

Algae from the Rhynie Chert

DAVID S. EDWARDS

*Department of Botany, University of Cape Coast,
Cape Coast, Ghana, West Africa*

AND

A. G. LYON

*17, The Square, Rhynie, by Huntly,
Aberdeenshire AB5 4HD*

Received January 1982, accepted for publication July 1982

New material collected from the Rhynie Chert Bed (Siegenian age) has revealed *new filamentous and unicellular algae*. Two of the filamentous forms and one palmelloid form are described. Filamentous and unicellular algae are particularly common in a white kind of chert not previously reported and which is interpreted as having been formed by the *in situ* silicification of a silicate-rich pond.

Some rhizoid-nodes of *Palaeonitella cranii* (Kidston & Lang) Pia and a possible rhizoid-borne proembryo are also described and compared with similar structures in living Charophyta.

KEY-WORDS:—Algae Charophyta Chroococcaceae - Devonian - fossil - Ulotrachaceae.

CONTENTS

Introduction	37
Material and methods	38
Discussion and systematic palaeontology	39
Filamentous algae	40
Palmelloid and coccooid algae.	50
General discussion	52
Acknowledgements.	54
References.	54

INTRODUCTION

Knowledge of Devonian algae is almost entirely confined to calcified forms of the Cyanophyta, Chlorophyta and Rhodophyta. Non-calcified filamentous and unicellular algal microfossils are far less well-known, the most widespread being the organic-walled cysts and resting spores of certain Prasinophyta (families Cymatiosphaeraceae, Tasmanitaceae, Leiophaeridiaceae—following the classification by Tappan, 1980) which were previously included in the heterogeneous group Acritarcha (see Downie, 1973; Tappan, 1980). The few other

forms known have been assigned to the Ulotrichales (Grüss, 1928; Baschnagel, 1942; Fairchild, Schopf & Folk, 1973; Wicander & Schopf, 1974), Zygnematales (Baschnagel, 1966), Oedogoniales (Baschnagel, 1966), Stigonematales (Croft & George, 1959; Tappan, 1980).

Previous studies of the algal flora of the Rhynie Chert, which is regarded as being of early Devonian, possibly Siegenian, age (see Richardson, 1967; Westoll, 1977) have recognized five taxa of cyanobacteria and a possible charophyte. Kidston & Lang (1921) described two species similar to modern *Oscillatoria*—*Archaeothrix oscillatoriformis* and *A. contexta*. The narrow filaments (3–4 μm diameter) of discoid cells of *A. oscillatoriformis* were found within a stem of *Rhynia gwynne-vaughanii* while the narrower (*c.* 2 μm diameter) filaments of *A. contexta* occurred in large masses lying loose in the matrix. Croft & George (1959) described three species of cyanobacteria—*Langiella scourfieldi*, *Kidstoniella fritschii* and *Rhyniella vermiformis* from a single chip of chert which also contains a vascular axis. *Langiella* and *Kidstoniella* had a heterotrichous growth habit with well-developed prostrate and erect systems, heterocysts and akinetes; Croft & George (1959) assigned both genera to the Stigonemataceae. The unbranched, non-heterotrichous mucilaginous filaments of *Rhyniella* were regarded by Croft & George (1959) as being of uncertain systematic position within the cyanobacteria; Tappan (1980) includes *Rhyniella* in the Scytonemataceae.

Possible algal unicells were described by Kidston & Lang (1921); additional specimens of similar unicells, together with a filamentous alga were found, but not described, by Lyon (1962).

Kidston & Lang (1921) also described some remains which they regarded as those of a probable charophyte. *Palaeomitella cranii* (Kidston & Lang) Pia includes branch whorls, possible bulbils and rhizoid-nodes; but no reproductive structures were found and Tappan (1980) considers its status questionable.

We describe a number of previously unknown filamentous and unicellular algae from the Rhynie Chert and provide additional information on *Palaeomitella cranii* (Kidston & Lang) Pia to support the interpretation of that plant as a charophyte.

MATERIAL AND METHODS

The essential features of the Rhynie Chert have been described by Kidston & Lang (1917, 1921). In general terms, the deposit is up to 2.5 m in thickness and consists of alternating beds of chert and sandstone. The chert is dark grey or black in hand specimens and contains well-preserved plant and animal fossils. Kidston & Lang (1921 : 891), in a detailed study of sections through the deposit, noted that algae were limited to certain horizons (designated A'' and F); Tasch (1957) has also pointed out that animal (principally crustacean) remains are also limited in occurrence, being most common in horizon A'', the most south-easterly of the chert horizons found by Tait (in Horne *et al.*, 1916) and regarded by him as the basal bed of the section.

Some of the material used in the present study was collected from the surface of the field which overlies the bedded chert and hence its relationship with the *in situ* chert is uncertain. Other material was obtained from a trench (designated No. 2a) which was excavated in the approximate position of Tait's trench No. 2 (in Horne *et al.*, 1916). While no algae were encountered in samples of bedded chert collected from the exposure, remains of such organisms were found in some loose blocks, a

lens of which was discovered embedded in an ochreous clay 31 m from the top (north-west end) of the bedded rock and 20.5 m from its lower (south-eastern) end. Hand specimens of this chert are white in colour and their identity with the deposit is confirmed by the occurrence within the blocks of *Rhynia major* axes bearing sporangia. For the most part these axes are aligned parallel to one another with the arms of their dichotomies all pointing in the same direction. This tends to suggest *situ* preservation. The matrix between the axes includes light grey and black areas which are usually localized in bands perpendicular to the *Rhynia* axes. Unlike the typical black chert of the deposit, the white chert, as a whole, is very porous, the grey areas having the highest porosity, the pure white ones, the lowest. Large (up to 5 mm diameter) cavities lined with crystalline quartz are also present. The algae are localized within the low porosity chert, most commonly in close proximity to *Rhynia* axes. (Fig. 7). Animal remains, largely disarticulated specimens of *Lepidocaris*, are more frequent in the areas of grey, high porosity, chert. Fungal hyphae and resting spores, isolated nematophytalean tubes and 'branch-knots' (Lyon, 1962) and *Rhynia major* spores also occur scattered throughout the matrix.

Material from Trench 2a was studied by means of ground sections; chip preparations were made from blocks gathered on the surface of the fields. All slides prepared from the white chert will be deposited in the Palaeobotanical Collection, Hunterian Museum, Glasgow, U.K., on completion of this study and are identified by the Hunterian Museum numbers allocated to them. Chip preparations made from the black chert are in the A. G. Lyon Collection. Stage co-ordinates for the individual fossils are not given in this paper since it is felt that they would be of limited usefulness for future workers. The general positions of the figured specimens has been indicated with a diamond scribe and outlined in ink on the bottom of the glass slides to which the sections are attached. Specimens in the Kidston Collection (Hunterian Museum) and the Lang Collection (Manchester Museum) have also been examined.

DISCUSSION AND SYSTEMATIC PALAEOBIOLOGY

The affinities of many fossil algae are uncertain since modern classifications (for example that of Bold & Wynne, 1978) emphasize biochemical and ultrastructural features which are rarely, and in most cases could never be, preserved (for example the number of flagella of motile stages of otherwise non-motile forms). The parallel trends in morphological complexity in many algal classes and the variations in form both within and between different stages of the life-cycle of a single species (for example *Stichococcus bacillaris* Naegeli (Hayward, 1974) make comparisons of fossil and living taxa extremely speculative. In addition, post-mortem diagenetic changes may obscure, or so alter, cell morphology, that the diagnostic features of the original organism are lost (Golubic & Barghoorn, 1977; Francis, Barghoorn & Margulis, 1978). Thus, although indications of cell contents can be seen in some of the Rhynie Chert algae, it is difficult to assess the relationship of these features to the original organelles and their relevance in indicating the affinities of the organisms. In accordance with current palaeobotanical practice (Schopf, 1968; Horodyski, 1980; Tappen, 1980) diagnosed taxa are referred to higher categories, but the doubtful usefulness of such a procedure must be emphasized.

Filamentous algae

DIVISION: Charophyta
SPECIES INCERTAE SEDIS: *Palaeonitella cranii* (Kidston & Lang) Pia

In their account of the Thallophyta of the Rhynie Chert, Kidston & Lang (1921) described some fragmentary remains which they regarded as probably representing the vegetative organs of a charophyte. These consisted primarily of branched septate filaments with dark contents which, in some cases, showed evidence of a nodal structure, as in modern charophytes. In the apparent absence of corticating cells, a particular comparison was suggested and implied in the provisional generic name *Palaeonitella*. This name has been accepted by most authors (Walton, 1953; Emberger, 1968; Tappan, 1980) rather than *Algites* Seward as originally proposed by Kidston & Lang (1921). Pia (1927) first used the generic designation *Palaeonitella* in referring to *Algites (Palaeonitella) cranii* Kidston & Lang; the currently accepted name is thus *Palaeonitella cranii* (Kidston & Lang) Pia.

