A NEW NON-CALCIFIED ALGA FROM THE UPPER SILURIAN OF MID WALES

by DIANNE EDWARDS

ABSTRACT. The alga, *Powysia bassettii* gen. et sp. nov., is described from the early Ludlow Series at Llangammarch Wells, Powys, mid Wales. The most complete specimen consists of a thallus differentiated into holdfast, stipe, and much branched distal region, all of which appear to have a tubular construction. Reproductive structures have not been found. Comparison is made with living and fossil algae, but the precise affinities of these Welsh fossils, in which a thallus of such marked morphological differentiation has an apparently simple internal structure, remain unresolved.

IN 1972, while collecting Silurian graptolites on a field excursion to the Builth Wells-Llangammarch Wells area of Powys in mid Wales, members of the Brecon County Naturalists Trust, led by Dr. M. G. Bassett, discovered two specimens in part and counterpart of a branching, non-calcified alga. The material came from an old quarry on the side of the road running eastwards along the south bank of the River Irfon, 250 m SE. of Llangammarch Wells Church (SN 9374 4720). Subsequently a third specimen was collected from the same locality. All the specimens came from scree on the quarry floor, but the lithology is undoubtedly that of the *in situ* rock, comprising hard dark grey, flaggy-bedded, slightly calcareous graptolitic siltstones and shales. The plants are preserved mainly as brown or yellow stained impressions but carbonaceous residues of the original thallus are present in some areas. In a few instances iron ?hydroxide casts of small fragments of axes are present. The flattened algae look remarkably like pressed herbarium specimens; the contrast between rock and fossil being enhanced by an area of powdery lighter rock immediately outside the thallus. A similar zone is also seen around some graptolites.

Although associations of graptolites and plants have been described from widely separated late Silurian and early Devonian localities (Bohemia, Obrhel 1962; Australia, Lang and Cookson 1935; Jaeger 1967; Alaska, Churkin *et al.* 1969), they have hitherto been only briefly recorded from Britain (see, for example, Straw 1953, p. 215). The plants from the Llangammarch locality, however, differ from those in previously described associations in that they are non-vascular. An account of the locality is given by Bassett in Baker and Hughes (in press) who list a faunal assemblage indicative of the lower *nilssoni* Zone (Eltonian). The presence of *Monograptus ludensis* (Murchison) in the assemblage possibly suggests that some of the beds may belong to the *ludensis* Zone of the uppermost Wenlock, although *M. ludensis* itself does occur in earliest Ludlow beds elsewhere. Graptolites accompanying the algae on the blocks have been identified by Dr. B. Rickards as follows:

NMW. 72 39G. 1a	*Bohemograptus bohemicus* (Barrande)
	? *Saetograptus varians* (Wood)
NMW. 72 46G. 1	*S. varians* (Wood)
NMW. 72 39G. 2b	*S. varians* (Wood)
	? *Pristiograptus dubius* (Suess)

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SYSTEMATIC PALAEONTOLOGY

Algae INCERTAE SEDIS
Genus POWYSIA gen. nov.

Type species. P. bassettii sp. nov.

Derivation of name. From Powys, the Welsh county.

Diagnosis. Macroscopic non-calcified alga with thallus differentiated into expanded basal region with short cylindrical outgrowths (holdfast), unbranched stipe, and much branched distal region. Branching irregular with axis width decreasing distally. Thallus composed of longitudinally aligned intertwined tubes (siphons or filaments) approximately the same size, numerous in the wider branches and stipe but decreasing to two or three in both the narrow ultimate and the short truncated lateral branches. Reproductive structures not seen.

Powysia bassettii sp. nov.

Plate 110, figs. 1–5; Plate 111, figs. 1–10

Diagnosis. As for genus.

Locality. Llangammarch Wells, Powys, Wales. Quarry opening off south side of road running eastwards along south bank of River Irfon, 250 m SE. of Llangammarch Church (SN 9374 4720). Plants associated with graptolites on darkish grey flaggy-bedded shales; blocks loose on quarry floor. Faunal assemblage indicative of lower *nilssoni* Zone (Eltonian), Ludlow Series, Upper Silurian.

