle Bridge

Quarry. Dashed square indicates study area. B) Map for Craswall locality

(starred). Grey shading = Brecon Beacons National Park.
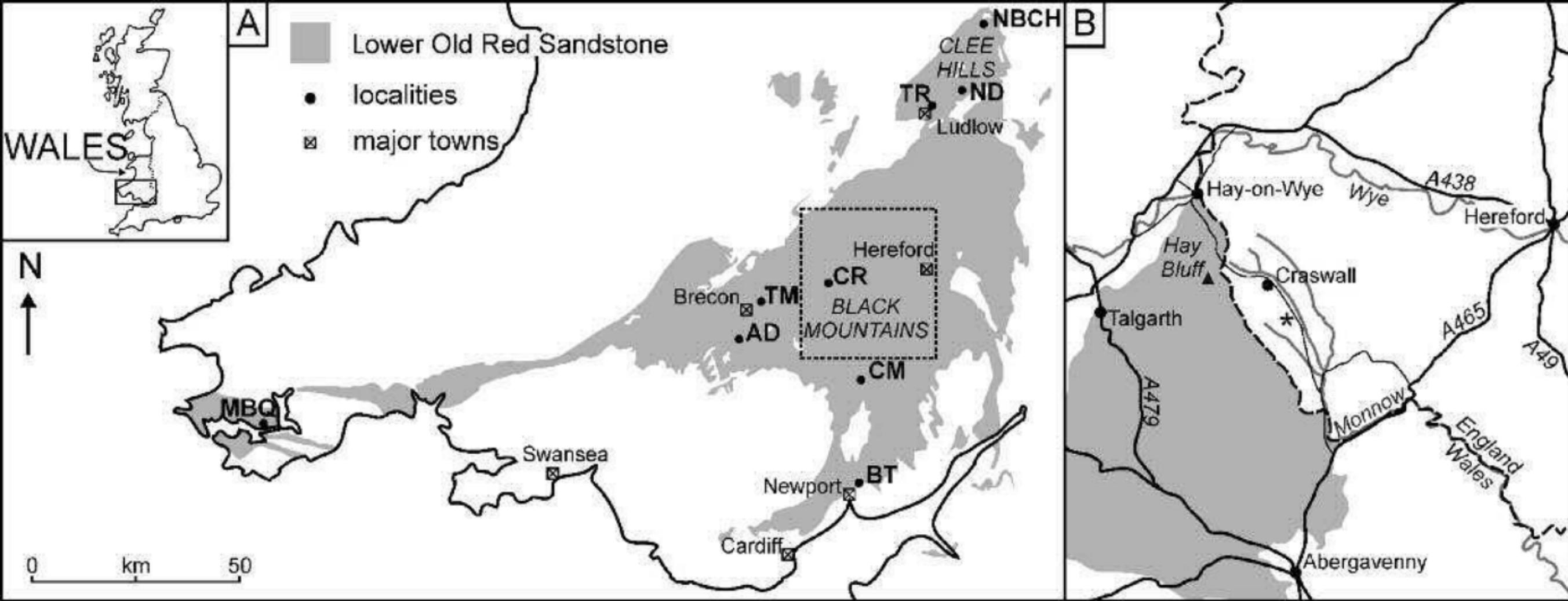
Figure 2. Stratigraphic chart after Barclay et al. in press, with Lochkovian

palaeobotanical localities marked. See Figure 1 for location abbreviations.

Age(My)	Stage	Vertebrate zonation scheme	Spore zonation scheme	Unit	Pembrokeshire (N of Ritec Fault)	Brecon Beacons/Black Mts/South Wales	Clee Hills Shropshire
407.6	PRAGIAN	(dunesis)	PE	Cossheston Subgroup	Mill Bay Formation	Senni Formation	
410.8	LOCHKOVIAN	leachi	BZ		Llanstadwell Formation ● MBQ	● AD	● ND
		crouchi	uMN	Milford Haven Subgroup		● CR ● CM ● BT	● NBCH
		leathensis	mMN				● TR
			lMN		Freshwater West Formation	● TM	
419.2		symondsi	A. sp E		Moor Cliffs Formation		
		pococki					

EARLY DEVONIAN

Figure 3. Outlines of fertile specimens from Craswall.

Type 1a: Intermediate cooksonioid sporangia. 1) & 2) V.68526. Type 1b: *Monnowella bennettii* gen. et sp. nov. 1) V.68559. 2) V.68528. 3) V.68562. 4) V.68561. 5) V.68561. 6) V.68546. 7) V.68550. 8) V.68535. 9) V.68550. 10) V.68550. 11) V.68561. 12) V.68535. 13) CR119A-2. 14) V.68543. 15) V.68546. 16) V.68548. 17) V.68550. 18) V.68562. 19) V.68534. 20) V.68537. 21) V.68561. 22) V.68534. 23) V.68557. 24) V.68550. 25) V.68548. 26) V.68561. 27) V.68562. 28) V.68562. 29) V.68539. 30) V.68567. 31) V.68568. Type 1c: 1) – 3) *Cooksonia hemispherica*. 1) V.68549. 2) V.68544. 3) V.68535. Type 1d: Other *Cooksonia* and cooksonioid specimens. 1) – 2) *Cooksonia* cf. *pertoni*. 1) V.68550. 2) V.68563. 3) - 7) *Cooksonia* cf. *cambrensis*. 3) V.68550. 4) V.68549. 5) V.68551. 6) V.68550. 7) V.68540. 8) – 9) Cooksonioid mesofossils. 8) V.68550. 9) V.68566. Type 1e: 'Zosterophylloid' sporangia. 1) V.68527. 2) V.68535. 3) V.68542. 4) V.68527. 5).68539. 6) CR083-1. 7) V.68544. 8) V.68532. Type 1f: *Aberlemnia* sp. V.68567. Type 2d: 'Urn shaped' sporangia. V.68563.