Associated with these axial structures were tubular elements lacking obvious contents, but with occasional oblique septa. In connection with these, groups of cells were developed and, in some cases, large oval or spherical vesicles. The former were interpreted as rhizoid-nodes, the latter as bulbils such as are formed by certain contemporary charophytes.

Some rhizoid-nodes from the new material were so orientated and preserved that a very close comparison with similar structures in living material has been possible.

In the development of a charophyte rhizoid-node, a curved oblique septum is laid down across the rhizoid in such a way as to give the ends of the resultant cells the appearance of two feet placed sole-to-sole (Groves & Bullock Webster, 1920). The 'toe' of one of these subsequently enlarges and divides to form a group of cells, some of which form secondary rhizoids.

Figure 3 shows a fossil node (Specimen No. 1) in side view. Although the cells of the nodal cluster are obscured by black granular material, the undivided 'toe' is prominently displayed and conforms very closely in relative size and position to comparable structures similarly orientated in living material. An interpretation of all visible structures is given in Fig. 1A and for purposes of comparison, a photograph of a rhizoid-node of *Nitella* sp. appears as Fig. 2.

Like specimen No. 1., specimen No. 2 (Figs 4, 8) is also orientated with its long axis parallel to the surface of the chip. In spite of its excellent preservation, it has proved difficult to obtain a satisfactory overall photograph, as slight differences in plane, coupled with the relatively high magnification required, fail to show clearly all the details of structure which can be resolved by differential focusing. An interpretation of all visible structure is given in Fig. 1B. In this specimen, three branch rhizoids can be seen arising from the cells of the nodal cluster and the longest of these seems, itself, to have developed a septum (seen in face view) with associated slight swelling of the ends of the two cells thus formed. While the undivided 'toe' of the larger node occupies a rather more prominent position than might be expected from the orientation of the specimen as a whole, this could be accounted for by slight twisting or displacement prior to petrification. Although the primary rhizoid can be traced, passing obliquely through the matrix for some

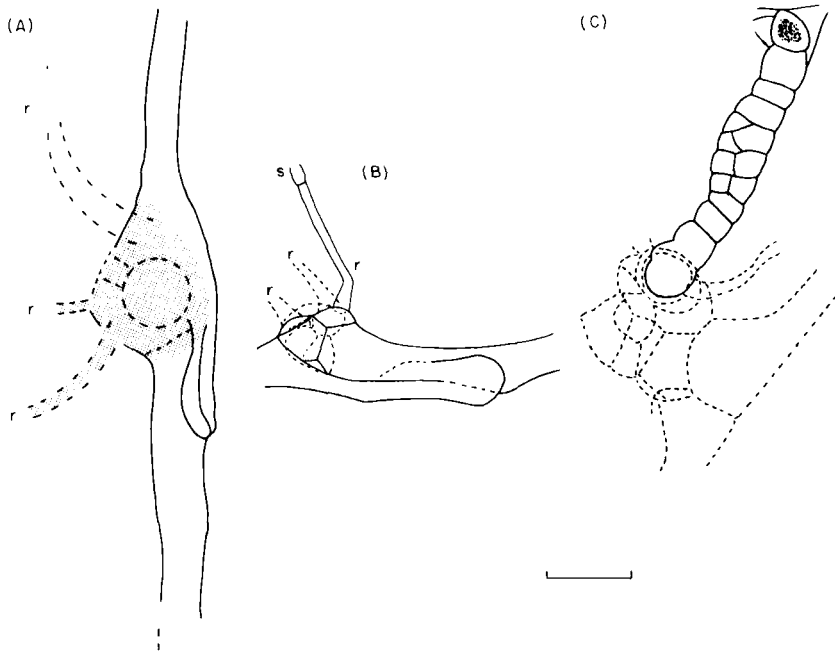


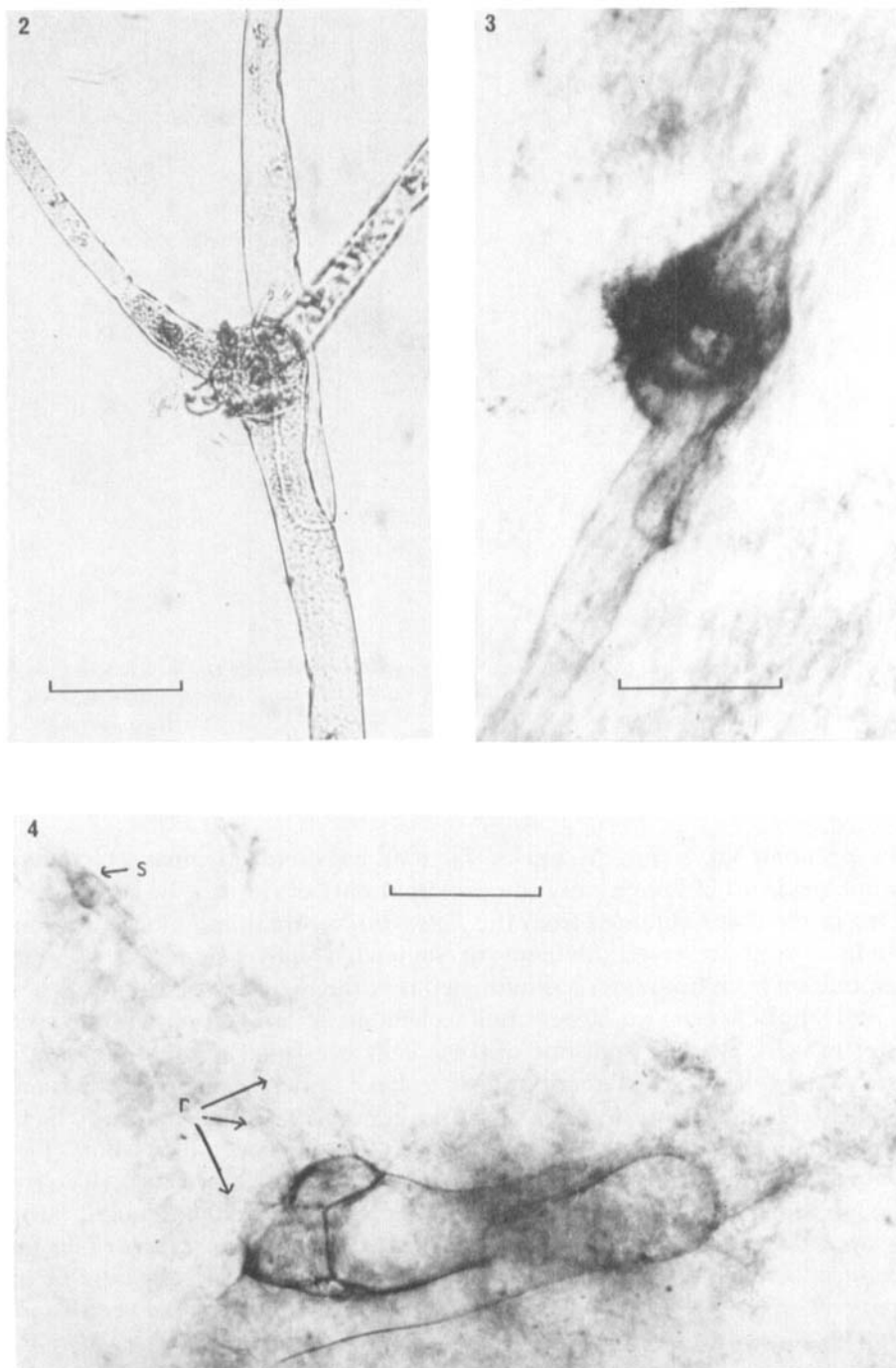
Figure 1. *Palaeonitella cranii*. A. Rhizoid-node No. 1. r,r,r, = branch rhizoids. cf. Fig. 3. B. Rhizoid-node No. 2. r,r,r = branch rhizoids. s = septum. cf. Fig. 4 & Fig. 8. C. ? rhizoid-borne pro-embryo. cf. Fig. 6. Scale bar equivalent to 100 μm .

distance on one side of the node, no connection with any axial structure can be detected.

