A NEW CALCAREOUS GREEN ALGA FROM THE MIDDLE JURASSIC OF ENGLAND: ITS RELATIONSHIPS AND EVOLUTIONARY POSITION

by GRAHAM F. ELLIOTT

ABSTRACT. *Leckhamptonella llewellyae* gen. et sp. nov., is described from the Middle Jurassic (Inferior Oolite; Aalenian) of the Cotswold district, England. Although known only from fragmentary material, it is recognizable as the remains of a new serial-segmented member of the Udoteaceae (Chlorophyta). It is compared with *Boueina* and *Arabicodium* (both Mesozoic) and *Halimeda* (Cretaceous-Recent), and shows certain affinities with the latter especially. The evolution of serial-segmented Udoteaceae from Lower Palaeozoic to Recent is briefly reviewed.

THE fossil described below occurs as pieces and fragments of original small calcareous-walled hollow ovoids, near-circular in transverse section and curved-elongate in vertical section. The walls show a very distinctive structure formed by irregular but characteristic branching pores, with possible vestiges of a structure interior to the wall. The material studied occurs in an oomicrite with subordinate echinoderm, molluscan, brachiopod, and other organic fragments, often worn and encrusted and presumed current-swept and not on the site of growth.

The new fossil does not show the optical extinction of echinoderm-calcite pieces, nor the laminar structure of molluscs or brachiopods. The wall-structure is not that of stromatoporoids or hydrozoa, and has not the spicular mesh of any known sponge. It does, however, have the characteristics of certain green calcareous algae, notably the Order Dasycladales and the family Udoteaceae of the Order Caulerpales. The resemblance is very much with the cortical structure of the 'serial-segmented' members of the Udoteaceae (*Halimeda*, and various extinct genera discussed below). It possesses the marked irregularity in detail which is so characteristic, and the general pore-plan is that of yet another variant of the branching utricles of the family. It does not, in most specimens, show clearly the longitudinal medullary threads appropriate to this interpretation, but two well-preserved pieces show traces of this structure, which has to be carefully distinguished from peripheral diagenesis and staining of the clasts. The absence is probably due to the rolled state of the fragments and the usual originally weak medullary calcification in the Udoteaceae. In the Permian *Tauridium*, normally found fragmented, very much more abundant material than is available with the present fossil still leaves reconstruction a difficult task.

If comparison is made with the Udoteacean *Ovulites* (Cretaceous, Cenozoic), the external dimensions and shape of the Cotswold fossil as so far known are comparable with those of *O. margaritula* (Lmk.) Munier-Chalmas (cf. Massieux 1966). In these, however, and other *Ovulites* spp., the calcareous wall is thinner, the pores near-uniformly straight, thin, and radial, and no trace survives of medullary structures. *Ovulites* is usually regarded as remains of a plant comparable with the living *Penicillus*, the 'Neptune's Shaving Brush', where the thallus is of different morphology to that of *Halimeda*. *Ovulites* and *Halimeda* both appear in the Cretaceous, and it is interesting that the new Jurassic fossil brings both to mind, even if apparently much more similar to the latter in structure.

If the present remains are envisaged as those of a dasycladalean, they are anomalous in showing udoteacean irregularity and not a verticillate arrangement. The thin calcification of the swollen heads of the Jurassic *Petrascula* and *Coniporella* belongs to very much larger individuals.

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It would thus seem that the fragments can be interpreted as those of ovoid serial-segments of a new udoteacean, the medullary part originally weakly calcified and now largely missing in the worn fragments available.

SYSTEMATIC PALAEONTOLOGY

Division CHLOROPHYTA (Green Algae)
Order CAULERPALES Feldmann 1946
Family UDOTEACEAE Feldmann 1946
Genus LECKHAMPTONELLA gen. nov.

Udoteacean segments with calcified cortical zone showing swollen branching utricles each dividing into several thinner outer parallel utricles which again divide peripherally. Type-species *Leckhamptonella llewellyae* sp. nov., dedicated to Dr. Llewellya Hillis-Colinvaux in recognition of her extensive studies of the living *Halimeda*.

Leckhamptonella llewellyae sp. nov.