Type 1b: *Monnowella bennettii* gen. et sp. nov.
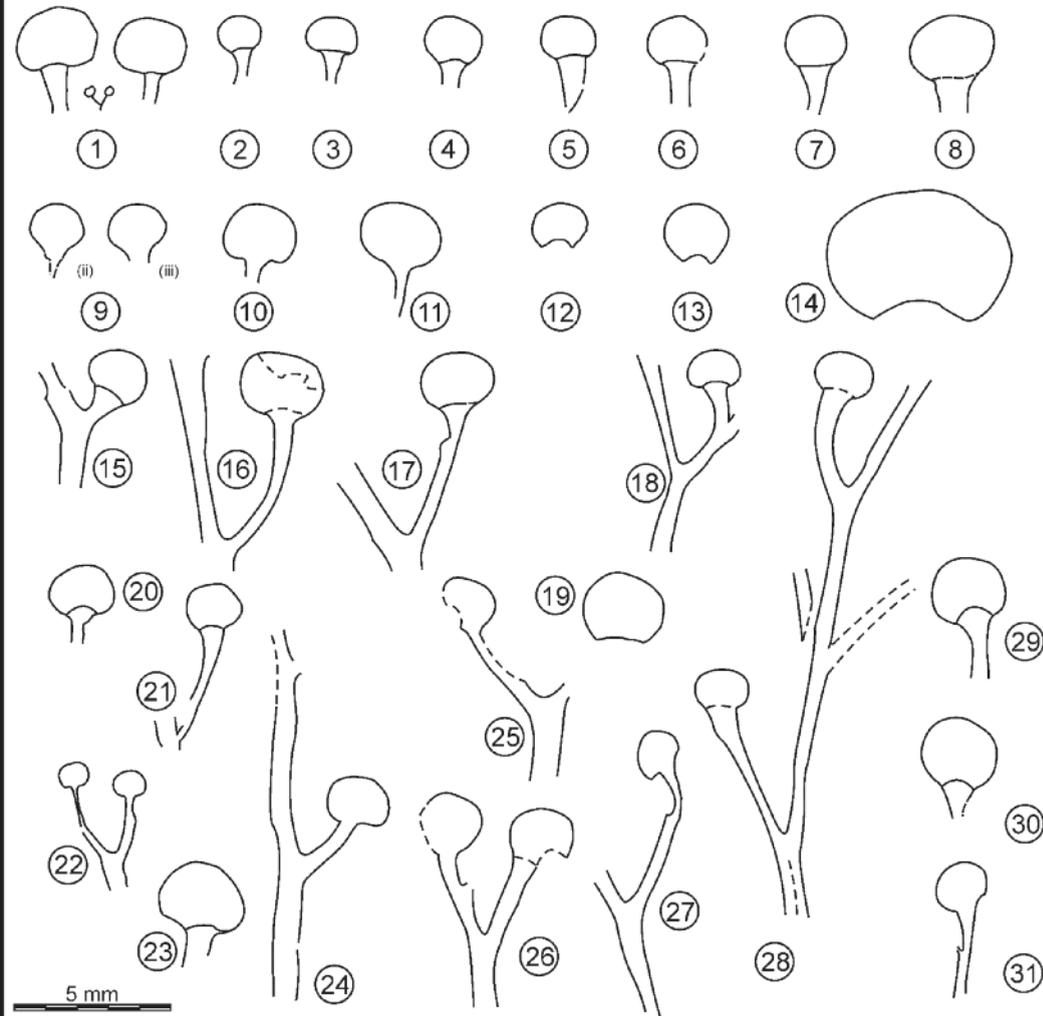
Type 2d
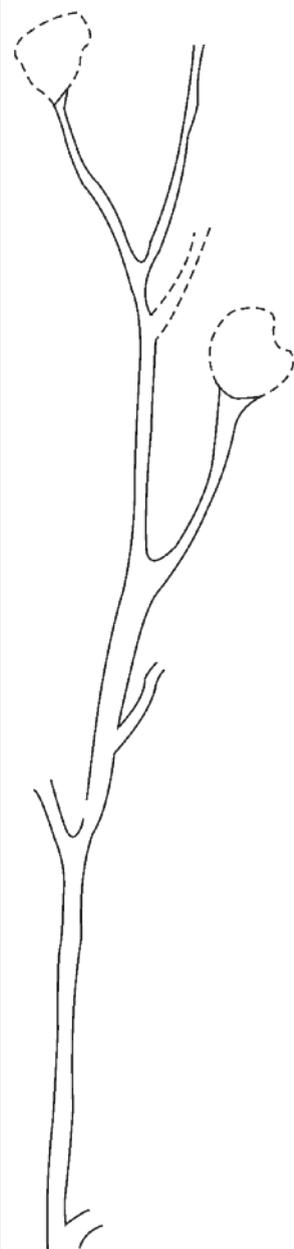
Type 1a : indeterminate cooksonioid
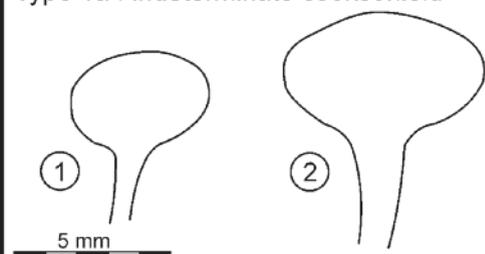
Type 1c: *Cooksonia hemisphaerica*
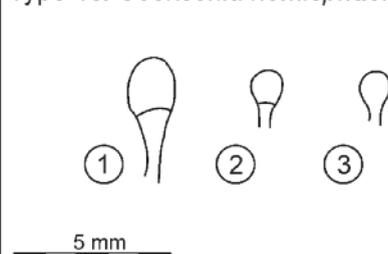
Type 1d: Other *Cooksonia* spp.
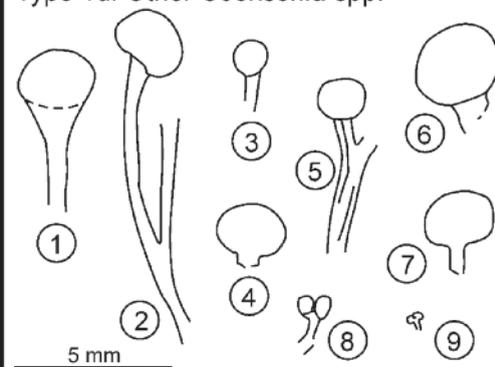
Type 1e: "Zosterophylloid" sporangia
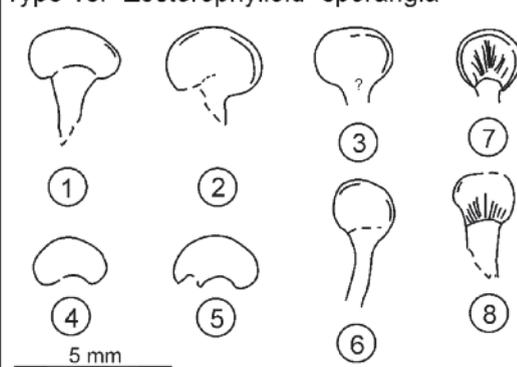
Type 1f: *Aberlemnia* sp.
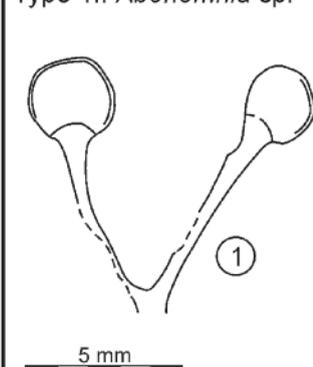
Figure 4. Outlines of indeterminate cooksonioids from Craswall. 1) V.68550. 2)

V.68551. 3) V.68538.

Indeterminate cooksonioids

1

2 mm

2

3
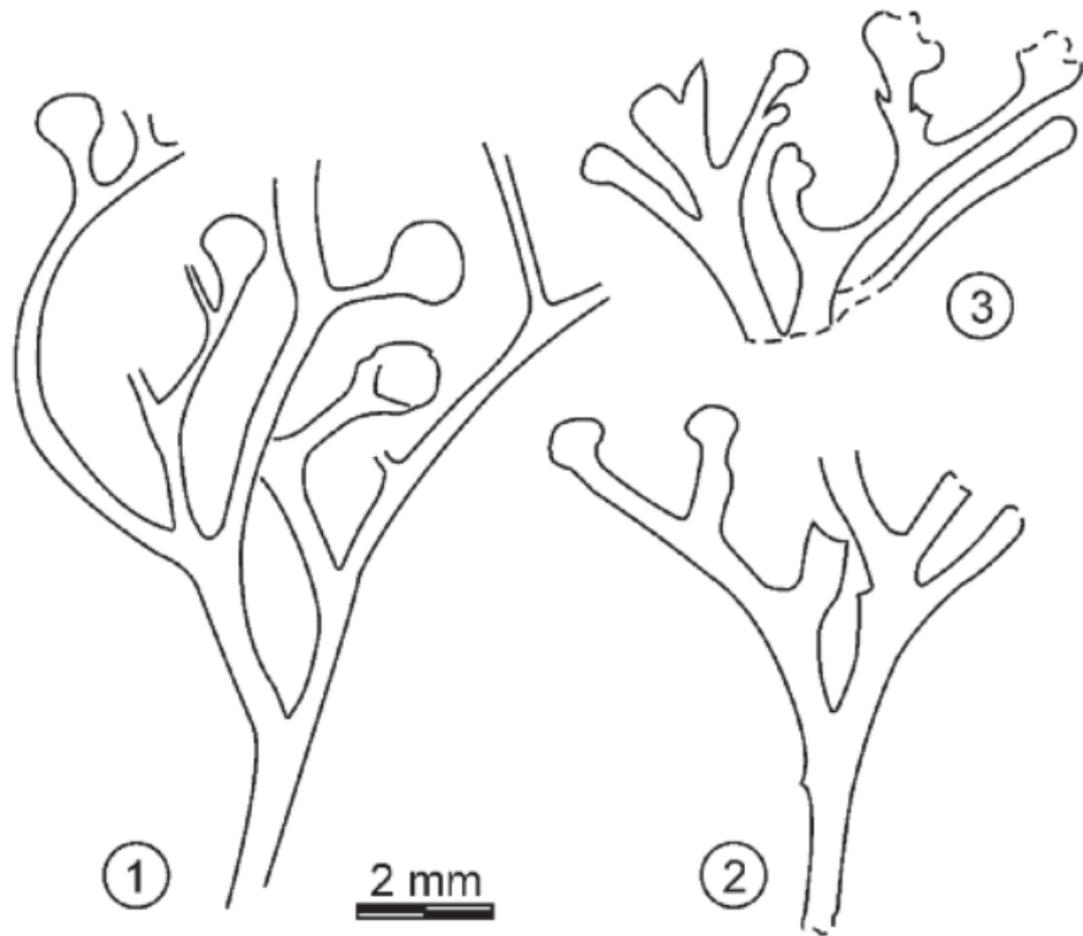
Figure 5. Outlines of sporangia that are longer than wide from Craswall. Type 2a: *Salopella allenii*: 1) V.68568. 2) V.68565. 3) V.68568. 4) V.68561. 5) V.68567. 6) V.68568. 7) V.68547. 8) V.68548. 9) V.68548. 10) V.68552. 11) V.68552. 12) V.68558. 13) V.68552. 14) V.68552. 15) V.68553. 16) V.68555. 17) V.68553. 18) V.68554. 19) V.68555. 20) V.68555. 21) V.68558. 22) V.68549. Type 2b: *Salopella/Tortilicaulis* sp.: 1) V.68563. Type 2c: Vertically elliptical sporangia: 1) V.68550. 2) V.68556.

