

THE INTERRELATIONSHIPS OF SOME CRETACEOUS CODIACEAE (CALCAREOUS ALGAE)

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ABSTRACT. The anatomy and evolution of fossil codiacean calcareous algae referred to *Arabicodium* and *Boueina* (Jurassic-Cretaceous) and *Halimeda* (Upper Cretaceous-Recent) are discussed. It is considered that all are referable to one botanical genus *Halimeda*; differentiation of the earlier species-groups (*Boueina* and *Arabicodium*) was followed by hybridization and selection in the Upper Cretaceous, leading to *Halimeda* s.str., a group of species of more vigorous growth and showing a combination of characters from the older species-groups.

THE genus *Halimeda* (Chlorophyta, family Codiaceae) is one of the most successful of modern warm-water marine algae. It abounds in clear shallow lagoonal and coastal waters throughout the tropical and subtropical areas of the Indo-Pacific, and the Atlantic with its adjacent Caribbean and Mediterranean. Since the segments or internodes of the *Halimeda* fronds are usually heavily calcified and growth of the plants is rapid, it is an important sediment-former, as directly evidenced by borings on atolls (Hinde 1904, Johnson 1961). Throughout the Tethyan area remains of *Halimeda* are common in the appropriate facies of Tertiary limestones, and segments of similar forms to those of some of the Recent species are known from rocks as old as the Eocene (e.g. *H. eocaeica* and *H. praemonilis*; Morellet and Morellet 1941). The origin of *Halimeda* is clearly pre-Tertiary.

SOME CRETACEOUS CODIACEAE

Segmented codiaceae in the Cretaceous are represented by assemblages of dissociated segments which have been referred to three genera: *Arabicodium*, *Boueina*, and *Halimeda*. Although typical segments for each differ in size and shape, and in internal thread-detail, they all agree in possessing longitudinal medullary threads and a zone of more or less radial cortical threads, and it seems reasonable to conclude that they came from plants of similar general morphology to that of the living *Halimeda*, and of close relationship to it. This was suggested for *Boueina* and *Halimeda* by Steinmann (1899) and Pia (1926, 1927). *Boueina* and *Arabicodium* have Lower Cretaceous type species, and are represented earlier in the Jurassic. *Halimeda* does not appear before the Upper Cretaceous. There are also numerous Cretaceous species from Aptian to Senonian, which are difficult to assign conclusively to any of the three genera since they show intermediate characters.

Boueina (type species: *B. hochstetteri* Toulou 1884 from the Lower Cretaceous of Serbia) shows elongate cylindrical segments, circular in cross-section, and not flattened or branched as are those of most Tertiary and Recent *Halimeda*. In thin-section they show a medullary zone of coarse tangled threads (Pl. 23, fig. 1), and a cortex of approximately radial finer branching threads, whereas in *Halimeda* the central coarse threads are mostly longitudinally directed, and the cortical threads show constrictions and

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swellings (Pl. 23, fig. 2). Steinmann (1899), in his comparison of the two, indicated a frequent triple branching of the swollen cortical threads of *Halimeda* as compared with a corresponding double branching of the slimmer *Boueina*-threads.

Arabicodium (type species: *A. aegagrapiloides* Elliott 1957, from the Lower Cretaceous of Arabia) occurs as slim cylindrical segments, occasionally showing incipient terminal branching. In thin-section they show a medullary zone of fine slightly wavy longitudinal threads, with cortical zones of very fine radially directed threads (Pl. 23, figs. 3, 4).

These two genera, well differentiated, both appear in the Jurassic and extend into the Lower Cretaceous. *B. hochstetteri liasica* was described from the Middle Lias of Morocco (Le Maitre 1937), and recorded from about the same level in Iraqi Kurdistan (Elliott 1960, and Pl. 23, fig. 1). In the Lower Cretaceous, besides the type-occurrence, there are Italian records of the species (Zuffardi-Comerci 1937) and of a variety *B. hochstetteri moncharmonti* (de Castro 1960). *Arabicodium* is recorded from the Middle Jurassic of France (Dufaure 1958), is known from the Upper Jurassic of Borneo, and has been seen from Tethyan Lower Cretaceous localities other than the type-locality.