Plate 45, figs. 1–6

Description. *Leckhamptonella* with presumed ovoid segments of observed length up to 2·70 mm and estimated matching diameter of approximately 1·80 mm (but a section of 2·40 diameter may indicate larger segments). Medullary zone mostly missing in fossil pieces: thickness of presumed medullary filaments where preserved about 0·030 mm. Thickness of calcified cortical zone about 0·36 mm; inner half of this occupied by a zone of outwardly directed waisted and swollen branching utricles of 0·030–0·090 mm diameter. These each divide into several straight, thin, near-parallel outer utricles of about 0·015 mm diameter. These are at right angles to the longitudinal axis of the segment, and divide again just below the segment-surface, to short adjacent peripheral utricles of 0·010 mm or less diameter, which expand up to 0·020 mm terminal diameter, almost touching.

Holotype. The specimen figured in Pl. 45, fig. 1; British Museum (Natural History), Dept. Palaeontology registered number V.60703. Middle Jurassic, Lower Inferior Oolite (Aalenian *bradfordensis* subzone); Upper Freestone facies of Scotsquar Hill Limestone (Mudge 1978): Leckhampton, Cheltenham, Gloucestershire.

Paratypes. The specimens figured in Pl. 45, figs. 2–6; registered numbers V.60704–60708 incl.; same locality and horizon.

Other material. About thirty-five fragments in thin-sections: same locality and horizon.

THE EVOLUTION OF THE 'SERIAL-SEGMENTED' UDOTEACEAE

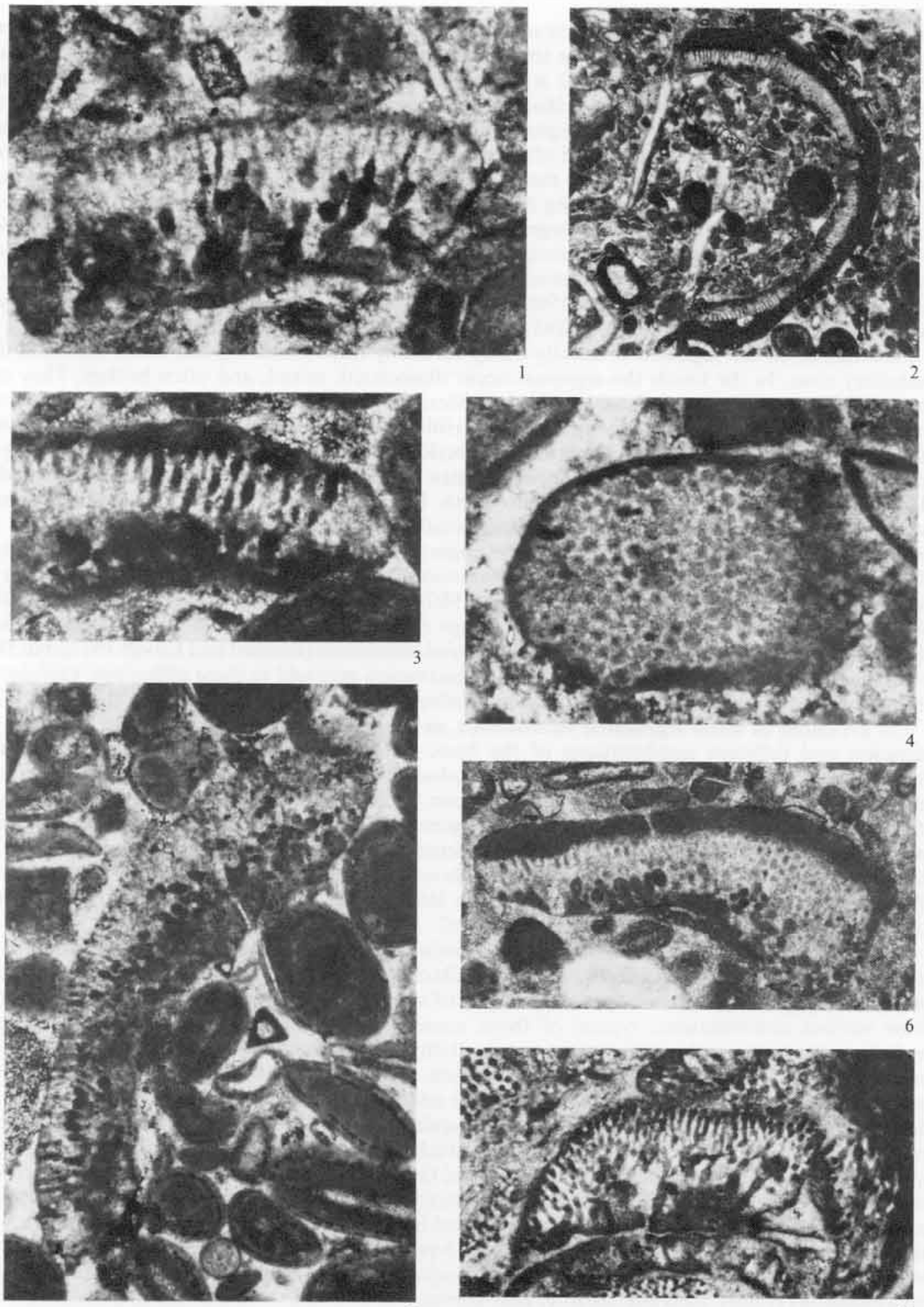
The members of the Udoteaceae, to which *Leckhamptonella* is referred, show a structure of repeatedly branching threads, much intertangled and interwoven. In *Udotea* itself the whole thallus is a single