Type 2c
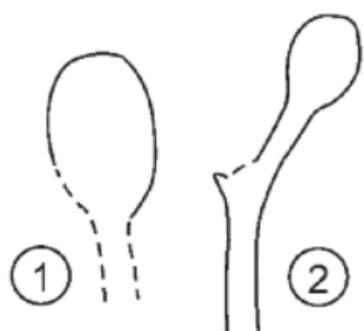
Type 2b

Type 2a: *S. allenii*
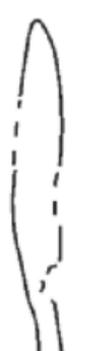
Figure 6. Outlines of laterally borne sporangia from Craswall and Newton Dingle. Darker shade of grey indicates sporangial material. Type 3a: *Zosterophyllum* strobili from Craswall. 1) V.68564. 2) V.68549. 3) V.68529. 4) V.68545. 5) V.68557. 6) V.68560. 7) V.68561. 8) V.68567. 9) V.68557. 10) V.68553. Type 3b: *Craswallia haegensis* gen. et sp. nov., from Craswall. V.68527. Type 3c: *Zosterophyllum* sp. from Newton Dingle. 1) V.68581. 2) V.68582.

Type 3a: *Zosterophyllum* strobili

① ② ③ ④ ⑤ ⑥ ⑦ ⑧ ⑨ ⑩

5 mm

Type 3b: *Craswallia haegensis* gen. et sp. nov.

1 cm
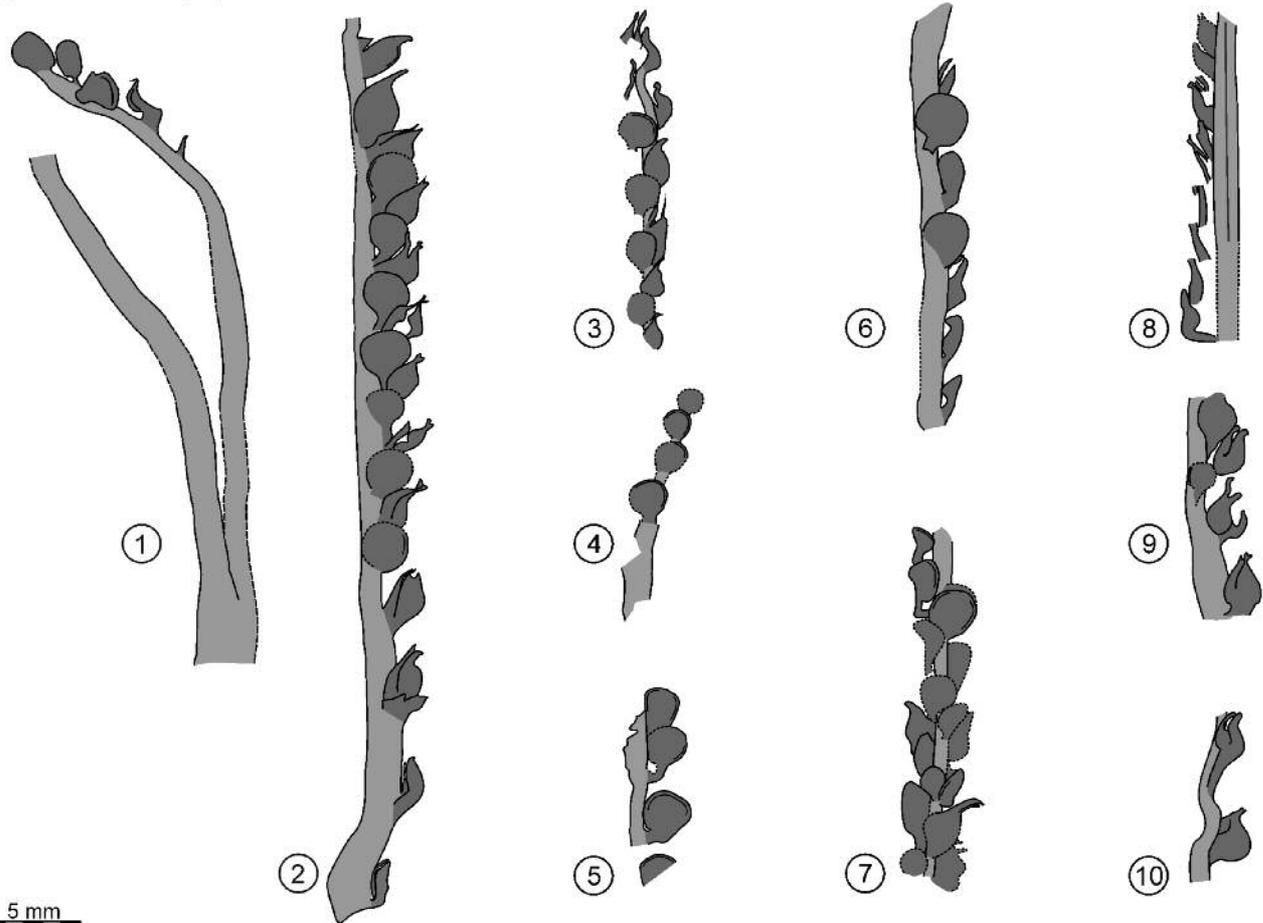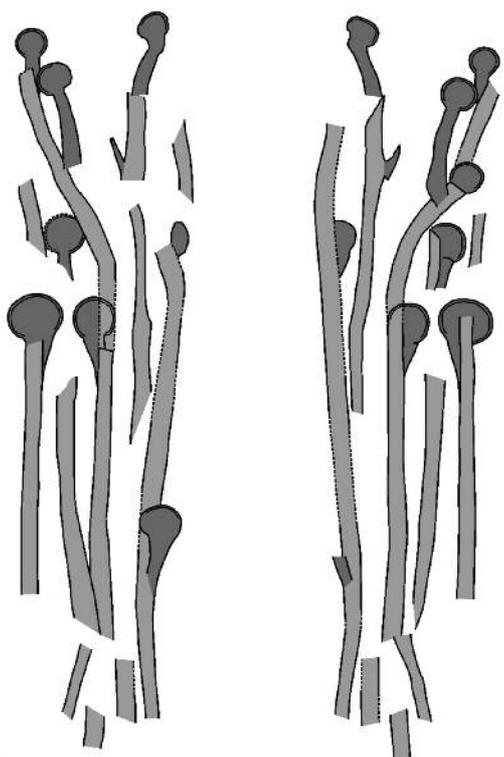
Type 3c: *Zosterophyllum* from Newton Dingle

