

A CORALLINE-LIKE RED ALGA FROM THE LOWER ORDOVICIAN OF WALES

by ROBERT RIDING, JOHN C. W. COPE *and* PAUL D. TAYLOR

ABSTRACT. A new alga, *Arenigiphyllum crustosum* gen. et sp. nov., from the lower Ordovician (lower Arenig Series, Moridunian Stage) of the Llangynog Inlier, Carmarthenshire, Wales, has a thin crustose dorsiventral thallus. The single specimen is preserved as limonite. Construction is dimerous, consisting of juxtaposed vertical filaments arising from prostrate bases. Cells are closely spaced. There is no evidence of cell fusions, pit connections or reproductive structures. In size and thallus structure, *Arenigiphyllum* closely resembles vegetative parts of extant coralline algae. It is the oldest well-preserved example of a coralline-type alga described to date.

CORALLINALEANS are an important order of red algae that includes the extant Corallinaceae and Sporolithaceae (Verheij 1993). Heavy calcification of the cell wall gives both families an excellent fossil record from the Lower Cretaceous to Recent (Edwards *et al.* 1993, p. 36). However, despite attempts to elucidate their earlier history, the Palaeozoic antecedents of coralline algae have long been uncertain. At first, it was believed that members of the Solenoporaceae held the key to their origins (Nicholson and Etheridge 1885; Brown 1894), but these comparisons encountered difficulties. The central problem was the perception that solenoporaceans had simpler thallus organization and lacked the reproductive structures commonly preserved in corallines (Johnson 1960). As a result, attention switched to Late Palaeozoic fossils that became known as 'ancestral corallines' (Wray 1977, pp. 71–77), in particular to genera such as *Archaeolithophyllum* Johnson (Johnson 1956). However, *Archaeolithophyllum* has not been recorded from rocks older than Carboniferous, leaving the question of possible earlier coralline-like algae unresolved. Blackwell *et al.* (1982) refocused attention on the Lower Palaeozoic by describing reproductive structures in *Solenopora richmondensis* (Miller) Blackwell, Marek and Powell from the upper Ordovician. *Petrophyton kiaeri* Høeg, from the middle–upper Ordovician, has until now been the oldest known Palaeozoic calcified red alga (Riding 1994, p. 428).

Here we describe an older fossil from the lower Ordovician (Arenig) of Wales which, although it lacks reproductive structures, shows closer similarities to coralline vegetative anatomy than either *S. richmondensis* or *P. kiaeri*. It represents the earliest record to date of a well-preserved, originally calcified, coralline-like alga.

LOCALITY AND MATERIAL

The single specimen is from the base of the Bolahaul Member of the Ogof Hên Formation (Fortey and Owens 1978), now referred to the Moridunian Stage of the Arenig Series (Fortey and Owens 1987). The locality is a small quarry in the northern part of the Llangynog Inlier (Cope 1982), 6 km south-west of Carmarthen in south-west Wales (Cope 1996, text-fig. 1). This locality was first mentioned by Strahan *et al.* (1909, p. 16), but their list of fossils is meagre and unremarkable. More recently, extraction of the fossils by one of us (JCWC), using bulk collection of the rock and splitting it in the laboratory, has yielded an extraordinarily diverse fauna, dominated by molluscs, 40 per cent. of which are bivalves constituting the most diverse early Ordovician bivalve assemblage yet

known (Cope 1996). This locality has also yielded the earliest parablattoid (Paul and Cope 1982) and the earliest fully documented bryozoan (Taylor and Cope 1987). In a collection of about 3100 fossils, obtained by splitting some 20 tonnes of rock, ten taxa are represented by single specimens, including the alga described here. The specimen is housed in the National Museum of Wales, Cardiff, with accession number NMW 88. 67G. 2. The specimen is now composed of limonite. Primary calcification is assumed because the preservation is similar to that of parablattoids (Paul and Cope 1982), bryozoans (Taylor and Cope 1987), molluscs, and articulate brachiopods from this locality. The alga is smoothly convex and encrusts what appears to be a trilobite free-cheek. However, substantiating this would require damage to the alga.