In the Upper Cretaceous codiaceans are common: they have been referred variously to *Boueina* or *Halimeda*, but sometimes also resemble the later-described *Arabicodium*. Pfender (1940) listed various circum-Mediterranean Upper Cretaceous records and referred to the difficulty of allocating them to *Boueina* or *Halimeda*, though she recorded the definite occurrence of the latter from the Syrian Turonian. Pia (1936) described *Boueina pygmaea* from the Cenomanian-Turonian of Libya: it is a much smaller species than the type, and without the distinctive medullary threads. It has been recorded from the Cenomanian of France and Spain (Pfender 1940) and the Turonian of the Trucial coast, Arabia (Elliott 1960). In describing *Halimeda nana* from the Moroccan Danian Pia made the generic allocation on the occurrence of a branching segment and not on the internal structure, which was not well preserved (Pia, Pfender, and Termier 1932). Records of this species from the Palaeocene of the Middle East (Elliott 1955, 1960) are based on similarly small segments which, however, show a more markedly halimeditiform thread-structure than may be distinguished in the type-figures.

EXPLANATION OF PLATE 23

- Fig. 1. *Boueina hochstetteri* Toulou var. *liasica* Le Maitre, longitudinal thin-section, $\times 28$; coarse irregularly directed medullary threads, cortical threads mostly ill-preserved. Lower Jurassic, Sekhaniyan Formation (Middle/Upper Lias); Sekhaniyan, Surdash, Sulemania Liwa, NE. Iraq. Brit. Mus. (Nat. Hist.), Dept. Palaeont., V 51381.
- Fig. 2. *Halimeda praemonilis* Morellet, longitudinal thin-section, $\times 28$; coarse longitudinally directed medullary threads and characteristic cortical layer. Palaeocene, Sinjar Formation; Rowanduz, Erbil Liwa, NE. Iraq. V 41615.
- Figs. 3, 4. *Arabicodium aegagrapiloides* Elliott, longitudinal thin-sections, $\times 28$. 3, Outline and fine threads of cortical layer. 4, Distinctive fine longitudinally directed medullary threads. Basal Lower Cretaceous, Hugf area, Oman, Arabia. V 41625.
- Fig. 5. *Halimeda* sp., random thin-section of damaged segment, $\times 40$. Upper Cretaceous, Tanjero Formation (Maestrichtian); Balambo, Sulemania Liwa, NE. Iraq. V 51380.

EXPLANATION OF PLATE 24

- Figs. 1, 3-5. *Boueina* spp., thin-sections, $\times 40$. 1, 5, Upper Cretaceous (Cenomanian), Djebel Meketsi, Algeria. V 51383, V 51384. 3, 4, Lower Cretaceous (Upper Aptian), Ain Keiriane, Algeria. V 51382.
- Figs. 2, 6. *Boueina* cf. *pygmaea* Pia, thin-sections, $\times 40$. Upper Cretaceous (Cenomanian), Bou Saâda, Algeria. V 51385.

Emberger (1961), in fossil-lists for successive Cretaceous stages in Algeria, listed codiacean remains as *Boueina* in the Neocomian, and as *Boueina-Halimeda* for Albian, Cenomanian, and Senonian. A selection of Algerian codiacean material is now figured, from Upper Aptian and Cenomanian (Pl. 24). All these segments are relatively small, when compared with those of type *Boueina* or *Arabicodium*, or with most Tertiary *Halimeda*-segments. Those from the Aptian, all considered referable to one species, are most similar in medullary threads to *Boueina*, though not always sharply distinct in this character from *Arabicodium*. Cenomanian examples are varied: two species appear to be represented, with differing medullary thread-structures, typical neither of *Arabicodium* nor of *Boueina*.

In the Middle East the Cretaceous codiacean remains listed by Elliott (1960), which include *Boueina pygmaea*, are usually extremely fragmentary. Segments definitely of *Halimeda*, however, occur in the Maestrichtian of Iraqi Kurdistan (Pl. 23, fig. 5). Andrusov's record (1939) of a Senonian *Halimeda* from the Carpathians, although of a true *Halimeda*, is now known to be of a Palaeocene occurrence (Misik and Zelman 1959).