EXPLANATION OF PLATE 45

Figs. 1–6. *Leckhamptonella llewellyae* gen. et sp. nov. All pieces in thin-section from the Middle Jurassic, Aalenian *bradfordensis* subzone, Lower Inferior Oolite; Leckhampton, Gloucestershire, England. 1, portion of vertical section of calcareous wall, showing presumed medullary thread at base, swollen branching cortical utricles, radial utricles, and terminal peripheral utricles (shown a little left of top centre); × 80; Holotype, British Museum (Natural History), Department of Palaeontology, registered number V.60703. 2, portion of transverse section of large unit, with external dark crust, × 30; V.60704. 3, portion of vertical section, showing two presumed medullary threads (bottom right), swollen utricles and radial utricles, × 80; V.60705. 4, tangential subsurface section, showing close-set peripheral utricles, × 80; V.60706. 5, slightly oblique vertical section of whole side of unit, × 40; V.60707. 6, tangential-longitudinal section of wall showing swollen and radial utricles, heavy dark crusting externally, × 40; V.60708.

Fig. 7. Oblique cut, piece of *Tauridium* sp. for comparison; Upper Permian, Southern Tunisia, × 40; V.54052.

PLATE 45



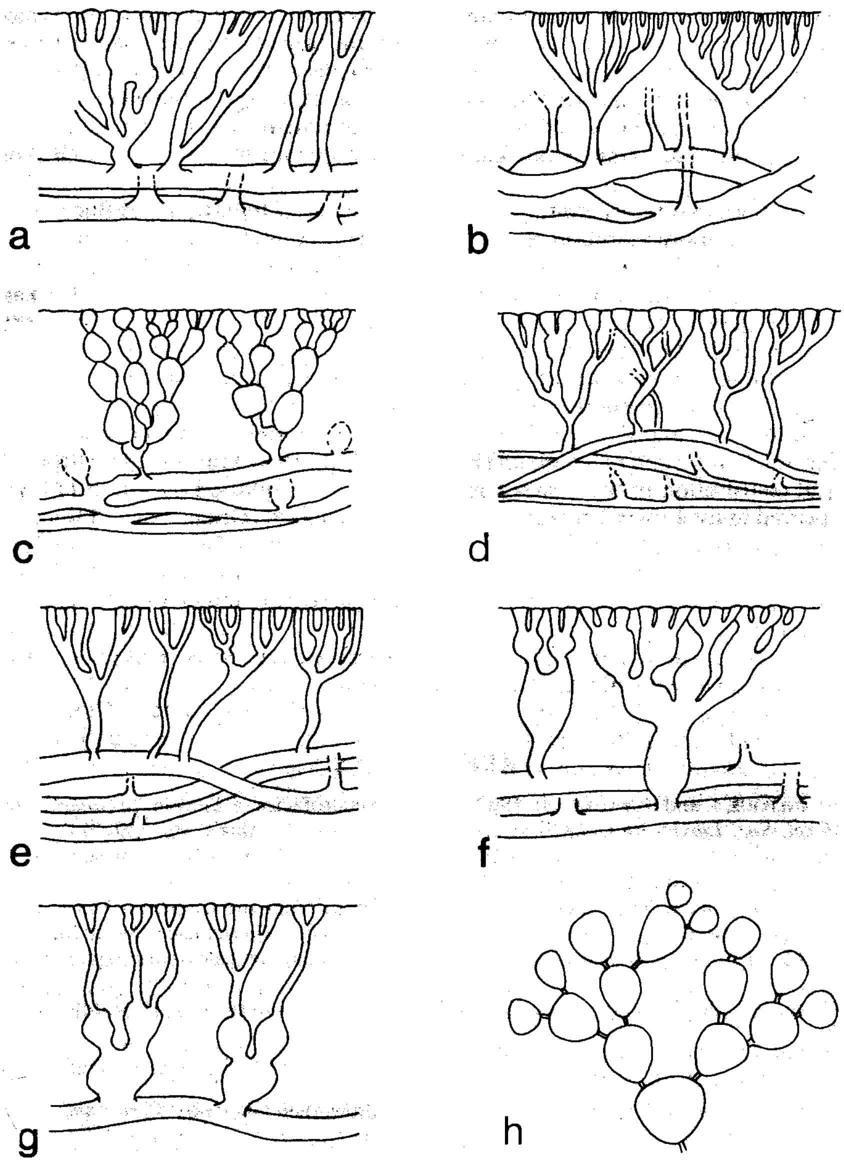
ELLIOTT, calcareous green alga

fan-shaped structure, but another common growth-form, of which *Halimeda* is the modern representative, is shown by what may be termed 'the serial-segmented udoteaceans'. In these, known since the Lower Palaeozoic, the plant is (or is presumed to have been) a clump of branching successions of numerous individual calcified segments, connected by uncalcified threads or filaments. Each segment shows internal coarse longitudinal medullary filaments from end to end, and an outer cortical zone of lateral, branching, and often swollen utricles which terminate in a surface layer of closely packed peripheral utricles. The medullary filaments give rise distally during growth to new segments beyond the old, the connecting filaments being either separate or partially or completely fused at the nodes, so uniting the whole segmented plant as a flexible structure. The peripheral utricles are concerned with the assimilatory functions, and the swollen inner cortical utricles with eventual transference of their content to deciduous reproductive outgrowths (gametangia) at the times of sexual reproduction (Hillis-Colinvaux 1980). These last are only really known in the living *Halimeda* (one fossil record in Pfender 1940, p. 245) and our knowledge is incomplete.

Calcification of the segments is usually heavy cortically (interutricular), but much less so in the medullary zone. In the fossils the segments occur dissociated, mixed, and often broken. They are preserved because of the calcification. The behaviour of the medullary filaments at the nodes, so important in classification of the living *Halimeda* (Hillis-Colinvaux 1980) is thus not normally known in the extinct genera. A solitary example in the collections of the British Museum (Natural History) of an undescribed udoteacean from the Upper Permian of Tunisia, reg. no. V.54065, shows the nodal filaments parallel and