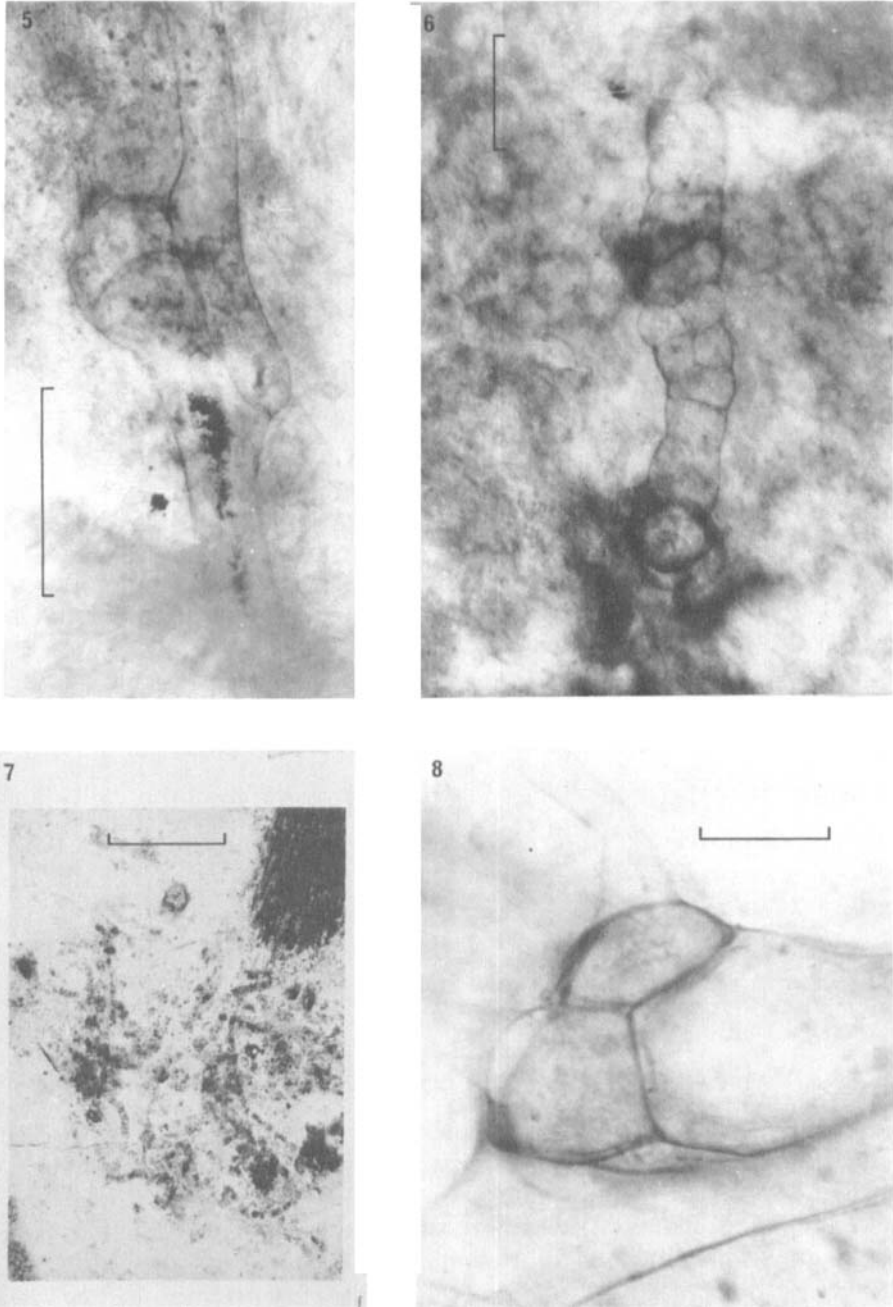
In specimen No. 3 (Fig. 5), one of the 'toes' has divided transversely and formed a branch rhizoid although only the proximal part of this can be seen.

One of the chips obtained from the *Palaeonitella*-containing blocks was found to include a well-preserved filament of somewhat barrel-shaped cells (Fig. 6). Examination from both sides has indicated that this distinctive structure is borne at the junction between two large tubular elements in association with an irregular cluster of cells. Arising from one of these cells is a small rhizoid-like outgrowth. Some of the cells of the filament appear to have undergone vertical divisions and one of the (?) two conical cells at its apex contains a brownish mass which may reflect former cell contents. The appearance of the specimen as a whole (Fig. 1C) is somewhat suggestive of a vegetative pro-embryo developed at a rhizoid-node, although the filament shows no clear indication of incipient nodal structure. However, the small size of the object and the rather granular texture of the matrix, make it difficult to distinguish between true cell walls and what might be merely superficial creases. It is also possible that development might have been abnormal. Although the septum between the two large tubular elements appears transverse, the junction cannot be interpreted as an axial node owing to the absence of an internodal cell. Occasional rhizoid-nodes with apparently transverse septa have been encountered and an example of such a node was figured by Kidston & Lang (1921: fig. 10).

In the absence of any direct evidence of continuity between the organs which have been grouped as *Palaeonitella cranii*, the question as to whether they all



Figures 2-4. Fig. 2. Rhizoid-node of *Nitella* sp. Scale bar equivalent to 100 μ m. Fig. 3. *Palaeonitella cranii*. Rhizoid-node No. 1. cf. Fig. 1A & Fig. 2. A. G. Lyon Collection Slide R.144. Scale bar equivalent to 200 μ m. Fig. 4. *Palaeonitella cranii*. Rhizoid-node No. 2. r,r,r=branch rhizoids; s=septum on branch rhizoid. Scale bar equivalent to 100 μ m.



Figures 5-8. Fig. 5. *Palaeonitella cranii*, Rhizoid-node No. 3. Enlarged 'toe' has divided once and formed a branch rhizoid. Scale bar equivalent to 200 μm . Fig. 6. (?) *Palaeonitella cranii*, ? rhizoid-borne pro-embryo. cf. Fig. 1C. A. G. Lyon Collection; Slide 137. Scale bar equivalent to 100 μm . Fig. 7. General view of filaments in white chert close to *Rhynia major* axes (bottom left of figure); some of the filaments are *Mackiella rotundatus*, others have not been described in this paper; Slide FSC 2202. Scale bar equivalent to 500 μm . Fig. 8. *Palaeonitella cranii*, rhizoid-node No. 2 enlarged to show details of divided 'toe'. Scale bar equivalent to 50 μm .

represent parts of a single species cannot yet be settled, although it remains likely. Furthermore, as no trace of reproductive organs of the characteristic charophyte type have ever been found in the Chert, conclusive evidence as to the nature of the remains is still lacking. Nevertheless, the highly distinctive structure of the rhizoid-nodes shown so clearly in these specimens, may serve to maintain and give added support to the belief that *Palaeonitella cranii*, either in whole, or in part, was probably a charophyte.

DIVISION: Chlorophyta
 CLASS: Chlorophyceae
 ORDER: Ulotrichales
 FAMILY: Ulotrichaceae

Mackiella D. S. Edwards & A. G. Lyon **genus novum**

DERIVATION: Named after Dr W. Mackie who discovered the Rhynie Chert.

Unbranched, unattached, uniseriate filaments with straight or rarely curved cross walls. Individual cells cylindrical, length approximately equal to diameter, rarely half that of diameter. Terminal cells rounded, longer than median cells of filament. Cell walls thin, non-stratified, mucilaginous sheath absent. Where preserved the cell contents are largely uniform and include fine granular material and a single darker body. Reproduction unknown.

TYPE SPECIES: *Mackiella rotundata* D. S. Edwards & A. G. Lyon (Figs 9–16).

Mackiella rotundata D. S. Edwards & A. G. Lyon **sp. nova**

DERIVATION: The specific epithet refers to the proportions of the individual cells.

Cell width 28–40 μm (\bar{x} 34 μm); cell length; normal intercalary cells 23–41 μm (\bar{x} 31.5 μm); terminal cells, 29–49 μm ; short cells, 16–18 μm (\bar{x} 17 μm) filament length, 3–25 cells.