① ②

1 cm
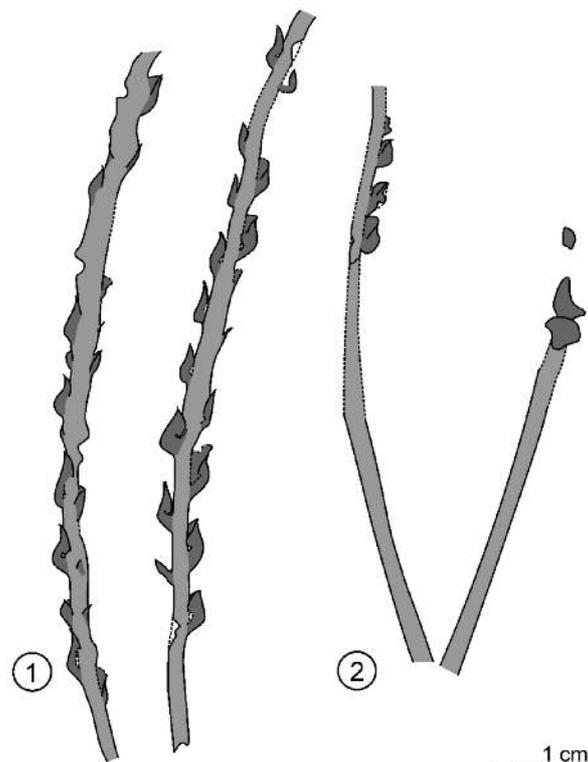
Plate I. Assemblage overview and sterile axes from Craswall. 1) Plant fragments preserved in a conglomeratic sandstone; V.68533. 2) Sandstone bedding planes packed with fossils; V.68530. 3) Higher plant axes intermingled with nematophytes fragments; V.68535. 4) Parallel-aligned sterile axes; V.68527. 5) Disordered alignment of axes; V.68550. 6) Long flexuous sterile axis; V.68528. 7) Isotomously branched wide axis; V.68528. 8) Anisotomously branched wide axis, with two close dichotomies; V.68554. 9) Wide axis with central strand (arrow); V.68527. 10) & 11) Isotomously branched narrow axes. 10) V.68527. 11) V.68527. 12) Anisotomously branched narrow axis; V.68539. 13) Anisotomously branched narrow axis; V.68546. 14) Alignment of axes on one side; V.68539. 15) - 17) Highly branched narrow axes; 15) V.68537. Possible terminal sporangium arrowed. 16) V.68538. 17). V.68548. 18) H branching; V.68567. 19) Condensed branching; V.68550. Scale bars: 1), 3), 6), 9), 10), 14) = 1 cm. 7), 8), 12), 13) = 0.5 cm. 2), 4), 5), 11), 15), 17), 18) = 2 cm. 16), 19) = 0.2 cm.
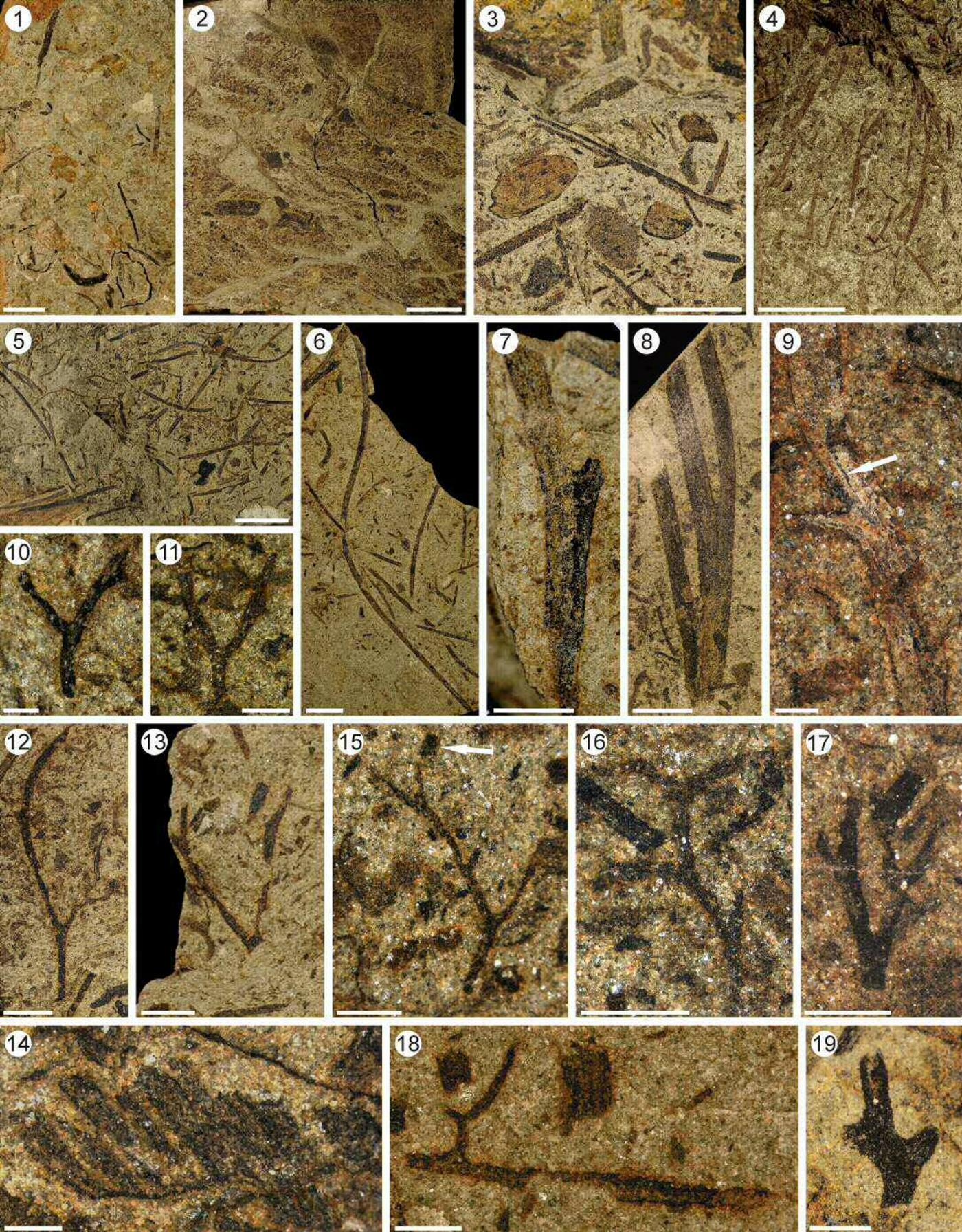
Plate II. Fertile specimens from Craswall; indeterminate cooksonioid sporangia and *Monnowella bennettii* gen. et sp. nov. 1) – 3) Type 1a: Indeterminate cooksonioid sporangia; V.68526. 1) Arrow a marks possible dichotomy. Arrow b indicates aligned stems that likely were once continuous. 2) Magnification of right-hand sporangium. 3) Magnification of left-hand sporangium. 4) - 15) Type 1b: *Monnowella bennettii* gen. et sp. nov. 4) – 5) Isolated sporangium. 4) V.68534. 5) V.68541. 6) – 8) Sporangia on short subtending axes. 6) V.68528. 7) V.68561. 8) V.68557. 9) Three closely associated stems with terminal sporangia; V.68550. Arrow indicates well-defined junction between sporangium and stem. 10) Isotomously branched axes, with slight overtopping, terminated by cooksonioid sporangia; V.68534. 11) – 14) Anisotomously branched axes with terminal sporangia. 11) V.68548. 12) V.68548. 13) V.68562 (holotype, part). 14) V.68562 (holotype, counterpart). Arrows indicate position of sporangia. 15) V.68550. Scale bars: 1) = 1 cm; 2) – 3), 8) – 9), 11) - 15) = 2 mm; 4) – 7), 10) = 1 mm.
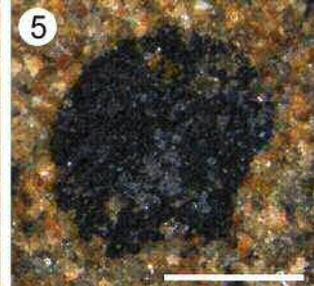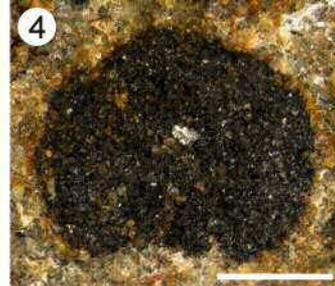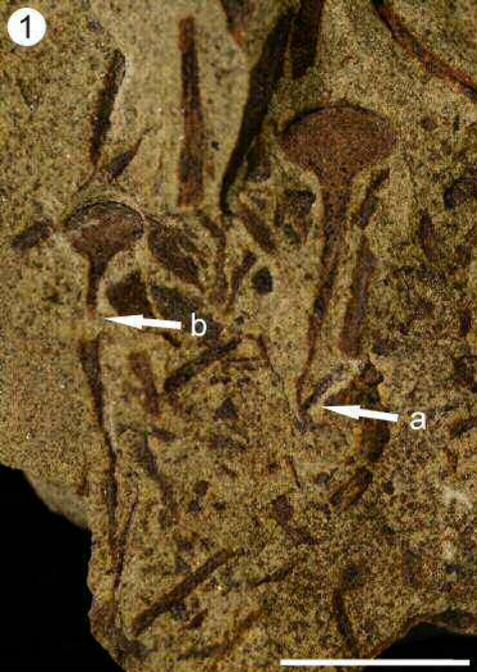
Plate III. Fertile specimens from Craswall; *Cooksonia hemispherica* and other *Cooksonia* and cooksonioid sporangia. 1) - 3) *Cooksonia hemisphaerica.* 1) V.68549. 2) V.68544A. 3) V.68535. 4) - 7) *Cooksonia* cf. *pertoni*; 4) – 5) V.68550. 5) Magnification of sporangium after dégagement. 6) V.68563. Isotomously branched specimen with terminal elliptical sporangium. 7) V.68550. 8) – 12) *Cooksonia* cf. *cambrensis*. 8) V.68550. 9) V.68540. 10) V.68551. 11) Magnification of sporangium and subtending axis illustrated in 10. Note central strand within axis (arrow). 12) V.68550. 13) - 14) Cooksonioid mesofossils. 13) V.68550. 14) V.68556. 15) – 17) Indeterminate cooksonioids. 15) V.68550. Arrow a = putative sporangium with diffuse outline. Arrow b = sporangium with well-defined outline. 16) V.68551. Arrow indicates possible sporangium. 17) V.68538. Arrow indicates possible sporangium. Scale bars: 1), 4), 5), 6), 7), 10), 12), 15), 16), 17) = 2 mm; 2), 3), 8), 9), 11), 14) = 1 mm; 13) = 500 μm.
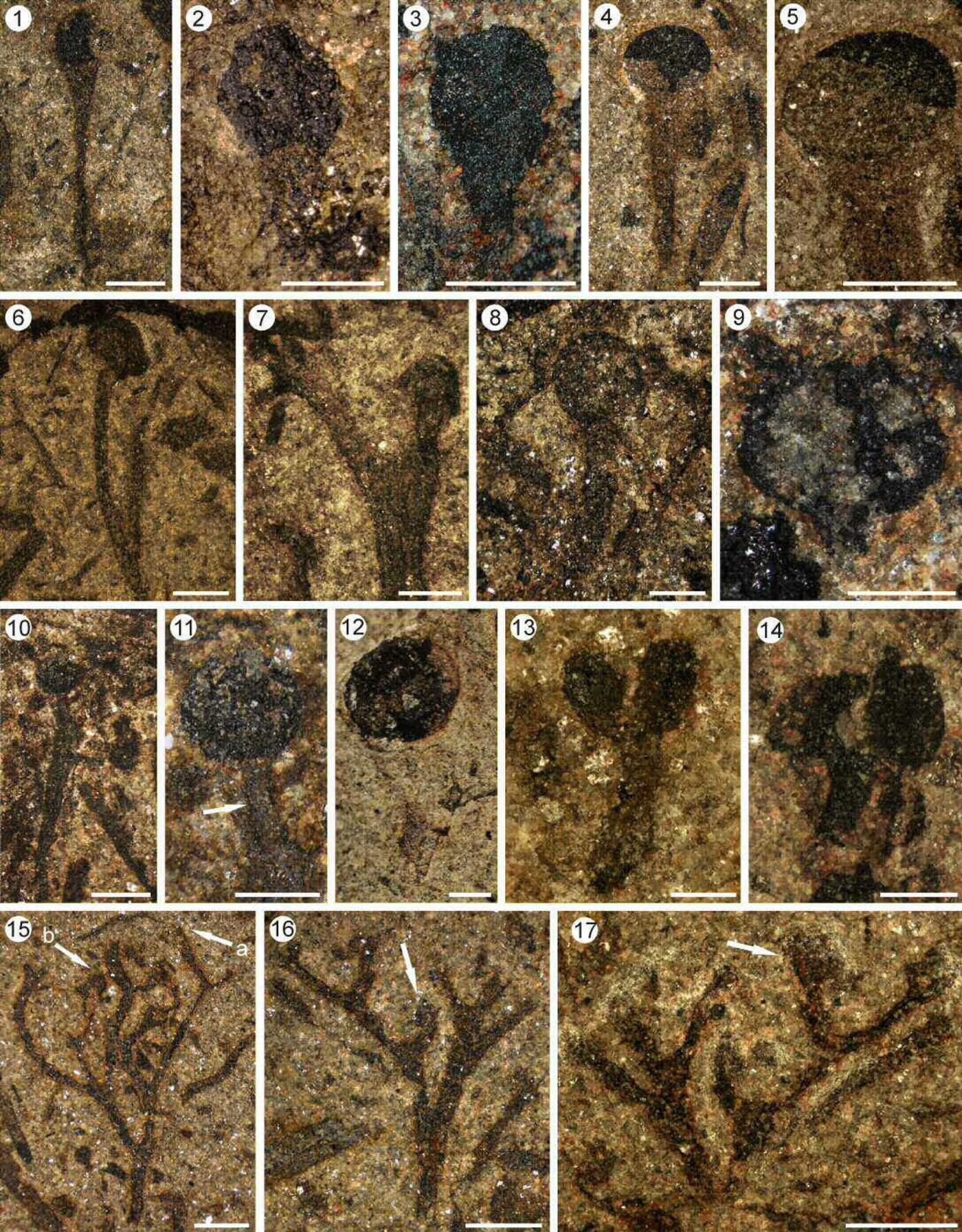
Plate IV. Fertile specimens from Craswall.