in contact along their length, but apparently not fused (if this is the correct interpretation of their slightly different mineralizations). The variation in detail and degree of structure and calcification between older and younger segments of individual plants, between those of different individuals of the same species, and between those typical of different species, as known in living *Halimeda* (Hillis 1959; Hillis-Colinvaux 1980) can make precise specific evaluation of the fragmentary resorted fossil remains difficult, though often occurrences seem to be of a single species. Ideally, one should have a real abundance of material to describe (Conard and Rioult 1977), but this is not always available. The state of geological preservation may add to these difficulties, explaining such records as *Boueina/Arabicodium*, *Boueina/Halimeda* (Bismuth, Bonnefous, and Dufaure 1967).

The evolution of serial-segmented udoteaceans, as preserved fossil, appears to have consisted of variation and different combinations of the basic structures outlined above, from the Lower Palaeozoic onwards (text-fig. 1). Thus *Dimorphosiphon* (Ordovician) shows a coarse thread-structure and *Palaeoporella* (Ordovician-Devonian) a fine one, while *Maslovina* (Silurian) has the dense layer of small peripheral utricles typical of some later genera (Obrhel 1968), but not present in the other two. Text-fig. 1 shows a selection of patterns in different genera from *Dimorphosiphon* to *Halimeda*. Is this evolution more or less random, or does it show some progression in time with the surviving *Halimeda* as the most advanced as well as the latest of its kind? And does the new Jurassic *Leckhamptonella* throw any light on this problem?

It can be seen from text-fig. 1 that the central medullary filaments can be thick or thin, straight or tangled in varying degree in different genera. Similarly, the cortical utricles, while often branching, vary much in spacing or crowding, and in degree of swelling between genera. The examples figured show various combinations, typical of those genera. On mechanical grounds, strong straight medullary filaments, with some fusion and flexibility at the nodes, would equip such a plant to withstand a moderate degree of water-movement and enable it to colonize moderate-energy environments, other conditions being suitable. In addition, swollen cortical utricles and a layer of close-set peripheral utricles would provide for quick segment-growth and eventually for rapid production of gametangia at times of sexual reproduction. This combination, familiar in *Halimeda*, is apparently first achieved in the Permian *Tauridium*, though with different proportions in the utricles, but these were extremely fragile plants post-mortem, almost invariably found as debris or comminuted. Apparently calcification was thin and mostly outer-cortical, and in life the plant was probably confined to quiet waters. In *Halimeda*, however, calcification is heavy, and its success as witnessed by abundance, wide distribution, and occurrence in a range of low to moderate energy-environments (Hillis-Colinvaux 1980) is well known.