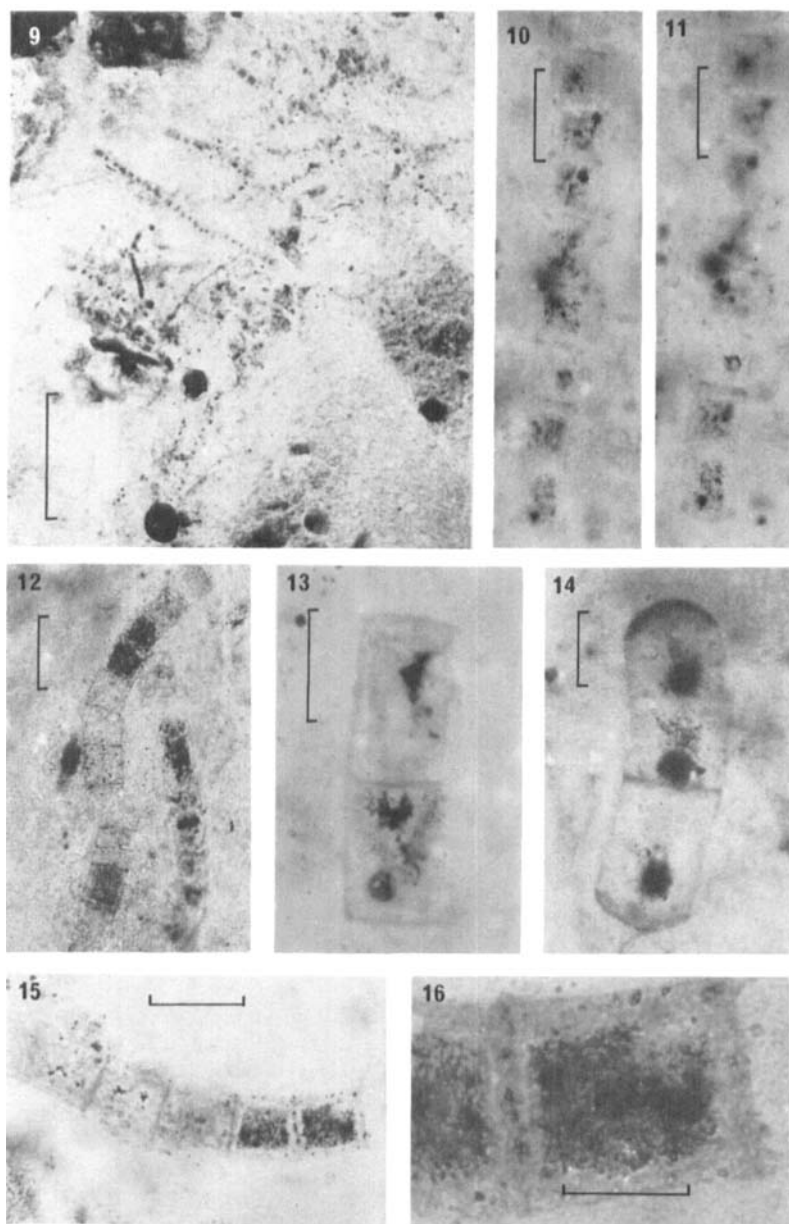
TYPE: Holotype from slide F.S.C. 2204, Hunterian Museum Palaeobotanical Collection, Glasgow. Illustrated in Fig. 10.

LOCALITY: Rhynie, Aberdeenshire.

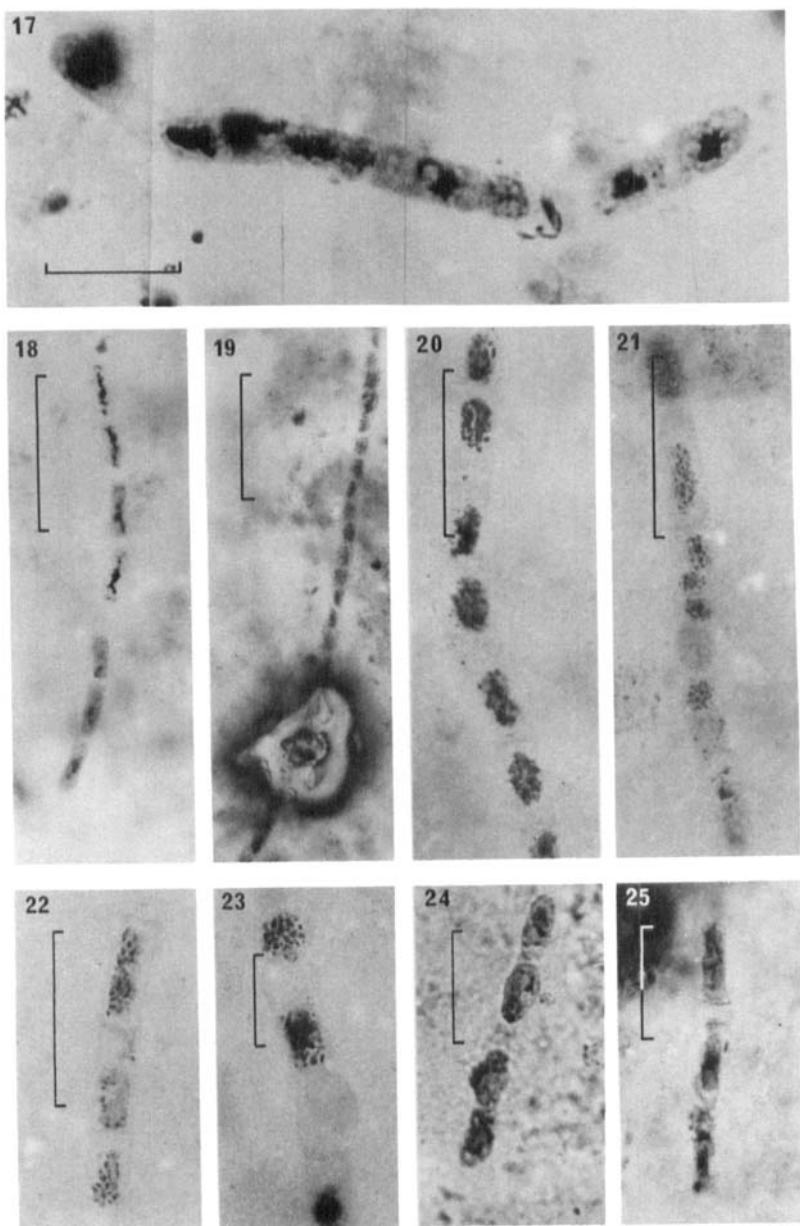
HORIZON: Rhynie Chert Bed, Scottish Lower Old Red Sandstone (Siegenian).

Filaments of this alga are fairly common in the white chert (to which it is confined), particularly in close proximity to *Rhynia major* axes, although it has not been found attached to that plant (Fig. 9). While cell width is fairly constant between different filaments, cell length varies both between and within filaments. Most filaments include one or two short cells amongst longer cells, possibly indicating a generalized capacity for cell division; in addition to this variation, some filaments consist of cells which are generally rather shorter. A few filaments have been found which are shorter than most—the shortest being of three cells (Fig. 13) and this may indicate a tendency for the filaments to fragment.

In most cases cell contents are a uniform light-brown with included granular areas; a regular feature is a larger spherical body (about 3.5 μm diameter), usually located towards one end of the cell. The best-preserved examples (Figs 10, 11, 14) show the brown background material (here interpreted as cytoplasmic remnants) to have contracted from the wall in some areas. The nature of the single dark body



Figures 9–16. Fig. 9. General view of filaments close to *Rhynia major* axis (off picture to bottom right); mostly *Mackiella rotundata*, the large dark circular bodies are spores of *R. major*; Slide FSC 2204. Scale bar equivalent to 300 μm . Figs 10–16. *Mackiella rotundata*. Figs 10 & 11. Views at two different focal planes of the type specimen, showing the single spherical body and dispersed cytoplasm in each cell; Slide FSC 2204. Scale bars equivalent to 50 μm . Fig. 12. 12-celled broken filament at left with all but three cells empty; these contain dense granular material; two short cells in the lower part of filament; Slide FSC 2203. Scale bar equivalent to 50 μm . Fig. 13. Two (of three) cells of a narrow incomplete filament, showing contraction of the cytoplasm which remains attached to the cross wall between the cells; Slide FSC 2229. Scale bar equivalent to 20 μm . Fig. 14. Three-celled (?) young filament, showing prominent dark spots; the cytoplasm is less conspicuous than in most filaments and is dispersed throughout the cell. Slide FSC 2204. Scale bar equivalent to 20 μm . Fig. 15. Short, incomplete filament with two granular cells; unlike the filament shown in Fig. 12, the remaining cells contain poorly preserved contents; Slide FSC 2204. Scale bar equivalent to 50 μm . Fig. 16. Granular cells of Fig. 15; the granules are not resolvable; Slide FSC 2204. Scale bar equivalent to 20 μm .