1) – 9) 'Zosterophylloid' sporangia. 1) V.68527A. 2) V.68535. 3) V.68542. 4) V.68527A. 5) V.68539. 6) - 8) V.68544. Arrow in 6 indicates possible branch point. 9) V.68532. 10) – 11) *Aberlemnia* sp. 10) Isotomously branched axes terminated by cooksonioid sporangia. V.68567. 11) Close up of sporangium with peripheral zone of persistent coalified material. Counterpart of specimen illustrated in 10). Scale bars: 1) - 4), 6), 9), 11) = 1 mm; 5), 10) = 5 mm; 7), 8) = 0.5 mm.
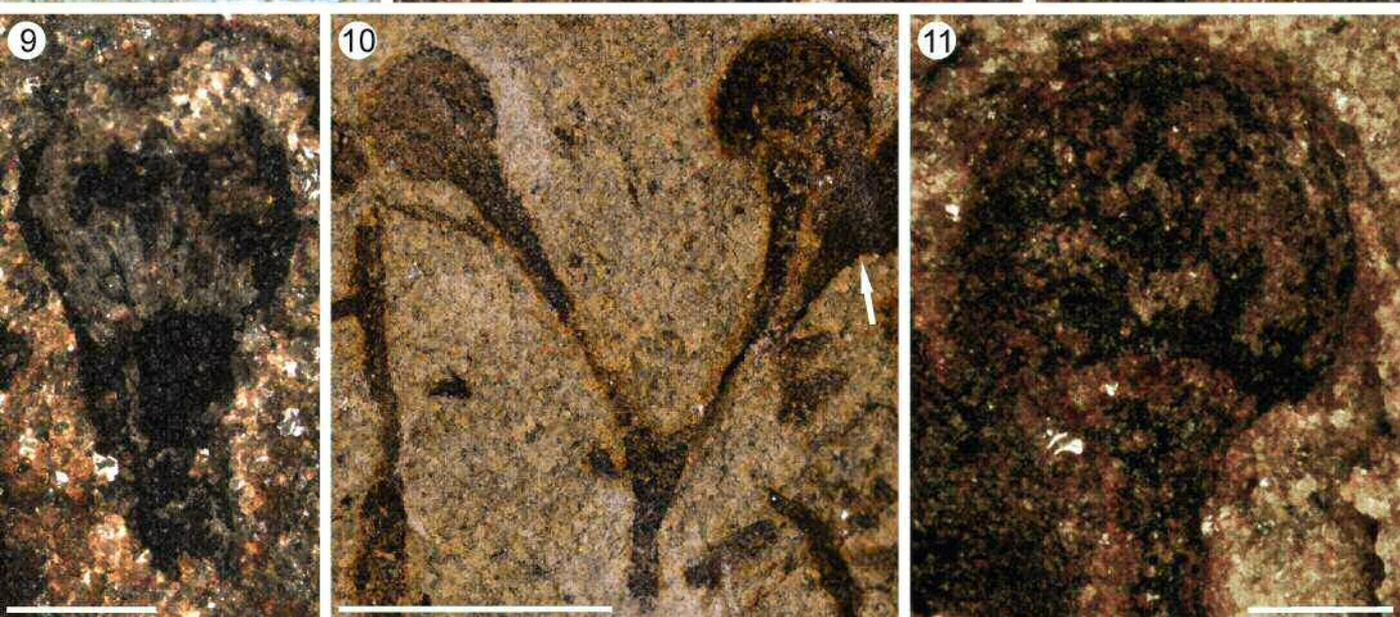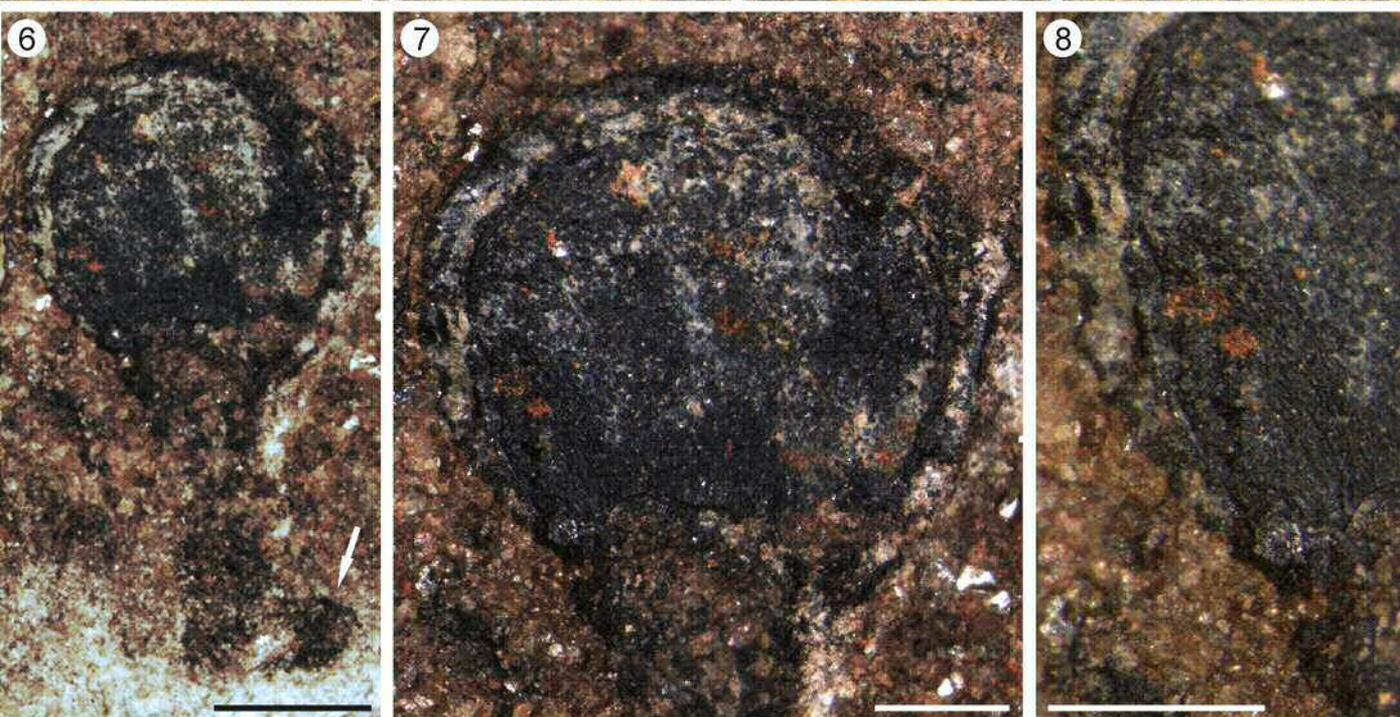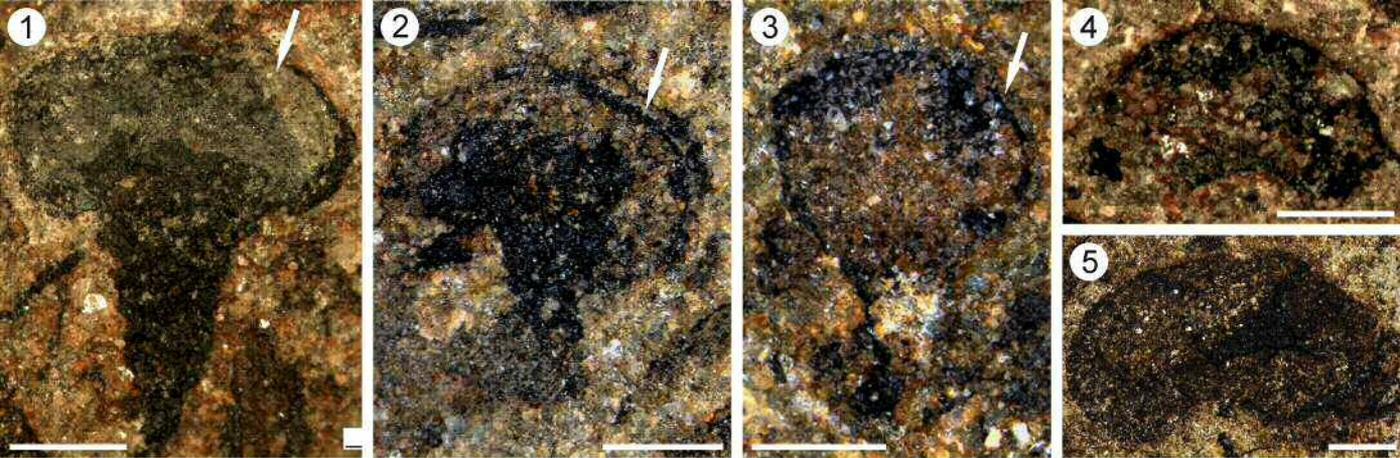
Plate V. Fertile specimens from Craswall.