In this paper, thin section photography and locality and material description are by JCWC. SEM photographs of *Arenigiphyllum* are by PDT. The systematic section and remainder of the paper are by RR.

SYSTEMATIC PALAEOLOGY

Division RHODOPHYTA Wettstein, 1901

Class RHODOPHYCEAE Rabenhorst, 1863

Order CORALLINALES Silva and Johansen, 1986? or GIGARTINALES Schmitz, *in* Engler 1892?

Family uncertain

Genus ARENIGIPHYLLUM Riding gen. nov.

Type species. Arenigiphyllum crustosum gen. et sp. nov.

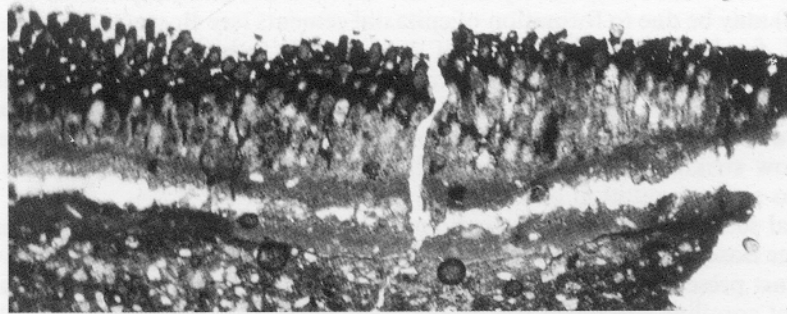
Derivation of name. After the Arenig Series, in which the fossil was found.

Diagnosis. Thin foliose thallus, with dorsiventral dimerous construction of erect prismatic filaments with rounded interiors, arising from a prostrate base; cell walls closely spaced.

Affinities and comparisons. In general size and filament arrangement, *Arenigiphyllum* closely resembles coralline algae (Pl. 1; Text-fig. 1). At this scale, size becomes a significant criterion and the small size of the filaments and cells makes superficial similarities with sponges, tabulates and bryozoans untenable. In addition to its size, *Arenigiphyllum* distinctly resembles coralline algae in structure. The thallus is thin (less than 1 mm thick) with dorsiventral dimerous construction, i.e. with a basal cell layer (of unistratose basal filaments) and erect upper portion. For example, *Arenigiphyllum* resembles the extant coralline *Exilicrusta* Chamberlain in its thin prostrate thallus and upward curving elongate filaments (compare fig. 5 in Chamberlain 1992 with Pl. 1, fig. 5), and the cell walls (cross partitions) visible in thin section (Text-fig. 2) are comparable to those illustrated by Woelkerling (1988, fig. 219) for *Melobesia*. However, all coralline groups may exhibit the thallus thinness and organization shown by *Arenigiphyllum*, and, in the absence of reproductive structures, it is not possible to decide whether *Arenigiphyllum* could be placed in either of the extant families Sporolithaceae and Corallinaceae.

It is also possible that *Arenigiphyllum* represents a member of the Peyssoneliaceae Denizot (also known as Squamariaceae (Agardh) Hauck). Although not included in the Corallinales, these red algae have broadly similar thallus construction and typically form thin foliose thalli similar to that seen in *Arenigiphyllum*. Peyssoneliaceans have a confirmed record from Lower Cretaceous to Recent (Edwards *et al.* 1993, p. 36), and have been compared to some Late Palaeozoic phylloid algae (Wray 1977, p. 53). A difference from members of the Corallinales is that the peyssoneliacean skeleton is aragonitic. We have no information concerning the original mineralogy of *Arenigiphyllum*. Furthermore, extant peyssoneliaceans show dichotomous division of cell filaments which results in a reduction in cell size as the filament grows (e.g. Buchbinder and Halley 1985, figs 6, 7a–b; Wray 1977, figs 37–38). This is not seen in *Arenigiphyllum*. Thus, although an affinity with the Peyssoneliaceae cannot be excluded, comparisons with corallines are closer.