Figures 17-25. Figs 17-24. *Rhynchertia punctata*. Fig. 17. Composite picture of a vegetative filament, each cell with dispersed cytoplasm filling the lumen and containing a single large body (? chloroplast); in one cell this body appears to have uncoiled and broken through the cell wall; Slide FSC 2204. Scale bar equivalent to 40 μm . Fig. 18. Vegetative filament with contracted cell contents and granular contents (lower portion) and carbonized cells (upper portion); Slide FSC 2229. Scale bar equivalent to 100 μm . Fig. 19. Long (37-celled) reproductive filament, each cell of which contains large numbers of ovoid bodies (? spores); Slide FSC 2234. Scale bar equivalent to 100 μm . Fig. 20. Type specimen; a 13-celled reproductive filament; Slide FSC 2235. Scale bar equivalent to 40 μm . Fig. 21. Filament with cells of varying lengths and contents, some containing ovoid bodies, others with a more uniform appearance; Slide FSC 2235. Scale bar equivalent to 40 μm . Fig. 22. Three-celled (incomplete) reproductive filament with well-defined cell walls; Slide FSC 2235. Scale bar equivalent to 40 μm . Fig. 23. Filament with protuberant cells, provisionally assigned to *R. punctatus*. Cells with ovoid bodies alternate with empty cells in this filament; Slide FSC 2235. Scale bar equivalent to 20 μm . Fig. 24.

is unclear although three possibilities exist—it may be a collapsed chloroplast, a pyrenoid or a nucleus. Comparable bodies within fossil unicellular algae from the Bitter Springs Formation (Precambrian) have been interpreted as nuclei (Schopf, 1968, 1974) or as pyrenoids and associated chloroplasts (Oehler, 1977). While there is little direct evidence in support of either of these interpretations in *Mackiella*, the existence of discrete black areas within the spots could suggest a pyrenoidal rather than a nuclear nature. The lack of a distinct chloroplast may be a result of collapse and integration into the darker body. Some filaments contain dense granular material which is not resolvable into discrete units (Figs 11, 15). While it is possible that the granular nature of these cells reflects the presence of zoospores within them, it is equally likely that their appearance merely reflects a difference in preservation, particularly since filaments with this kind of cell have not been found in close proximity to those with indications of organelles.

Cell size, the presence of possible organelles and the distinctive contraction of cell contents suggest that *Mackiella* was a eukaryotic alga. No comparable fossil material has been found, but among extant algae, members of the orders Ulotrichales, Oedogoniales, Zygnematales (Chlorophyta) and Tribonematales (Xanthophyta) may be considered similar. Assignment of *Mackiella* to any of these orders is not possible since in each case *Mackiella* lacks at least one of the diagnostic vegetative features of these extant orders: Ulotrichales—fossil lacks the distinctive chloroplast; Oedogoniales—fossil lacks cap cells (although certain living members produce these only rarely) (Fritsch, 1935); Zygnematales—fossil lacks the distinctive chloroplasts; Tribonematales—fossil lacks 'H-pieces' in the cell wall (although they are frequent in some living taxa (*Bumilleria*) and absent in others (*Heterothrix*) (Fritsch, 1935; Smith, 1950)). Of these orders, the most similar forms to *Mackiella* are amongst the Ulotrichales—*Klebsormidium* has unattached filaments, cells with a single pyrenoid, and may fragment into short filaments (Bold & Wynne, 1978); however, cell width is rather narrow—up to 14 μm in *Hormidium* (*Klebsormidium*) *flaccidum* (Kütz.) A. Braun (from Ramanathan, 1964). Filaments of *Ulothrix zonata* (Weber & Mohr.) Kütz. have a similar cell width/length ratio with cells 11–45 μm wide, but typically the cell wall is thickened in older filaments (young filaments do not show this feature) (Ramanathan, 1964: 30). On the basis of these similarities, *Mackiella* is tentatively assigned to the Ulotrichales.

Rhynchertia* D. S. Edwards & A. G. Lyon *genus novum

DERIVATION: Named after the Rhynie Chert beds.

Unbranched, unattached, uniseriate multicellular filaments with cells of narrow diameter (8–17 μm) and variable length, most commonly twice the width of the filament, rarely much shorter. Terminal cells of filament slightly longer than median cells, bluntly rounded. Cells thin-walled, lacking a mucilage sheath. Cell contents uniform or with a single dark body or containing many small ovoid bodies. Reproduction (?) by the production of many spores per cell.

TYPE SPECIES: *Rhynchertia punctata* D. S. Edwards & A. G. Lyon

Short vegetative filament provisionally assigned to *R. punctatus* with cell walls not preserved but showing the protuberant nature of the cells; found in the gelatinous zone of *Nematoplexus*; Peel 38B/B. 17 (A. G. Lyon Collection). Scale bar equivalent to 150 μm . Fig. 25. Large-celled filament showing contraction of the cell contents; Slide FSC 2233. Scale bar equivalent to 150 μm .

***Rhynchertia punctata* D. S. Edwards & A. G. Lyon sp. nova**

DERIVATION: The epithet refers to the spots in some of the cells.

Cell width 8–16.5 μm (\bar{x} 11 μm), cell length about twice width 16–40 μm (\bar{x} 21.5 μm). Filaments vegetative, 'reproductive' or mixed.

TYPE: Holotype from slide FSC 2235, Hunterian Museum Palaeobotanical Collection, Glasgow. Illustrated in Fig. 20.

ILLUSTRATIONS: Figures 17–24.

LOCALITY: Rhynie, Aberdeenshire.

HORIZON: Rhynie Chert Bed, Scottish Lower Old Red Sandstone (Siegenian).

The narrow filaments of *R. punctata* are fairly common in the white chert and they have also been found in association with *Nematoplexus rhyiensis* Lyon where they are confined to a possible gelatinous (post-mortem degradation?) zone of the plant (Lyon, 1962).

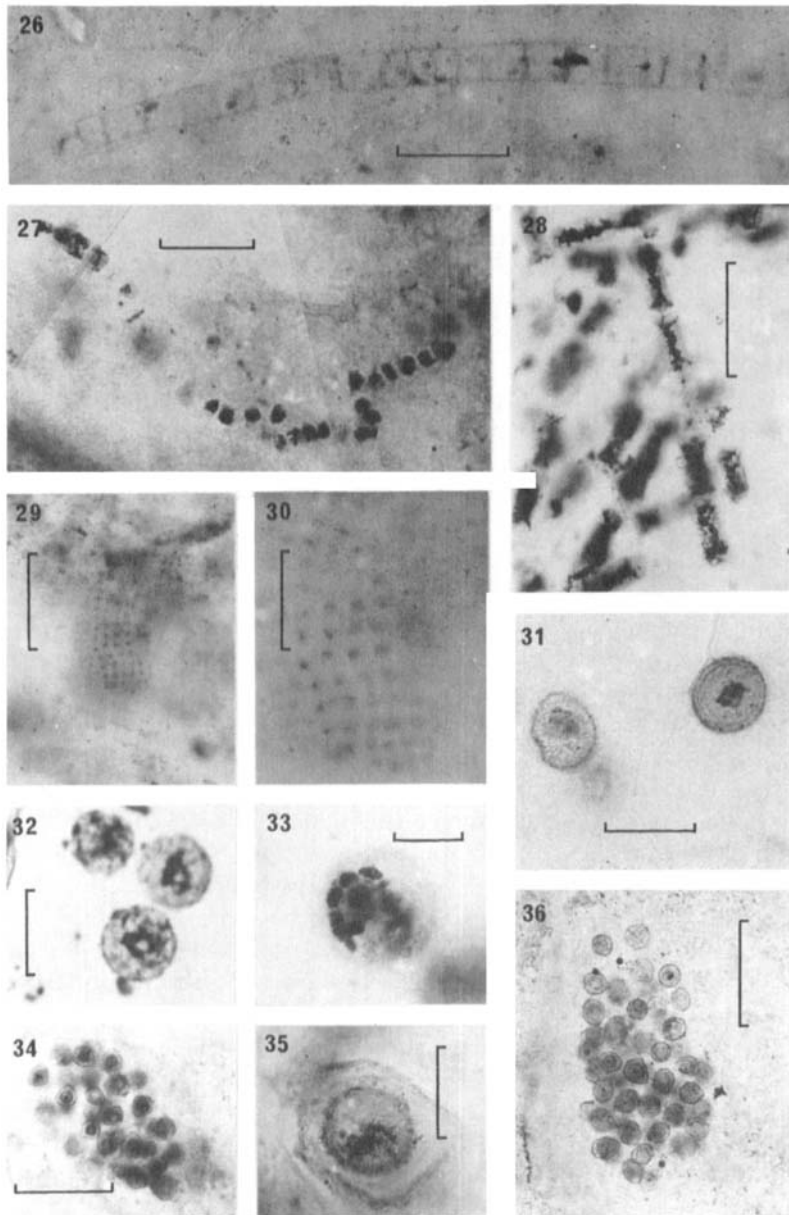
Most vegetative cells have poorly-defined walls and amorphous contents, but a few are better preserved. In these specimens there are indications of internal differentiation. A number of darker areas may be visible (Fig. 18) or a single rather irregular body may occupy the centre of the cell (Fig. 17). This body may be the remains of a single large organelle, possibly a chloroplast.