1) –17) *Salopella allenii*. 1) Narrow, spear-shaped sporangium with pointed tip and a difference in coal thickness between the sporogeneous area and the subtending stem; V.68536. 2) Narrow, spear-shaped sporangium; V.68548. 3) Narrow sporangium, with obliquely orientated longitudinal striations and slight constriction at base; V.68552. 4) Sporangium with pointed tip; V.68552. 5) Broad sporangium with rounded tip; V.68531. 6) Broad sporangium with rounded tip; V.68552. 7) Three-dimensionally preserved sporangial tip, producing a pointed, solid cone; V.68534. 8) Magnification of rounded tip; V.68531. 9) Constriction in stem directly beneath sporangium. Stem with longitudinal central strand (arrow); V.68550. 10) Rare branching of fertile stems; V.68558. 11) Sporangial surface with obliquely orientated longitudinal striations; V.68552. 12) Outlines of sporangial wall cells; V.68535. 13) & 14) Splits through sporangial walls (arrows), possibly for dehiscence. 13) V.68547. 14) V.68537. 15) – 17) Examples of short lengths of fertile stems that are approximately the same level and orientated such that it is likely they are attached. 15) V.68549. 16) Slightly anisotomously branched fertile stem; V.68565. 17) At least four closely associated fertile stems; V.68531. Scale bars: 1) - 8), 11), 12) = 1 mm; 9), 10) 13), 14), 15) = 2 mm; 16), 17) = 5 mm.
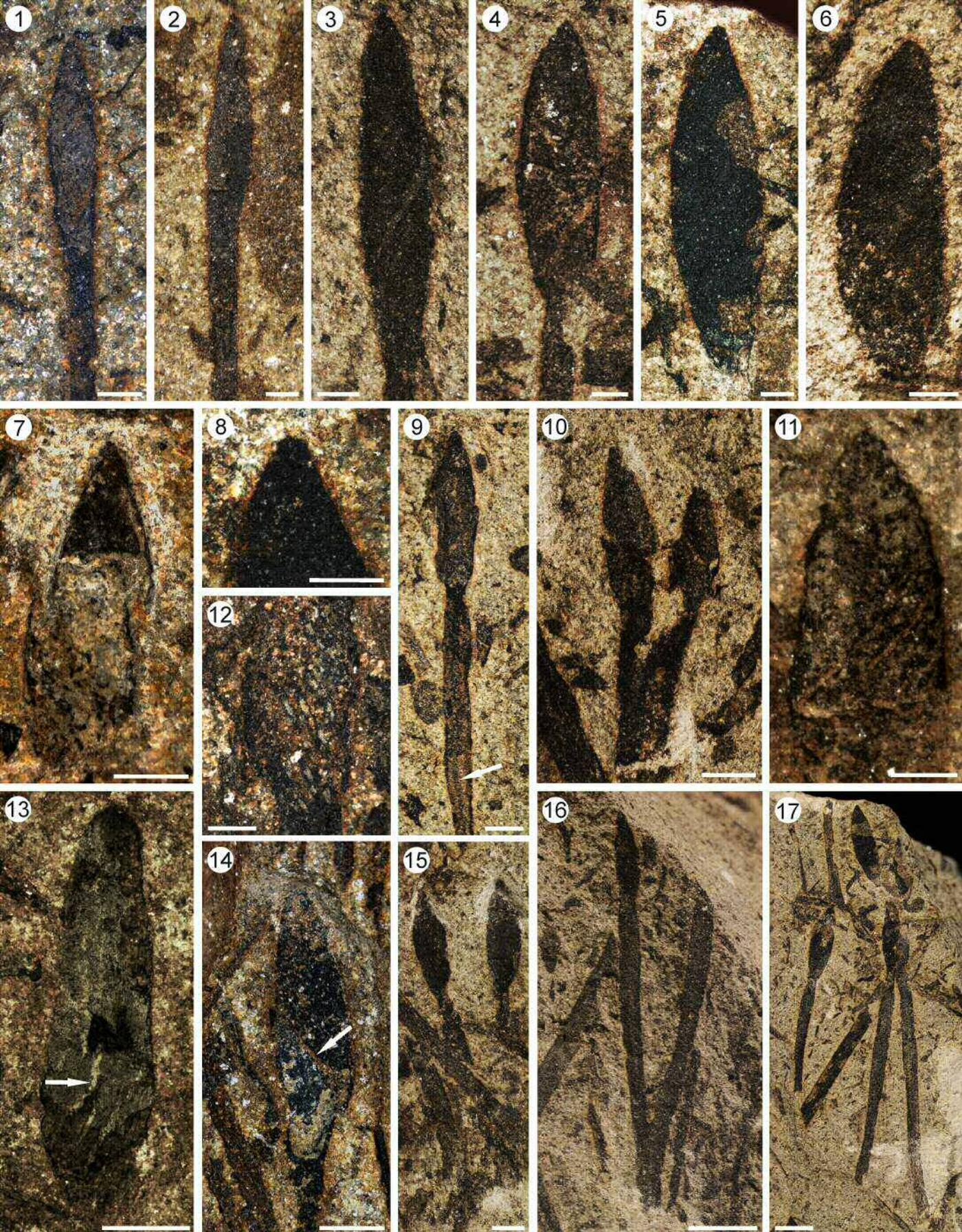
Plate VI. SEM images. 1) – 9) *Salopella allenii* from Craswall. 1) & 2) Sporangial walls. Traces of cells represented by longitudinal striations (arrows). 3) Compressed spores revealed underneath sporangial wall, associated with numerous pyrite crystals (arrow). 4) – 6) Compressed spores revealed beneath sporangial walls, associated with framboidal granular material (arrows). 7) Spores with smooth walls (arrow). 8) & 9) Spore surfaces pitted from cuboid pyrite crystals. 1), 2), 7) - 9) = V.68561. 3) - 6) = V.68552. Scale bars: 1), 2) = 50 μm. 3), 4) = 20 μm. 5), 7) - 9) = 10 μm. 6) = 2 μm.
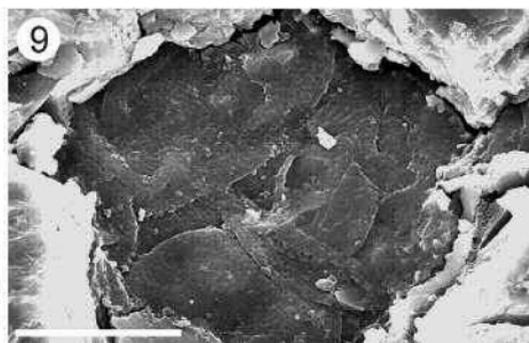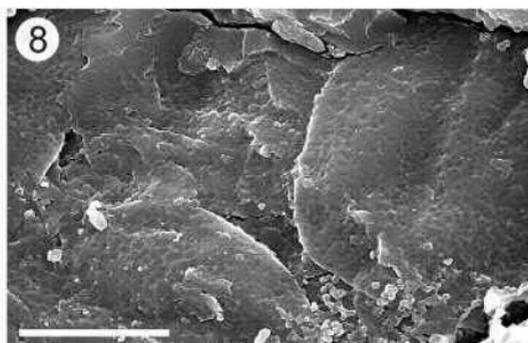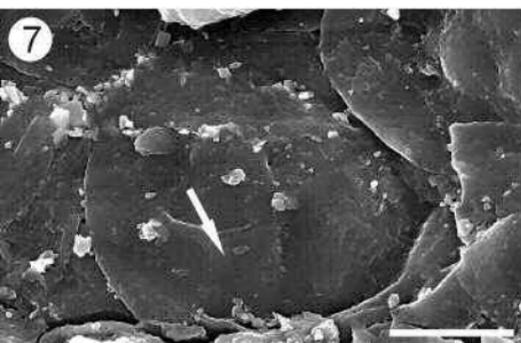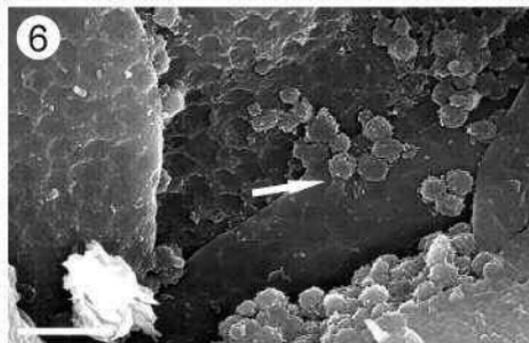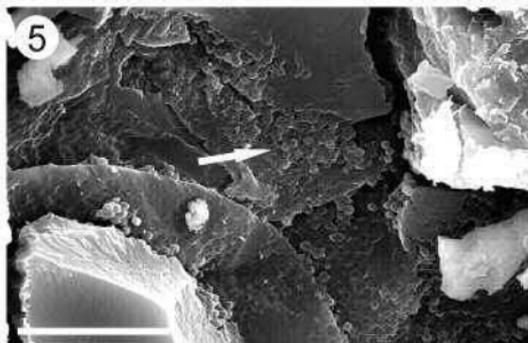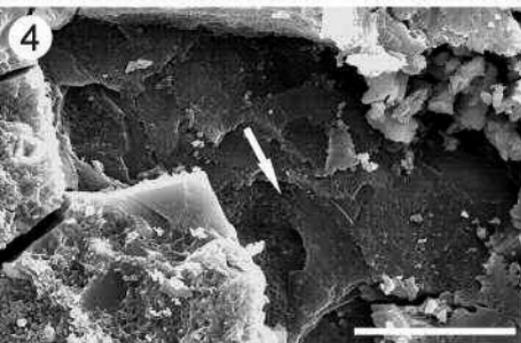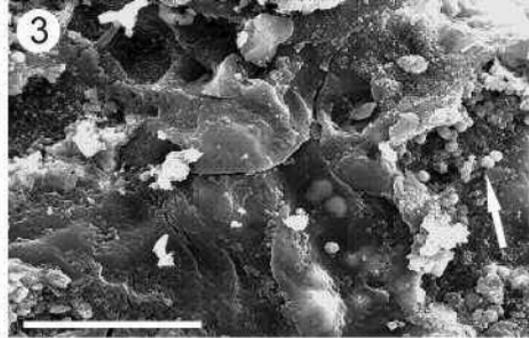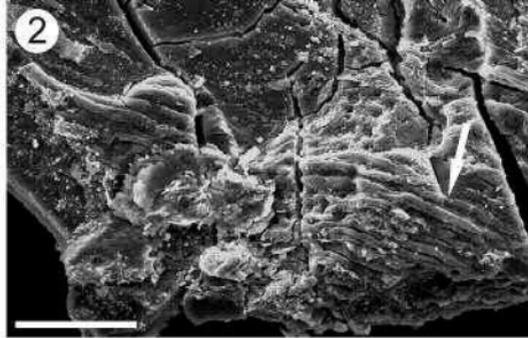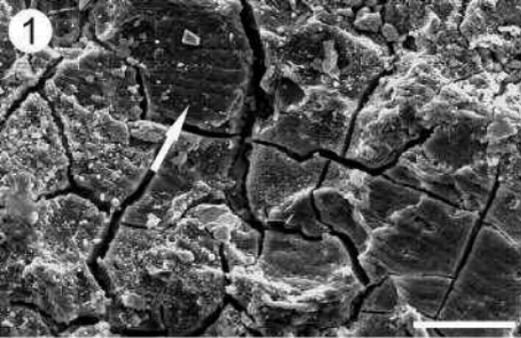
Plate VII. 1) – 4) *Salopella/Tortilicaulis* sp. from Craswall. 1) - 3) Dichotomously branched fertile stem; V.68563. 2) Magnification of right-hand sporangium, with acuminate tip. 3) Magnification of left-hand sporangium. 4) Narrow, spear-shaped sporangium; V.68568. 5) -7) Vertically elliptical sporangia. 5) & 6) V.68550. Arrows indicate possible position of two further branches. 6) Magnification of sporangium. Arrow indicates shallow grove running along the distal margin. 7) V.68556. 8 - 11) 'Urn-shaped' sporangia, attached to highly branched axis. V.68563. 8) Magnification of sporangium from 10). 9) Magnification of sporangium from 11). 10), 11) Whole specimen. Arrows indicate additional uncovered sporangium. Scale bars: 1), 5), 7) = 2 mm; 2) - 4), 6), 8), 9) = 1 mm; 5), 10), 11) = 5 mm.
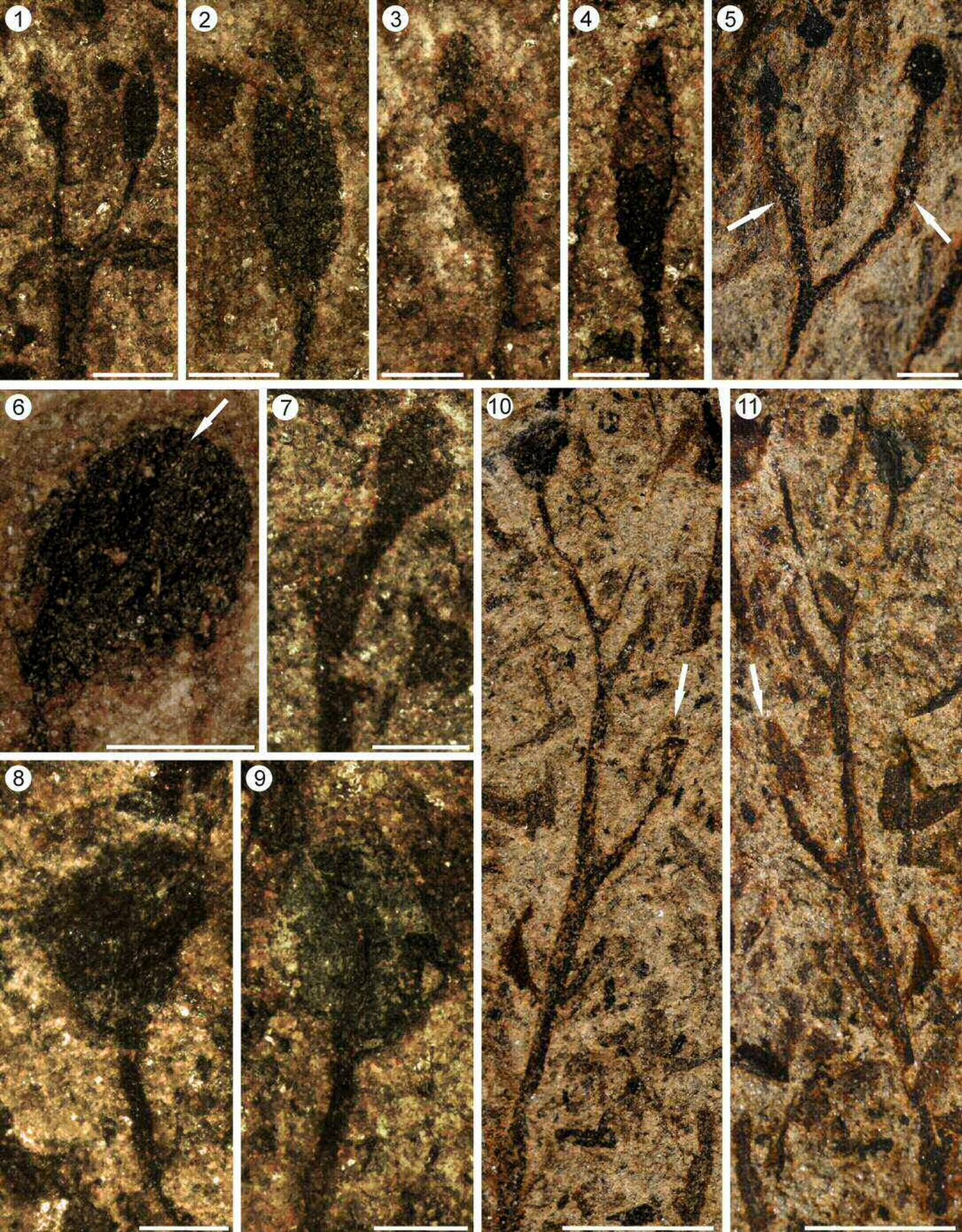
Plate VIII. *Zosterophyllum* strobili from Craswall.