Holotype. Specimens NMW. 72 39G. 1a and 1b. Department of Geology, National Museum of Wales, Cardiff.

Derivation of name. After Dr. M. G. Bassett who found the specimens.

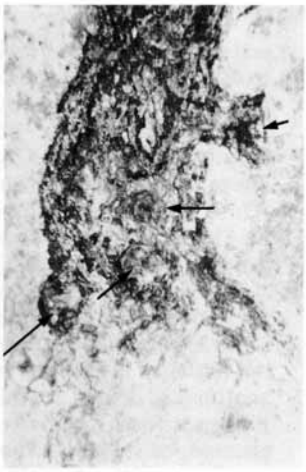
Description of plants. The following account is based on information from all three specimens. That designated the holotype (NMW. 72 39G. 1a) has been most informative for the gross morphology of the alga (Pl. 110, fig. 1). The thallus is differentiated into three regions; an expanded basal part, a short, stout stipe, and a distal much branched 'frond'. Its counterpart (NMW. 72 39G. 1b) was partially destroyed to provide samples for chemical analysis. The most fragmentary specimen (NMW. 72 46G. 1) which lacks a counterpart, has only branch tips present. Much of the evidence for the internal structure of the branches was obtained from the isolated fronds on specimen NMW. 72 39G. 2a and its counterpart (2b).

The slightly expanded region at the base of the stipe is interpreted as a holdfast (Pl. 110, fig. 2). Depressions and protrusions approximately a millimetre in diameter give an irregular appearance to the surface of the plant and the underlying rock

EXPLANATION OF PLATE 110

Figs. 1–5. *Powysia bassettii*. 1, holotype. Note part of graptolite alongside on the left. Arrow indicates central thickened region, ×1·7. 2, basal holdfast region enlarged. Protrusions are arrowed, ×7·1. 3, isolated tube in stipe region, ×30 (NMW. 72 39G. 1a). 4, counterpart of holotype from which organic material removed for analysis by Dr. K. Niklas. Isolated holdfast is arrowed, ×1·9 (NMW. 72 39G. 1b). 5, iron stained specimen with some structural detail, ×1·9 (NMW. 72 39G. 2b).

1



2

3

4

5

EDWARDS, Silurian non-calcified alga

matrix. One such protrusion is seen in profile: it is 1·2 mm high, 1·2 mm wide at its base, and increasing to 1·8 mm diameter distally (Pl. 110, fig. 2). It seems possible that these basal extensions were involved in the anchoring of the alga to the substratum. Details of the internal structure of the holdfast region are unknown. Very little carbonaceous residue remains particularly at the extreme base of the fossil where carbonaceous strands ramify between the irregularities in the rock surface. A further isolated holdfast was originally present on the counterpart (NMW. 72 39G. 1b; Pl. 110, fig. 4). This showed the same over-all features as the one described above, but was less well preserved. Traces of it are visible on the holotype.

The holdfast in the intact plant on the holotype passes into a short unbranched axis 3·5–4·0 mm in diameter and 5·0 mm long. The carbonaceous residue in this area is thick, particularly towards the centre suggesting that the organ was cylindrical and not flattened in life. The surface of the stipe is longitudinally striated but any further anatomical details are obscured by the regular cleat-like fracture of the carbon. Evidence for a tubular or filamentous construction comes from a parallel sided element, or strip of carbonaceous material 0·1 mm wide, projecting from the right-hand edge of the stipe (Pl. 110, fig. 3) and from similar, but less well preserved, structures on the frayed left-hand margin. Whether or not the stipe consists entirely of such elements longitudinally orientated cannot be determined.

The stipe divides unequally distally: the wider right-hand branch (2·7 mm diameter) branches repeatedly producing the main body of the thallus. The narrower left-hand branch (2·4 mm) divides again but soon peters out.

The thallus gives the over-all impression of irregular branching, in which it is possible to distinguish several different kinds of lateral branch. Many attempts have been made to demonstrate a pattern of branching, i.e. a repeated sequence of the different categories, and although these have been unsuccessful, a few generalizations may be made.