TEXT-FIG. 1. *Lithophyllum incrustans* Philippi, 1837; specimen TJ-24, deposited in the Museum of the Departamento de Estratigrafía y Paleontología, Universidad de Granada; fractured surface showing longitudinal section parallel to prismatic sinuous filaments; compare with *Arenigiphyllum* in Pl. 1, fig. 5; Miocene (Upper Tortonian), Almazora Corridor, south-east Spain; scanning electron micrograph of coated specimen using secondary electrons; $\times 221$.



TEXT-FIG. 2. *Arenigiphyllum crustosum* gen. et sp. nov; holotype, NMW 88. 67G. 2; 6 km south-west of Carmarthen; Bolahaul Member, Ogof Hên Formation; thin section showing sub-vertical filaments and closely spaced cell walls near the upper surface; $\times 27$.

The type species of *Solenopora*, *S. spongioides* Dybowski, was described from the upper Ordovician (Dybowski 1877), and the Solenoporaceae has generally been regarded as an extinct family of calcified red algae. However, the Solenoporaceae is a heterogeneous group based on an aggregation of disparate taxa some of which may not be algal (Riding 1977, p. 206, 1993; Brooke and Riding 1987). Corallinean algae have been recognized among Early Palaeozoic solenoporaceans. Blackwell *et al.* (1982) described sporangial compartments arranged in a sorus in *S. richmondensis* and compared it to the extant coralline *Sporolithon*. The cells of *S. richmondensis* are rounded to polygonal in cross section, are 30–110 μm wide and 60–140 μm long (Blackwell *et al.* 1982, p. 478, fig. 6), appear to be well-aligned between adjacent filaments, and closely resemble those of *Petrophyton kiaeri* from the middle-upper Ordovician. *Petrophyton* has also been recorded by Sinclair (1956) as *P. ? floreale* from the Ordovician of Québec, and as *P. kiaeri* from the Silurian of Québec (Mamet and Roux, in Héroux *et al.* 1977, p. 2898), but lacks reproductive structures. *Solenopora gotlandica* from the lower Silurian, possesses small cells, radial monomerous or diffuse

thallus organization, and tetrasporangia arranged in sori and also appears to be a sporolithacean (Brooke and Riding in press). Neither *S. gotlandica* nor *S. richmondensis* appears to be congeneric with *S. spongioides*.

Arenigiphyllum is distinguished from *Petrophyton* and species attributed to *Solenopora* by being thin and foliose in form, whereas these other taxa characteristically have inflated nodose thalli. *Arenigiphyllum* is distinguished from *Petrophyton* and *S. richmondensis* by having smaller cells that are wider than high. No pit connections are visible in *Arenigiphyllum*, but this does not preclude their absence since it can be difficult to observe pits even in present-day corallines where they are known to be present (J. C. Braga, pers. comm.). However, larger cell fusions between adjacent filaments do appear to be absent. Among corallines, absence of cell fusions is characteristic of the subfamily Lithophylloideae and some sporolithaceans. More rarely, some corallines lack any kind of cell connection between adjacent filaments. This is characteristic, for example, of the subfamily Austrolithoideae Harvey and Woelkerling, 1995, although these are very small uncalcified plants that are unknown as fossils.