TEXT-FIG. 1. Diagrammatic representations of filament and utricle structure in various udoteacean genera, mostly based on materials in the collections of the British Museum (Natural History): (*a*) *Dimorphosiphon* (Ordovician); (*b*) *Aphroditicodium* (Permian; BM(NH) Dept. Palaeont. reg. no. V.59461); (*c*) *Tauridium* (Permian); (*d*) *Arabicodium* (Jurassic–Cretaceous); (*e*) *Boueina* (Triassic–Cretaceous); (*f*) *Halimeda incrassata* (Ellis) Lamx (Recent) (Hillis 1959); (*g*) *Leckhamptonella llewellyae* Elliott (Jurassic); (*h*) diagrammatic growth-plan of serial-segmented udoteacean. See also comparisons for some other Palaeozoic genera in Obrhel (1968, fig. 1) and Guilbault and Mamet (1976, fig. 2).

Leckhamptonella llewellyae shows similarities in cortical utricle-structure to typical modern *Halimeda* spp. It differs in that the third layer of cortical branches are straight, thin, and parallel before dividing into peripheral utricles, whereas in the modern *Halimeda* spp. swollen branches and branchlets usually continue outwards to the peripheral utricles. In the light of the functional reasoning above this difference would be a primitive character is *Leckhamptonella*. The general appearance of the medullary zone is not known, and so cannot be compared with those of other genera.

Halimeda is itself known rarely from the Lower Cretaceous (Dragastan and Bucur 1979; possibly Wells 1944), becomes more common in the Upper Cretaceous, and is abundant throughout the Cenozoic to the present day. It has been considered as arising by hybridization from the earlier Mesozoic *Boueina* and *Arabicodium* (Elliott 1965) or as more closely related to *Boueina* as evidenced by comparable intrageneric species groupings (Conard and Rioult 1977). The fragmentary condition of the Middle Jurassic *Leckhamptonella*, as described above, precludes a detailed comparison of these four genera, but the cortical structure of *Leckhamptonella* appears closer to that of the later *Halimeda* than to those of the earlier genera.

Arabicodium, *Boueina*, and *Halimeda* were all Tethyan in origin: *Boueina* appears in the Upper Triassic of Central Europe and of Thailand (Flügel 1975; Kemper, Maronde, and Stoppel 1976) and its pan-tropical distribution in the Lower Cretaceous has been plotted by Elliott (1981). *Halimeda* may have appeared in the Lower Cretaceous of both hemispheres (Dragastan and Bucur 1979; Wells 1944) and was certainly widely distributed in the Upper Cretaceous (Elliott 1981). *Arabicodium* from the Jurassic-Cretaceous of the western Tethys (Mediterranean-Middle East) had a Jurassic straggler as far north as southern England (Elliott 1975) in the same area where *Leckhamptonella* occurs.

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ADDENDUM

AFTER completion of this paper, I read the memoir of Dr. D. Vachard (Doc. Trav. IGAL Paris no. 2, dated 1980, issued 1981) in which he suggests that various genera, including *Aphroditicodium* Elliott and *Tauridium* Guvenç should be considered as synonyms of *Permocalculus* (Vachard 1981, 382). *Aphroditicodium* he considers to be a well-preserved *Permocalculus fragilis.* The point is of some importance because it would transfer these two genera from Udoteaceae (green algae) to Gymnocodiaceae (red algae). I have examined material from Burma, much better preserved than the type of *Aphroditicodium*, and more extensive material of *Tauridium* from north Italy, in both of which the medullary structures and their relations to the cortical structures are well shown, better than in the types. However, in none of these specimens are reproductive structures to be seen (an absence to be expected in Udoteaceae), whereas in *Permocalculus* they are conspicuous in many individuals, even when preservation is poor. Whilst agreeing with Dr. Vachard as to the similarities of structural plan in these fossil genera, and as to the various changes in taxonomic allocation (to which I contributed) in the past, I consider that *Aphroditicodium* and *Tauridium* are Udoteacean genera, however wide a variation the Gymnocodiacean *Permocalculus* shows.