1) V.68564. Whole specimen; branched smooth axis terminated with strobilus. 2) V.68549. Axis with terminal strobilus. 3) – 5) Sporangia with marginal borders. 3) V.68564. 4). V.68529. 5) V.68545. 6) V.68529. Two rows of sporangia, no indication of a strobilar axis. 7) V.68560. Two rows of sporangia on one side of a strobilar axis, with straight edge on other side. 8) & 9) Two rows of sporangia, one row in face view, the other in side view (arrowed). 8) V.68549. 9) V.68549. 10) V.68545. Small fragment of a single row of sporangia in face view. 11) Strobilar axis with crowded and overlapping sporangia. V.68561. 12) Elliptically shaped sporangium; V.68560. 13) Sporangium with marginal border, with short stalk attached to stem; V.68557. 14) & 15) Sporangia, with concave abaxial margins. 14) V.68564. 15) V.68549. 16) & 17) Sporangia attached to short stalks which are curved distally so that valves are held upright. 16) V.68553. 17) V.68549. Scale bars: 1), 2) = 5 mm; 3) - 5), 12) - 14), 16), 17) = 1 mm; 6) - 11), 15) = 2 mm.
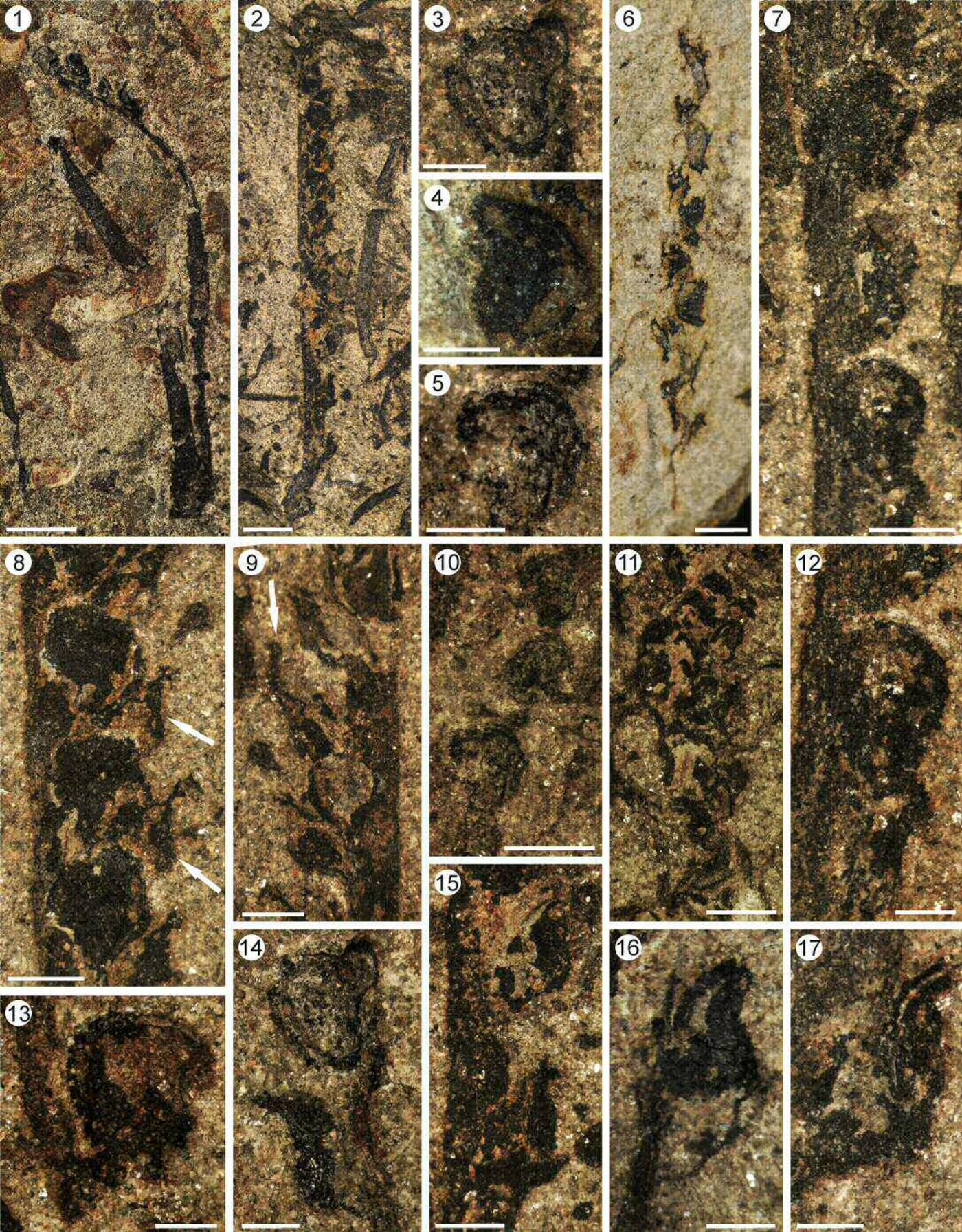
Plate IX. *Craswallia haegensis* gen. et sp. nov. V.68527, from Craswall. 1) & 2)