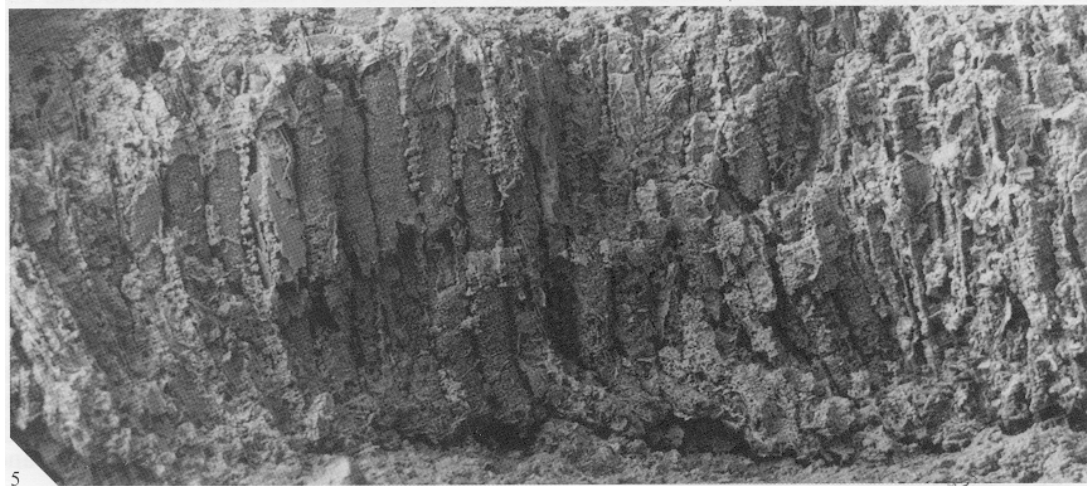
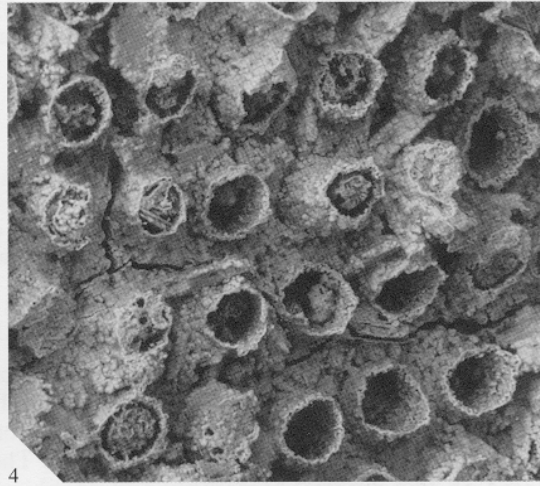
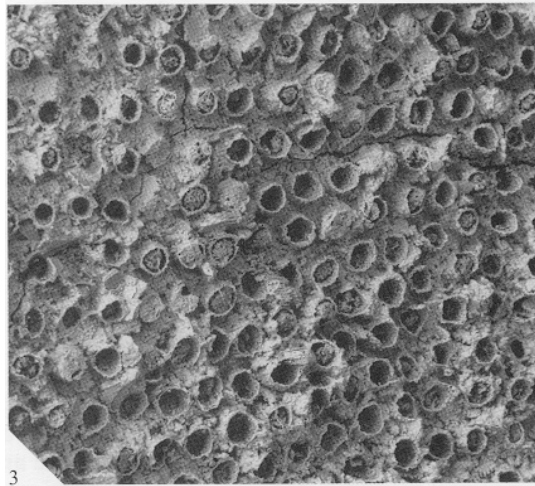
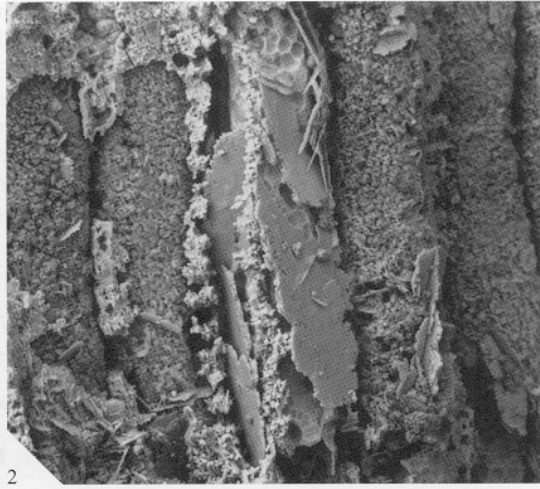
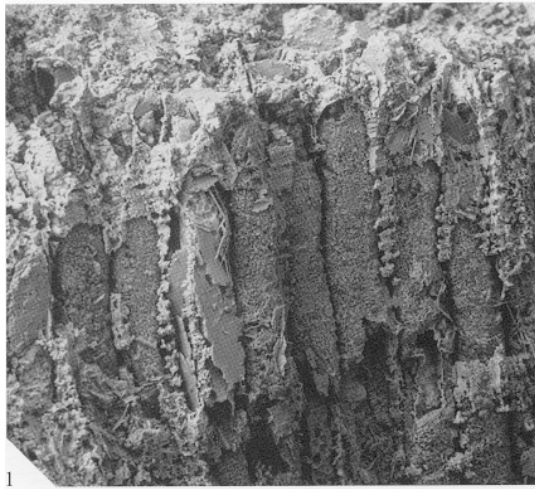
Despite the difficulties of elucidating *Arenigiphyllum*'s precise relationships with extant corallines, due to the absence of reproductive structures and information concerning original mineralogy, available evidence indicates that *Arenigiphyllum* is a calcified red alga closely allied with extant corallines and peyssoneliaceans. Accordingly, it is here tentatively referred to either the Corallinales or Gigartinales.