Some complete filaments (or individual cells of otherwise vegetative filaments), consist of cells which contain a large number of small (about 0.4 μm maximum length) opaque ovoid bodies (Figs 19, 20). These bodies are interpreted as being reproductive (? zoospores or gametes) since possible differences in preservation seem insufficient to explain the regularity of their occurrence and the mixed nature of some filaments. It has not been possible to count the exact number of bodies within an individual cell but there are about 30–50.

Extant zoospore-producing unbranched filamentous uninucleate algae are found in the Ulotrichales and while details of the chloroplast structure are lacking for *Rhynchertia*, it is reasonable to assign the plant to that order on the basis of gross morphology: in particular, *Ulothrix cylindricum* Prescott has cells of similar shape and size (10–12.5 μm diameter, 2–3 times as long as wide) (Ramanathan, 1964: 36).

Commonly associated with filaments of *R. punctata* are filaments of similar size and general appearance (? spores in some cells, other cells containing one or two discrete bodies), but which include cells with lateral protuberances (Figs 23, 24). Filaments may contain several such cells or just a single cell of this kind. The other cells are often of variable length, frequently slightly shorter than typical *R. punctata* cells, and may even appear spherical rather than cylindrical. The bulges on the sides of the cells are somewhat suggestive of early stages in branching as found in extant Cladophorales and Chaetophorales, although in these taxa the protuberances are confined to one end of the cell. *Hormidium* (*Klebsormidium*) *rivulare* (Kütz.) A. Braun shows a similar variation in cell shape when the filaments undergo false branching or become geniculate (Ramanathan, 1964); these latter features have not been observed in the fossil material.

In the absence of any sharp distinction between cell length or width or cell contents, it seems likely that these filaments represent a different growth form of *R. punctatus* and they are tentatively referred to that taxon.



Figures 26–36. Fig. 26. Composite photograph of narrow, well-preserved filament with short and long cells, most of which contain a single darker spot; Slide FSC 2244. Scale bar equivalent to 30 μm . Fig. 27. Composite photograph of filament with spherical cells (to right) each containing a large dark body and elongate empty cells (centre left). The elongate structure (centre top) is a fungal hypha; Slide FSC 2204. Scale bar equivalent to 50 μm . Fig. 28. Five-celled filament of relatively large cells, each containing a carbonised reticulum; Slide FSC 2202. Scale bar equivalent to 100 μm . Figs 29 & 30. *Rhyniococcus uniformis*, type specimen; The spherical cells containing a central dark spot have poorly defined cell walls (visible in Fig. 30 centre); Slide FSC 2235. Scale bars equivalent to 50 μm —Fig. 29, to 20 μm .—Fig. 30. Figs 31 & 32. Unicells with irregular contents A. G. Lyon Collection. Fig. 31—slide FSC 2242. Scale bar equivalent to 20 μm . Fig. 32—Peel 38B/B.8, Scale bar equivalent to 20 μm . Fig. 33. Unicell containing ovoid bodies; a larger spherical body can be seen in the upper left of the cell; Slide FSC 2240. Scale bar equivalent to 10 μm . Figs 34–36. Unicells with two outer coverings; the middle layer remains attached to the thin outer one in one area in many examples (at right in Fig. 35); Figs 34 & 35, chip preparation 83. A. G. Lyon Collection. Fig. 36 Slide R1187, Lang Collection. Scale bars equivalent to 100 μm —Figs 34 & 36; to 10 μm —Fig. 35.

Filamentous algae incertae sedis: The affinities of the large-celled filamentous algae shown in Fig. 25 and Fig. 30 are not clear. The smaller form (cell width $22\text{--}32\ \mu\text{m}$, mean $27\ \mu\text{m}$; cell length $53\text{--}73\ \mu\text{m}$, mean $60\ \mu\text{m}$) is confined to two sections from a single block and a single filament from another block, while the larger form (cell width $24\text{--}33\ \mu\text{m}$, mean $30\ \mu\text{m}$) is found in several blocks of the white chert. The short-celled form is generally poorly-preserved with little indication of cell contents apart from a carbonized reticulum, and is often found as individual cells dispersed through the matrix. The longest filament found has five cells with the terminal cells having bluntly rounded ends. The larger-celled filaments have better-preserved cell contents, with indications of contents but, possibly due to the thickness of the sections relative to cell length, filaments longer than three cells have not been observed.

The large cell size of these filaments invites comparison with certain Chlorophyta, particularly members of the Cladophorales and Zygnematales (for example *Zygnema ornatum* (Li) Transeau, in Randhawa, 1959: 248): but lack of cell contents or reproductive bodies in the fossil material precludes a more definite assignment.

Figure 26 shows the only specimen of a well-preserved filament which has been found. The cells are about $12\ \mu\text{m}$ wide and fall into two length groupings—the longer cells being about $14\ \mu\text{m}$ long and the shorter, (two groups of four cells), about $7.5\ \mu\text{m}$ long. One of the terminal cells is much longer (about $29\ \mu\text{m}$) and is bluntly rounded, the other appears almost spherical. Cell contents are indistinct but in some cells there is a single faint darker spot. The filament is similar in general appearance to macrandrous species of *Oedogonium* with the shorter cells representing antheridia, but the lack of cap cells limits this comparison.

One specimen of a poorly-preserved filament (Fig. 27) also contains two sizes of cells—the shorter 16 cells are rectangular in section, between 11 and $13\ \mu\text{m}$ wide and include a single dark spherical body with indications of internal differentiation, while the larger five cells are between 26 and $40\ \mu\text{m}$ long and appear empty. Although comparisons based on a single specimen are highly speculative, it is worth noting that the cell diameter is similar to that of *Langiella fritschii* (vegetative cells $9\text{--}12\ \mu\text{m}$, akinetes up to $18\ \mu\text{m}$) (Croft & George, 1959) but this specimen lacks the mucilage sheath and has longer cells than *Langiella*. In addition, the occurrence of discrete spherical bodies within the cells is more compatible with a eukaryotic rather than a prokaryotic organization, particularly since in *Langiella* the cell contents are extremely uniform and have contracted uniformly (see Oehler, 1977) away from the walls.

Palmelloid and coccoid algae

DIVISION:	Cyanophyta
CLASS:	Schizophyceae
ORDER:	Chroococcales
FAMILY:	Chroococcaceae

Rhyniococcus D. S. Edwards & A. G. Lyon **genus novum**

DERIVATION: A coccus from the Rhynie Chert bed.

Colonial alga consisting of a one cell thick flat, or nearly flat, sheet of cells. Cells regularly arranged in rows, not grouped within the sheet. Reproduction unknown.

TYPE: *Rhyniococcus uniformis* D. S. Edwards & A. G. Lyon

***Rhyniococcus uniformis* D. S. Edwards & A. G. Lyon sp. nova**

DERIVATION: Referring to the uniform spacing of the cells in the sheet.

Cells 4 μm diameter, separated by approximately 1 μm . Cell contents indistinct, consisting of a central dark spot.

TYPE: From slide FSC 2235, Hunterian Museum Palaeobotanical Collection, Glasgow. Illustrated in Figs 29 & 30.

LOCALITY: Rhynie, Aberdeenshire.

HORIZON: Rhynie Chert Bed. Scottish Lower Old Red Sandstone (Siegenian).

Both the Chlorophyta and Cyanophyta include forms with a similar organization—*Prasiola* (Ulvales) and *Merismopedia* (Chroococcales) include species with cells arranged in rows and not (as is usual in both genera) arranged in groups of two or more (e.g. *P. furfuraceae* (Nert.) Menegh.—Pascher (1914); *M. trolleri* Bachman—Pascher (1925) and some forms of *M. tenuissima* Lemm.—Desikachary (1959)). The small size of the cells of *R. uniformis* is more typical of a prokaryotic rather than a eukaryotic alga (Schopf & Oehler, 1976) and is comparable with several species of *Merismopedia*; *Rhyniococcus* is therefore referred to the Chroococcales.

Unicellular algae Incertae Sedis: The three kinds of unicellular algae which have been distinguished will not receive formal taxonomic treatment at the present time. The most common kind has been found in both the white and the black chert. Two size classes can be recognized, the larger having a diameter of 11–21 μm (\bar{x} 15 μm) and the smaller with a diameter of 8–11 μm (\bar{x} 10 μm). The larger (Fig. 31) has been found in the white chert and in the zone surrounding *Nematoplexus* (Lyon, 1962); the smaller is confined to the black chert. The ‘? algal unicells’ figured in Kidston & Lang, (1921: Pl. VII, figs 77, 78) fall into the smaller-celled category. Apart from differences in size, unicells of both categories are similar in general appearance. The cell contents have contracted slightly from the wall and in some cases consist of a single large dark body which does not appear uniform. In other cases, smaller irregularly shaped units are dispersed throughout the cell.