Branching angles vary: those in the proximal branches are wide, those of the narrower distal branches are more acute. The diameter of the branches decreases on the whole from base to apex. The nearest approach to dichotomous branching is seen in the widest basal axes, but the branches produced are not absolutely equal in diameter. These main branches divide repeatedly in a monopodial fashion in which a main axis maintains its diameter while producing laterals of various types. Some of

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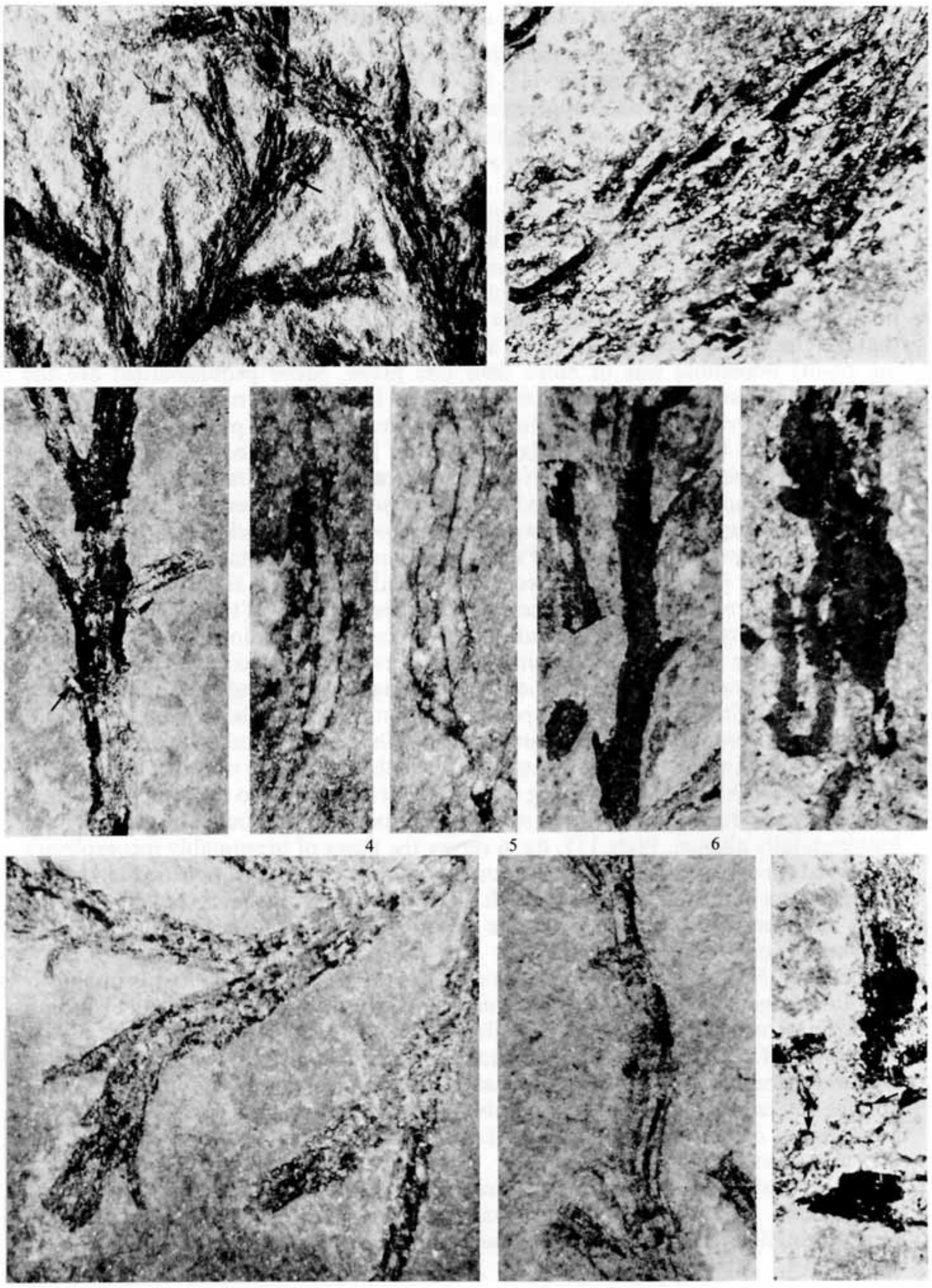
EXPLANATION OF PLATE 111