Whole specimen, part and counterpart. 3) Fertile region of specimen

(counterpart), with small, circular sporangia. 4) Sporangium attached via

sporangial stalk to main stem. 5) Same sporangium as shown in 4, after the main

stem has partially been removed to reveal more of the sporangium beneath. 6)

Magnification of a sporangium margin, with broad conspicuous border. 7)

Smallest sporangia in the most distal region of the specimen, with circular shape.

Scale bars 1, 2, 3 = 1 cm; 4, 5, 6 = 1 mm; 7 = 2 mm.
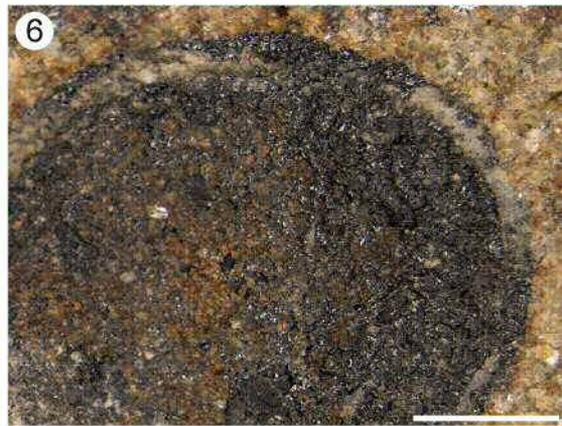
Plate X. Newton Dingle assemblage. 1) – 8) Naked sterile axes and axial-like fragments. 1) Longest sterile axis with central strand; V.68579. 2) Siltstone bedding plane packed with plant debris and malachite; V.68578. 3) Axis delimited by coalified bands; V.68575. Arrow indicates central strand. 4) & 5) Isotomous branching axes. 4) V.68575. 5) V.68580. 6 – 8) *Prototaxites / Nematasketum* complex. 6) V.68574. 7) & 8) V.68576. 9) – 10) Indeterminate fertile material. 9) ?*Cooksonia hemisphaerica*; V.68583. 10) Ellipitical sporangium; V.68577. 11)-13) *Zosterophyllum* sp.; V.68582. 11) Whole specimen. 12) Right hand strobilus. Arrow indicates sporangium in face view. 13) Left hand strobilus. Scale bars: 1), 2) = 1 cm; 3), 10), 12), 13) = 2 mm. 4) - 7), 11) = 5 mm. 9) = 1 mm.

Plate XI. *Zosterophyllum* sp. from Newton Dingle (V.68581).

1) & 2) Whole specimen, part and counterpart. 3) Basal naked portions of axes.

4) Incomplete distal ends of axes. 5) – 7) Axes with laterally-attached sporangia

in two rows on the side. 8) – 10) Magnification of individual sporangia. Scale bars:

1) – 3) = 1 cm; 4), 5) = 5 mm; 6), 7) = 2 mm; 8) – 10) = 1 mm.