The existence of possible evidence of organelles and cytoplasmic contraction is suggestive of a eukaryotic rather than a prokaryotic alga. Possible eukaryotic unicellular algae have been reported from several Precambrian deposits (e.g. *Maculosphaera* from the Beck Spring Dolomite (Licari, 1978); *Caryosphaeroides*, *Glenobotrydion* and *Globophycus* from the Bitter Springs Formation (Schopf, 1968; Oehler, 1977) but most of these consist of individuals with a single prominent central or eccentric spot; rarely is there any indication of discrete contents and the eukaryotic nature of such cells has been questioned (Knoll & Barghoorn, 1975; Colubic & Barghoorn, 1977; Knoll, Barghoorn & Awrmik, 1978; Francis, Barghoorn & Margulis, 1978). The Rhynie Chert unicells differ from typical spot cells in that their contents are made up of several discrete bodies, partially or completely fused into one larger entity and are thus not strictly comparable with Precambrian material (e.g. *Glenobotrydion* Schopf and *Caryosphaeroides* Schopf) which is tentatively accepted as eukaryotic by some authors (Oehler, 1977; Tappan, 1980).

A second kind (Fig. 32) of thin-walled unicell (diameter 16–20 μm) has been found in several sections of the white chert and differs from the first kind in that the cells contain a number of opaque bodies, each about 3.75 μm long and up to 2.0 μm wide. A larger black spherical body is also present in some cells. Although these structures may be merely crystals, they could be gametes or aplanospores, the larger body being two or three of the smaller ones clumped together, or they may represent pyrenoids, the chloroplast having degenerated. The organization of this alga (which may be the larger of the first type in a reproductive state) is similar in many respects to extant Chlorococcaceae which reproduce by zoospores or aplanospores and which have one to several pyrenoids in each cell (Fritsch, 1935; Bold & Wynne, 1978), and its affinities may be in that direction.

While the affinities of the unicells described above may be with Chlorophyta, the relationships of the organisms shown in Figs. 34–36 are less obvious. The central sphere (*c.* 14 μm diameter) often contains a spot, although sometimes the cell contents appear more diffuse. It is surrounded by an envelope which appears to have contracted from a thin-walled, outer covering 24–34 μm (\bar{x} 27 μm) in diameter but remains attached to it at one point, giving the impression of an exit pore. Specimens of these unicells are found in groups in the black chert, and in two examples (Chip preparation 83 and slide R1187, Lang Collection, Manchester Museum) there is an indication of a boundary layer to the cell group, suggesting that they were embedded within mucilage or developed within a larger structure. Slide R1187 also contains remains of *Lepidocaris* and fragments of *Palaeonitella* but the unicells appear unconnected with either of these organisms. Unicells of similar morphology have been described as “encysted cells of *Caryosphaeroides pristina* ?” by Schopf (1968: 682) cells of *Gleodinopsis lamellosa* described by Schopf & Blacic (1971) and *Cumulasphaera lamellosa* described by Edhorn (1973) also show similarities to the Rhynie unicells. Tappan (1980) regards these as of uncertain systematic position, possibly of chroococcacean affinity.

GENERAL DISCUSSION

It is apparent from the above descriptions that the Rhynie Chert microflora includes a wide range of algae, many of which are of an eukaryotic aspect. However, the algae are localized within the deposit—the prokaryotic forms being largely confined to the black chert and the eukaryotic to the white. Algae are rare in the black chert; *Kidstoniella*, *Langiella* and *Rhyniella* all occur in a single chip (Croft & George, 1959) and we know of no other specimens, *Archaeothrix oscillatoriformis* was also reported from a single group of samples (Kidston & Lang, 1921) although a few additional specimens have since been found. *Archaeothrix contexta* is more common and several specimens of this have been encountered. *Palaeonitella cranii* is much more widespread and occasionally occurs in quite compact masses. Algae are far more common in the white chert with five being confined to this rock. However, filaments of *Rhynchertia* and unicells have also been found in the black chert, particularly in association with nematophytalean remains. It is likely that the differences in the algal flora reflect a difference in the environmental or preservation conditions. In this connection it is interesting to note that cyanobacteria are absent from acid waters with a pH of less than 4 (Brock, 1973), possibly indicating a more acid environment for the algae in the white chert.

Kidston & Lang (1921 : 895) thought that the tracheophytes in the deposit had grown on a substrate saturated with hot siliceous acid water and that the chert as a whole had silicified from the base upwards. Tasch (1957) favoured their original interpretation (Kidston & Lang, 1917 : 764) that the bed silicified after its full thickness had accumulated—but also suggested an influx of hot siliceous water at an early stage in the history of the deposit (Bed A'') to explain the restricted distribution of algal and animal fossils which were washed in amongst the vascular plants. The latter interpretation is more in keeping with the rarity of algae in the black chert—in comparison with present day hot spring waters the deposit is very deficient in cyanobacterial remains.

The algae in the white chert seem more likely to have been growing amongst axes of *Rhynia major*—the stratification of the blocks, the alignment of the axes and their localized occurrence, indicates gradual flooding of a stand of *R. major* (which then started to decay), the growth of the algae and subsequent silicification. This suggests a sequence of chertification similar in some ways to that proposed for the Pleistocene deposits of some East African natron lakes (e.g. Lake Nagadi) in which a sudden lowering of pH in a silica-saturated environment resulted in a deposition of silicates (Nagadiite); subsequent freshwater leaching of the silicates formed bedded chert (Surdam & Eugster, 1976; Collinson, 1978). However, such a sequence commences in an alkaline environment and this in turn suggests either that the pH controlled algal distribution indicated above is incorrect or that the algae in the white chert were very limited temporally within the sequence. Further examination of this possibility and an explanation for the white colour of the algal containing chert requires a detailed petrological examination which we have not attempted.

Fossil floras comparable with that of the Rhynie Chert are rare—most Precambrian and Cambrian microfossil assemblages are stromatolitic with a high proportion of cyanobacteria and were formed under saline or intermittently saline, shallow (rarely deep) water conditions (see Monty, 1977), although some shale-facies microbiotas are also known (Horodyski, 1980; Zhongying, 1982). The flora of the Middle Devonian Onondaga Chert consists of possible freshwater algae which were suggested to have been washed into an off-shore shallow water environment before preservation (Baschnagel, 1942, 1966) and includes forms similar to modern Ulotrichales (cf. *Geminella*, Oedogoniales (*Palaeoedogonium*) and Zygnematales (*Palaeoclosterium*). The algal flora of the Kalkberg Limestone (Lower Devonian) is very poorly-preserved (mainly as pyrite casts) but includes possible Ulotrichaceae, Nostocaceae, Chroococcaceae and Scytonemataceae forms (Wincander & Schopf, 1974); the depositional environment was similar to that of the Onondaga Chert—a shallow marine shelf. Although the Rhynie Chert contains similar elements to both these floras, the difference in depositional environments limits any meaningful comparison.

Palaeonitella described from the Late Devonian Caballos novaculite (Fairchild, Schopf & Folk, 1973) may be a pseudofossil (Schopf, 1974) as may also be the other filamentous forms from that deposit, particularly since the formation has recently been reinterpreted as a deep-water deposit (Folk & McBride, 1976; Jenkyns, 1978). The algal flora described by Grüss (1928) from the Devonian of Germany includes ulotrichalean forms but, as has been pointed out by Fairchild *et al.* (1973), these filaments may be modern contaminants since they were found in macerates rather than in thin sections. The siphonaceous *Courvoisiella* described by

Niklas (1976) was apparently epiphytic on *Archaeopteris* but no siphonaceous or epiphytic forms have been found in the chert.

The algal flora of the Rhynie Chert thus occupies a rather isolated position in relation to other floras but serves to emphasize the diversity of forms in a freshwater (siliceous) habitat during early Devonian time. It also provides one of the earliest records of non-calcareous filamentous chlorophytes and suggests that the vegetative structure of the Charophyta was well-developed by that time.

ACKNOWLEDGEMENTS

We would like to thank Dr J. Franks (Herbarium, Manchester Museum) and Dr W. D. I. Rolfe (Hunterian Museum, Glasgow) for the loan of specimens in their care. Part of this work was carried out at University College, Cardiff, during the tenure of a Science Research Council studentship (awarded to D.S.E.).