Figs. 1–10. *Powysia bassettii.* 1, part of holotype photographed using unilateral illumination showing corrugated appearance. Arrowed is the base of a tube projecting from the surface of the thallus, ×8. 2, area of thallus in which short lengths of carbonaceous tubes are visible, ×20. 3, note the short lateral branches, the one to the right comprising two tubes, abruptly truncated distally. Arrowed is a short theca-like projection, ×10 (NMW. 72 39G. 1a). 4 and 5, outlines of individual tubes in ultimate branches, ×30. 6, part of petrified axis (?limonite) with bases of lateral tubes, ×10 (NMW. 72 39G. 2a). 7, petrified tubes, ×30 (NMW. 72 39G. 2a). 8, part of the distal region of the holotype showing truncated tips and short lateral branches composed of one or two tubes, ×10 (NMW. 72 39G. 1a). 9, wider axis in which several aligned tubes are visible, ×10 (NMW. 72 39G. 2a). 10, area of carbonized thallus showing bases of tubes (arrowed), ×20 (NMW. 72 39G. 1a).



1 2 3 4 5 6 7 8 9 10

EDWARDS, Silurian non-calcified alga

these act as main axes themselves and branch further. Others are narrow, of varying length and remain undivided (Pl. 111, fig. 3) while others divide just once or twice. Plate 111, fig. 8 illustrates the appearance of part of a fan-shaped cluster of ultimate branches. Note that in this region a slight increase in axis diameter may occur. It should be emphasized that this frond although lying alongside the main axis is not attached.

Like the stipe, the widest basal branches possess a considerable thickness of carbonaceous residue and are longitudinally striated. Plate 110, fig. 1 shows a branch in which a prominent thicker central band is present. It is therefore concluded that the wider branches were cylindrical and not flattened in the original plant. Although the holotype itself gives the impression that the whole frond was planated, it seems likely that in at least the basal regions (where axes sometimes overlie each other at a branching point) branching was in more than one plane. More problematical are the splayed out ultimate branches which may indeed have been flattened in life.

Most of the evidence for the detailed internal structure of the plant comes from the narrower distal branches. While the wider ones have a striated surface, narrower branches present an irregular longitudinally corrugated appearance (Pl. 111, fig. 1) suggesting groups of intertwining tubes of some sort. Even where the carbonaceous residue has disappeared, the yellow to brown iron stained rock beneath bears the pronounced imprints of the tubes. Further information was obtained from carbonaceous examples in less well preserved areas of thallus (Pl. 111, fig. 2) and from iron petrifactions, presumably casts of the original tubes or groups of tubes (Pl. 111, fig. 6). A combination of these two preservation types is seen on the holotype where petrified brown tubes are scattered on the surface of a heavily carbonized portion of thallus. The tubes themselves are parallel sided, on average 0·1 mm wide and have smooth featureless longitudinal walls. It is postulated that these must have been quite rigid to produce the impressions of individual tubes on the rock. The tubes are unbranched, at least for the two to three millimetres over which they can be traced. The frequent changes in depth of the intertwining tubes made it impossible to follow a single tube over any great distance. Individual tubes are occasionally sinuous. The majority are longitudinally aligned. Plate 111, fig. 6 shows the bases of presumably incompletely preserved tubes arising from a central bundle. In one case only a petrified U-shaped tube has been preserved (Pl. 111, fig. 7). It was impossible from these types of preservations to determine whether or not the tubes consisted of rows of cells, i.e. were filamentous or were siphoneous.

Specimen NMW. 72 39G. 2a and its counterpart are impression fossils on which very little organic material remains. This occurs as very fine longitudinally running black lines, marking the outlines (walls) of tubes on the various branches at the extremities of the frond (Pl. 111, figs. 4 and 5). These lines are also visible on the holotype where the carbonaceous material has flaked off. Transverse lines are not present, nor are any indications of branching tubes. Here again the tubes could be traced for a maximum of only two millimetres. Tube diameter varies between 0·08 mm and 0·15 mm (average 0·11 mm).

While the absence of transverse walls suggests a siphoneous rather than filamentous construction, it is possible that cross walls, if more delicate than longitudinal ones, were originally present but escaped preservation. Indeed as only comparatively short lengths of tubes (up to 3 mm) are visible, it is also considered possible that the thallus consisted of filaments of very elongate cells.