Remarks. The specimen is preserved as limonite. It is assumed that the original specimen was calcified and that preservation involved infilling by cements and/or matrix, followed by dissolution and replacement. The walls are relatively thick and the final size and shape of the preserved central tube (Pl. 1, fig. 4) may be due to formation of epitaxial cements (see Bosence 1991, figs 1b, 2f; Braga *et al.* 1993, pl. 1, fig. 2) that left the centres of the filaments to be infilled subsequently by matrix. If limonite replaced the calcareous skeleton and cement, but not the matrix-filled tubular filament centres, this would produce the square outer filament surfaces, thick walls and rounded centre. However, it should be noted that present-day corallines such as *Exilicrusta parva* (see Chamberlain 1992, fig. 5) show strikingly similar calcified filaments with planar outer surfaces and rounded interiors prior to any cementation or infilling.

In longitudinal section, the outer planar bounding surface (Pl. 1, figs 1–2) is interpreted as the inner cell wall (see Bosence 1991, fig. 1a, for terminology), which may have been dissolved and infilled to provide the cast preserved. Differential dissolution of parts of the cell wall occurs in dilute acid etching of Recent coralline specimens (see Braga *et al.* 1993, pl. 1, figs 1–2). Cell walls are partially preserved (Text-fig. 2; Pl. 1, figs 1–2). They are unusually closely spaced; most extant corallines have cells whose height is equal to or greater than the filament width. However, some near-surface cells of melobesioids are closely spaced and have a flat appearance similar to those in *A. crustosum* (J. C. Braga, pers. comm.).

EXPLANATION OF PLATE 1

Figs 1–5. *Arenigiphyllum crustosum* gen. et sp. nov.; holotype, NMW 88. 67G. 2; scanning electron micrographs of the uncoated specimen imaged using back-scattered electrons; Llangynog, 6 km south-west of Carmarthen, Wales; Bolahaul Member, Ogof Hên Formation. 1, vertical prismatic filaments, detail of 5; locally ladder-like remains of cell walls are preserved between adjacent filaments; $\times 110$. 2, detail of 1, showing smooth prismatic inner wall of the middle filament, which is removed from adjacent filaments to reveal the surface of the lining or infilling to the filament; $\times 225$. 3, transverse section of regular spaced circular openings interpreted as filaments on the upper surface of the thallus; $\times 90$. 4, detail of 3, showing local infilling of tubes by cement/matrix; intervening material is interpreted as filament wall possibly with cement rims; rectilinear cracks may represent inner walls of filaments; $\times 210$. 5, fractured surface of foliose thallus showing dorsiventral dimerous construction with sub-vertical prismatic filaments arising from a prostrate base; $\times 80$.