REFERENCES

- BASCHNAGEL, R. A., 1942. Some microfossils from the Onondaga Chert of Central New York. *Bulletin of the Buffalo Society of Natural Sciences*, 17: 1-8.
- BASCHNAGEL, R. A., 1966. New fossil algae from the Middle Devonian of New York. *Transactions of the American Microscopical Society*, 85: 297-302.
- BOLD, H. C. & WYNNE, M. T., 1978. *Introduction to the Algae*. New Jersey: Prentice-Hall Inc.
- BROCK, T. D., 1973. Lower pH limit for the existence of blue-green algae: evolutionary and ecological implications. *Science*, 179: 480-482.
- COLLINSON, J. D., 1978. Lakes. In H. G. Reading (Ed.), *Sedimentary Environments and Facies*: 61-79. Oxford: Blackwell.
- CROFT, W. N. & GEORGE, E. A., 1959. Blue-green algae from the Middle Devonian of Rhynie, Aberdeenshire. *Bulletin of the British Museum (Natural History), Geology*, 3: 341-353.
- DESIKACHARY, T. V., 1959. *Cyanophyta*. New Delhi: Indian Council of Agricultural Research.
- DOWNIE, C., 1973. Observations on the nature of acritarchs. *Palaentology*, 16: 239-259.
- EDHORN, A. S., 1973. Further investigations of fossils from the Animikie, Thunder Bay, Ontario. *Proceedings of the Geological Association of Canada*, 25: 37-65.
- EMBERGER, L., 1968. *Les Plantes Fossiles*. Paris: Masson et cie.
- FAIRCHILD, T. R., SCHOPF, J. W. & FOLK, R. L., 1973. Filamentous algal microfossils from the Caballos Novaculite, Devonian of Texas. *Journal of Palaeontology*, 47: 946-952.
- FOLK, R. L. & McBRIDE, E. F., 1976. The Caballos Novaculite revisited, Part 1: origin of novaculite members. *Journal of Sedimentary Petrology*, 46: 659-669.
- FRANCIS, S., BARGHOORN, E. S. & MARGULLIS, L., 1978. On the experimental silicification of microorganisms. III. Implications of the preservation of the green prokaryotic alga *Prochloron* and other coccoids for interpretation of the microbial fossil record. *Precambrian Research*, 7: 377-383.
- FRITSCH, F. E., 1935. *The Structure and Reproduction of the Algae*. Cambridge: Cambridge University Press.
- GOLUBIC, S. & BARGHOORN, E. S., 1977. Interpretation of microbial fossils with special reference to the Precambrian. In E. Flugel (Ed.), *Fossil Algae, Recent Results and Developments*: 1-14. Berlin: Springer-Verlag.
- GROVES, J. & BULLOCK-WEBSTER, G. R., 1920. *The British Charophyta*, Vol. 1. London: Ray Society.
- GRÜSS, J., 1928. Zur Biologie Devonischer Thalophyten. *Paläobiologica*, 1: 487-518.
- HAYWARD, J., 1974. Studies on the growth of *Stichococcus bacillaris* Naeg. in culture. *Journal of the Marine Biological Association*, 54: 261-268.
- HORODYSKI, R. J., 1980. Middle Proterozoic Shale-facies microbiota from the Lower Belt Supergroup, Little Belt Mountains, Montana. *Journal of Palaeontology*, 54: 649-663.
- HORNE, J., MACKIE, W., FLETT, J. S., GORDON, W. T., HICKLING, G., KIDSTON, R., PEACH, B. N. & WATSON, D. M. S., 1916. The plant-bearing cherts at Rhynie. *Report of the British Association for the Advancement of Science, 1916*: 206-216.
- JENKYN, H. C., 1978. Pelagic environments. In H. G. Reading (Ed.), *Sedimentary Environments and Facies*: 314-371. Oxford: Blackwell.
- KIDSTON, R. & LANG, W. H., 1917. On Old Red Sandstone Plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part I. *Rhynia Gwynne-vaughanii* Kidston & Lang. *Transactions of the Royal Society of Edinburgh*, 51: 761-784.
- KIDSTON, R. & LANG, W. H., 1921. On Old Red Sandstone plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part V. The Thalophyta occurring in the peat-bed; the succession of plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. *Transactions of the Royal Society of Edinburgh*, 52: 855-902.

- KNOLL, A. H. & BARGHOORN, E. S., 1975. Precambrian eukaryotic organisms: A reassessment of the evidence. *Science*, 190: 52-54.
- KNOLL, A. H., BARGHOORN, E. S. & AWRAMIK, S. M., 1978. New microorganisms from the Aphebian Gunflint Iron Formation, Ontario. *Journal of Palaeontology*, 52: 956-992.
- LICARI, G., 1978. Biogeology of the Late Pre-phanerozoic Beck Spring Dolomite of Eastern California. *Journal of Palaeontology*, 52: 767-792.
- LYON, A. G., 1962. On the fragmentary remains of an organism referable to the Nematophytales, from the Rhynie Chert, "*Nematoplexus rhyniensis*" gen. et sp. nov. *Transactions of the Royal Society of Edinburgh*, 65: 79-87.
- MONTY, C., 1977. Evolving Concepts on the Nature and the Ecological Significance of Stromatolites. In E. Flugel (Ed.), *Fossil Algae. Recent Results and Developments*: 15-35. Berlin. Springer-Verlag.
- NIKLAS, K. J., 1976. Morphological and chemical examination of *Couroisiella ctenomorpha* gen. et sp. nov., a siphonous alga from the Upper Devonian, West Virginia, U.S.A. *Review of Palaeobotany and Palynology*, 21: 187-203.
- OEHLER, D. Z., 1977. Pyrenoid-like structures in Late Precambrian Algae from the Bitter Springs Formation of Australia. *Journal of Palaeontology*, 81: 885-890.
- PASCHER, A. (Ed.), 1914. *Die Süßwasser-Flora Deutschlands, Österreichs und der Schweiz. Heft 6, Chlorophyceae III*. Jena: Fischer.
- PASCHER, A. (Ed.), 1925. *Die Süßwasser-Flora Deutschlands, Österreichs und der Schweiz. Heft 12, Cyanophyceae*. Jena: Fischer.
- PIA, J., 1927. Thalophyta. In M. Hirmer (Ed.), *Handbuch der Paläobotanik, 1*: 31-136. Munich: Oldenbourg.
- RAMANATHAN, K. R., 1964. *Ulotrichales*. New Delhi: Indian Council of Agricultural Research.
- RANDHAWA, M. S., 1959. *Zygnemaceae*. New Delhi: Indian Council of Agricultural Research.
- RICHARDSON, J. B., 1967. Some British Lower Devonian spore assemblages and their stratigraphic significance. *Review of Palaeobotany and Palynology*, 1: 111-129.
- SCHOPF, J. W., 1968. Microflora of the Bitter Springs Formation, late Precambrian, central Australia. *Journal of Palaeontology*, 42: 651-688.
- SCHOPF, J. W., 1974. Palaeobiology of the Precambrian: the age of blue-green algae. *Evolutionary Biology*, 7: 1-43.
- SCHOPF, J. W. & BLACIC, J. M., 1971. New microorganisms from the Bitter Springs Formation (late Precambrian) of the north-central Amadeus Basin, Australia. *Journal of Palaeontology*, 45: 925-960.
- SCHOPF, J. W. & OEHLER, D. Z., 1976. How old are the eukaryotes? *Science*, 193: 47-50.
- SMITH, G. M., 1950. *The Fresh-water Algae of the United States*, 2nd ed. New York: McGraw-Hill Book Co.
- SURDAM, R. C. & EUGSTER, H. P., 1976. Mineral reactions in the sedimentary deposits of the Lake Magadi region, Kenya. *Bulletin of the Geology Society of America*, 87: 1739-1752.
- TAPPAN, H., 1980. *The Palaeobiology of Plant Protista*. San Francisco: W. H. Freeman & Co.
- TASCH, P., 1957. Flora and fauna of the Rhynie Chert; A paleoecological reevaluation of published evidence. *University of Wichita, Bulletin*, 32: 3-24.
- WALTON, J., 1953. *An Introduction to the Study of Fossil Plants*. London: A. & C. Black.
- WESTOLL, T. S., 1977. In M. R. House et al. (Eds), A correlation of Devonian rocks of the British Isles. *Special Report of the Geological Society of London*. 7: No. 8: 1-110.
- WICANDER, E. R. & SCHOPF, J. W., 1974. Microorganisms from the Kalkberg Limestone (Lower Devonian) of New York State. *Journal of Palaeontology*, 48: 74-77.
- ZHONGYING, Z., 1982. Upper Proterozoic microfossils from the Summer Isles, N.W. Scotland. *Palaeontology*, 25: 443-460.