Whether or not the thallus contained other types of tissue in addition to these tubes cannot be determined. Detailed internal organization cannot be detected in the wider branches, where longitudinal striations presumably represent longitudinally aligned tubes of the kind described above. In the narrower branches it is possible to distinguish up to ten individual tubes aligned in parallel, but there is no evidence of any additional tissues (Pl. 111, fig. 9).

Many of the branches bear short theca-like (in the zoological sense) lateral projections, usually seen in profile (Pl. 111, fig. 3). They often consist of just one tube, which ends abruptly close to the branch. Circular scars, of similar diameter to the tubes and present on the surface of some narrow branches, are thought to represent the bases of these short truncated projections (Pl. 111, fig. 10). Tubes are also visible in the individual lateral branches mentioned above. While up to three tubes occur at the base, there is a progressive reduction in number distally. Individual tubes are abruptly truncated and give a stepped appearance to the tip of the branch.

Some of the terminal branches have a similar organization. Where tubes (up to four) are visible, they end abruptly. It is possible that more delicate areas of tissue were originally present beyond the tubes but these were not preserved. A few branches end in sheets of featureless carbonaceous residue, lacking any indication of tubes or of apical organization (Pl. 111, fig. 8).

Habitat. The gross morphology of *Powysia* suggests a benthic alga, while its presence in graptolitic shales probably indicates a marine origin, although it must have been transported some distance from where it grew in shallow water. However, the possibility that it was a fresh water alga which was swept into the sea before burial cannot be ruled out.

COMPARISONS

Macroscopic non-calcified algae which are sufficiently well preserved to allow identification in terms of present-day taxa are rare in the early Palaeozoic. Indeed the early history of the group centres on calcified representatives and more recently, on microscopic algae preserved in cherts. Many of the identification problems in non-calcified algae result from lack of preserved anatomy and reproductive parts. Similarities in thallus form seen in various lines of extant algae serve as important reminders of the pitfalls of identification based on external morphology in compression fossils. Excellent examples of the necessary critical approach are found in Fry and Banks's description of apparently complete and highly distinctive algae from the Upper Devonian of New York State (Fry and Banks 1955) and in Elliott's taxonomic treatment of his new genus *Inopinatella* from the Upper Silurian of Britain (Elliott 1971). None of the algae described in these two papers sufficiently resemble the Welsh fossils to merit detailed comparisons, although two general points, relevant to any considerations on non-calcified algae, emerge. Firstly, there is Elliott's comment that *Inopinatella*, a non-calcified alga, shows marked similarities with the *juvenile* stage of *Neomeris* an extant calcified genus, and secondly, as Fry and Banks point out, there is a possibility that the calcium carbonate originally present in the plant has been subsequently leached out producing an apparently non-calcified fossil. It is concluded unlikely, however, that either possibility applies in the present study.

The genus *Buthotrephis* Hall is widespread in Ordovician and Silurian strata. While it is outside the scope of this paper to discuss in detail the affinities of the numerous *Buthotrephis* species, it seems likely that a few are indeed non-calcified algae (Johnson *et al.* 1959). Two such examples are *B. newlinii* and *B. divaricata* described by White (1901) from the Silurian of Indiana. In both, the ?fragment of the thallus consists of regularly dichtomizing axes of uniform width and with rounded apices. Species distinction is based on axis width and frequency of branching. Another possible non-calcified alga *B. nidarosiensis* (Høeg 1941) shows less regular branching, and in common with the other two species shows none of the over-all morphological complexities of *Powysia*. I consider it possible that many *Buthotrephis* specimens were distal branching fragments of much larger algae, perhaps with gross morphology similar to that in *Powysia*, although they are quite distinct from the distal branches of *Powysia* itself.

White (1903) also described *Thamnocladus clarkei* from the Upper Devonian of New York State, which he considered to be a non-calcified alga. It consists of an extensively branched thallus in which the regular branching is described as 'alternately dichotomous'. Individual axes are flexuous, gradually tapering, and have a central line. Whether or not this highly distinctive plant is indeed vascular is being investigated by Dr. D. Grierson in the United States. Although the distal regions of *Powysia* as seen in the more complete specimens bear a superficial resemblance to *T. clarkei*, I conclude they are unrelated.