MESOZOIC CODIACEAN EVOLUTION

A comparison of these fossil remains with what is known of living algae suggests that the evolution which occasioned the distribution outlined above may better be expressed by a taxonomic simplification. In Recent algae, not merely may two species of the same genus show strikingly different morphology (e.g. *Codium*), but even the sexual and asexual forms of the one species may be morphologically very different. Svedelius (1953) studied this in *Galaxaura*, and his work was applied by Elliott (1961) to the study of Cretaceous *Permocalculus*, where the fossil remains would not otherwise have been recognized as all belonging to the same species. Without invoking this degree of closeness of relationship, it seems that the Mesozoic codiaceans had by the Jurassic differentiated into two species-groups or variable long-range species, *Boueina* and *Arabicodium*, possibly as a result of geographical isolation. They are very similar in structure and morphology, and show little evolution through the Jurassic and Lower Cretaceous when compared with members of the other contemporary chlorophyte family, the Dasycladaceae. Their generic ranking is the result of initial studies of isolated distinctive assemblages, and has been difficult to apply as more and more material has been examined. By the beginning of the Upper Cretaceous hybridization occurred, and a plexus of intermediate forms resulted, typical neither of *Boueina*, *Arabicodium*, nor yet of the later *Halimeda*. *Halimeda* itself, appearing but not common at the end of the period, is a form in which the thickness of the tangled medullary threads of *Boueina* is combined with the longitudinal orientation of the thin medullary threads of *Arabicodium*. In the very detailed revision of Recent *Halimeda* by Hillis (1959), these coarse medullary threads are seen to be classifiable into several patterns according to the degree and nature of the fusion between them at the nodal points connecting adjacent segments: this character is connected with the growth of the new successive segments.

Once evolved, *Halimeda* rapidly replaced the older segmented codiaceans, which are not known after the Cretaceous. Records of Palaeocene *Boueina* (Rao and Vimal 1955, Elliott 1960) refer to *Halimeda* sp., and to poorly preserved dasyclads, respectively. *Halimeda* seems to have undergone rapid differentiation into some of the species-groups

represented in the living flora early in the Tertiary, along with an increase in segment-size, and probably size of the plants also, in many species. The occasional origin of new and vigorous species by hybridization is a well-known botanical phenomenon; the measure of the success with which *Halimeda* has fitted its warm-water niche is indicated by the extent of its contribution as a sediment-builder during the Tertiary and at the present day (Chapman and Mawson 1906, Johnson 1957).

All the fossil codiaceans discussed here are considered referable to a single genus: of available names, *Halimeda* Lamouroux 1812 has priority. *Boueina* and *Arabicodium* are available for use as subgenera for fossils of the appropriate species. *Halimeda* has already been used for some Cretaceous species interpreted here as hybrids (e.g. Pfender 1938).

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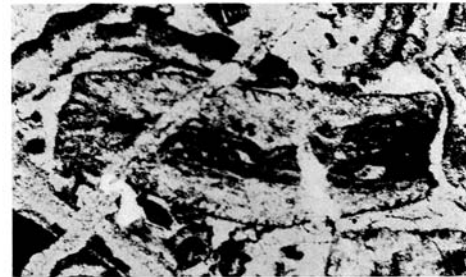
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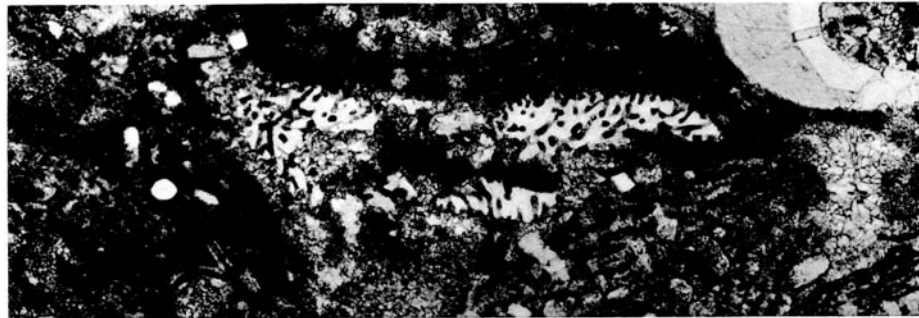
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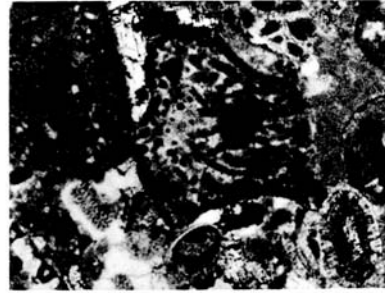
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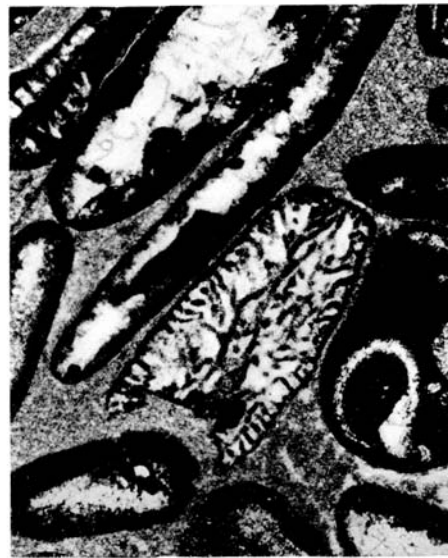
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