In transverse section, the spaced circular openings (Pl. 1, figs 3–4) are interpreted as cross sections of filaments (see Chamberlain 1992, fig. 5), and the material occupying space between the openings as cement/matrix and/or originally calcified cell wall (compare cement fills of coralline filaments shown by Bosence 1991, fig. 1b, and Braga *et al.* 1993, pl. 1, fig. 2). The circular openings also somewhat resemble epithallial surface concavities of extant corallines (see Woelkerling *et al.* 1985, figs 30–31; Chamberlain 1992, figs 2, 15). The complicated filament infillings observed locally (Pl. 1, fig. 4) appear to be due to replacement of various stages of cement and matrix. An apparent double wall has been produced during preservation of Silurian *Solenopora compacta* (see Rothpletz 1913, pl. 1, fig. 6, lower right centre).

Arenigiphyllum crustosum Riding sp. nov.

Plate 1; Text-figure 2

Derivation of name. From the thin crustose appearance of the fossil.

Holotype. Thin foliose fragment, NMW 88. 67G. 2; Plate 1; Text-figure 2.

Locality and horizon. National Grid Reference SN 3640 1639, Llangynog, Carmarthenshire, Wales. Approximately 5 m above the base of the Bolahaul Member, Ogof Hên Formation (Moridunian Stage, Arenig Series).

Diagnosis. As for genus.

Description. Thin domed layer 800 μm thick and 28 mm across, composed of erect filaments arising vertically from prostrate basal filaments. Filaments tubiform, diameter expanding from 20 μm in basal part up to 60 μm in erect part, where they maintain constant diameter; cell height 15–20 μm ; filaments juxtaposed; walls thick, outer surface polygonal with planar faces, inner surface circular.

DISCUSSION

The earliest red alga known is an uncalcified Proterozoic bangiophyte approximately 1000 My old from Somerset Island, Canada (Butterfield *et al.* 1990). Phosphatized red algae (*Thallophyca* Zhang) that probably were not calcified have been reported from the 680 Ma Doushantou Formation of China (Zhang 1989; Zhang and Yuan 1992). The oldest records of possible calcified red algae are based on two reports: Horodyski and Mankiewicz (1990) recorded *Tenuocharta* Horodyski and Mankiewicz from the Neoproterozoic (600–700 Ma) and suggested that it might be a red alga or cyanobacterium; and Grant *et al.* (1991) compared a younger (530–650 Ma) possible alga with phylloid algae, peyssoneliaceans, and corallines. Both of these fossils are calcified and foliose. *Tenuocharta* is distinguished from *Arenigiphyllum* by being extremely thin, apparently consisting of a single layer of 5–10 μm size cell-like structures. The specimens described by Grant *et al.* (1991) appear to have originally been aragonitic and are sheets up to 500 μm thick with elevated structures reminiscent of reproductive structures, which have not been observed in *Arenigiphyllum*. The overall size and appearance are broadly consistent with those of *Arenigiphyllum*, and the possibility that they are related cannot be ruled out. But, poor preservation of internal detail within the sheets precludes any precise comparison with *Arenigiphyllum*. Various early Cambrian calcified fossils have been referred to the red algae (Korde 1959), but are now regarded as probable cyanobacteria (Luchinina 1975; Riding 1991). None has the foliose and cellular structure seen in *Arenigiphyllum*.

Although *Arenigiphyllum* lacks reproductive structures, its possession of dimerous tissue differentiation is much more coralline-like in vegetative anatomy than either *S. richmondensis* (late Ordovician; Blackwell *et al.* 1982) or *P. kiaeri* (mid-late Ordovician; Høeg 1932, p. 32). *Arenigiphyllum* therefore predates these previous oldest records of confirmed calcified red algae and is the oldest example of a well-preserved coralline-type alga so far known.

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ROBERT RIDING

JOHN C. W. COPE

Department of Earth Sciences
Cardiff University
Cardiff CF1 3YE, UK

PAUL D. TAYLOR

Department of Palaeontology
The Natural History Museum
Cromwell Road, London SW7 5BD, UK

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