It would be unwise to exclude the enigmatic *Prototaxites* Dawson from any discussion on non-vascular plants of this age. However, I know of no *Prototaxites* species of such elaborate morphological differentiation and two sizes of tube are not recorded for *Powysia*, although, of course, this could be due to preservation failure.

AFFINITIES OF *POWYSIA*

The possibility that *Powysia* was an animal cannot be ignored. It has long been appreciated that many of the fossils described as algae in the last century under such genera as *Fucoides* Brongniart are trace fossils (Seward 1898). Indeed many *Buthotrephis* species may belong in this category and Simpson (1956) has assigned *B. gracilis*, Hall's type species to *Chondrites* von Sternberg, a trace fossil genus considered to represent the branching burrowing system of a worm. In addition, remarkable morphological similarities exist between certain invertebrate fossils and plants (Chaloner and Allen 1970; Lundblad 1972). Ruedemann (1916) postulated graptolitic affinities for *B. lesqueureuxii* and renamed it *Inocaulis lesqueureuxi*. Dr. B. Rickards has examined all the *Powysia* specimens and has confirmed that they are not dendroid graptolites. Geochemical analysis of carbonaceous residues from specimen NMW. 72 39G. 1b by Dr. K. Niklas, New York Botanical Garden (pers. comm.) supports the plant nature of the fossils.

The evidence presented above suggests that *Powysia* was an alga of marked morphological complexity but with relatively simple internal organization, the thallus consisting of intertwining filaments or siphons. As discussed earlier the reliability of the anatomical evidence is questionable: it is possible at least for the wider axes, that while tubes or filaments have been preserved, softer parenchymatous or pseudo-parenchymatous tissues have disappeared.

A morphologically complex thallus of siphoneous construction characterizes members of the Siphonales (Chlorophyta). Indeed the complete *Powysia* plant resembles the upright and rhizoidal portions of members of the Caulerpaceae. *Powysia*, however, lacks 'rhizomes', regularity of branching, and the complexity of internal structure typical of *Caulerpa* and allied genera. These two latter features also exclude relationships with *Codium* a non-calcified, non-rhizomatous member of the Codiaceae. On the limited data available it is impossible to assign *Powysia* to any living family within the Siphonales.

Filamentous organization of heterotrichous type, in which a basal prostrate system of filaments is accompanied by a system of upright branches, is present in many living algae. In the Chlorophyta, the heterotrichous habit is very well developed in the Chaetophorales, as in *Stigeoclonium*. The majority of the Chaetophorales have erect branches consisting of a single filament with the highest degree of internal differentiation in certain species of *Draparnaldia* and *Draparnaldiopsis* where lateral branches produce rhizoid-like structures which completely invest the main axis in its basal region. Aggregation of filaments in mucilaginous envelopes are seen in certain species of *Chaetophora* itself. None of these species are morphologically similar to *Powysia*.

Considered the simplest growth form in the brown algae, the heterotrichous habit is typical of the Ectocarpales. *Powysia* is best compared with those members in which erect branches consist of aggregations of filaments (multiaxial forms), but here again their internal organization is more complex than in the fossils because filaments are of varying size and orientation. Indeed some species have a pseudoparenchymatous organization in ultimate branches.

Similar problems arise when *Powysia* is compared with heterotrichous multiaxial members of the red algae and so it is concluded that the combination of morphological and anatomical characteristics seen in *Powysia* is not represented in modern heterotrichous forms in any of the major groups of macroscopic algae.

Finally, there are some red and brown algae which resemble *Powysia* in habit and size, but which have highly elaborate internal differentiation. In the browns, for example, the extant fucoid *Cystoseira* is superficially like *Powysia*, although the fossil lacks any small swellings, while in the reds, similarities exist with tough branching forms such as *Cystoclonium*.

It is, of course, possible that the fossil alga exhibits a combination of characters unknown in present-day forms. I feel, therefore, that until further, better-preserved specimens are found, *Powysia* should be considered an alga of uncertain affinities.

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