Halimeda: paleontological record and palaeoenvironmental significance

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Abstract. Udoteacean algae, identical or related to Halimeda, have been recorded in shallow-marine carbonate rocks since Upper Triassic. About 30 species have been described, most of which occur in Lower Cretaceous shelf carbonates. These species are conventionally attributed to four "genera" (Arabicodium Elliott, Boueina Toula, Halimeda Lamouroux, Leckhamptonella Elliott), but the validity of these taxa is a matter of discussion (generic or subgeneric position, or synonymy of Halimeda?) owing to wide discrepancies in the classification of fossil and recent species of halimediform algae. The paleoenvironmental setting of the Mesozoic and the Tertiary is comparable with that of recent Halimeda: lagoonal as well as reefal environments are already known from Upper Triassic occurrences. A reinvestigation of Boueina limestones described from Norian-Rhaetian lagoonal carbonates of Western Thailand indicates the important role of the alga (Boueina marondei n. sp.) in sediment accumulation from its very beginnings.

Introduction

Calcereous algae, identical or related to Halimeda, appear in the Tethyan Upper Triassic (Flügel 1975; Kemper et al. 1976) and are common in shallow-marine carbonate rocks during the Late Mesozoic and Cenozoic (Bassoullet et al. 1983). Several generic names are used in the classification of these algae: Halimeda Lamouroux, 1812; Boueina Toula, 1883; Arabicodium Elliott, 1857; Leckhamptonella Elliott, 1882. For a long time Halimeda, Boueina and Arabicodium were placed in the family Codiaceae of the chlorophycean group Caulerpaceae (e.g., Wray 1977). Following the scheme proposed for the classification of recent green algae, the genera are now included within the family Udoteaceae (cf. Hillis-Colinvaux 1980; Bassoullet et al. 1983).

Boueina, Arabicodium and Leckhamptonella are morphologically closely related to Halimeda. This relationship was emphasized very early by Steinmann (1899) in comparing Boueina and Halimeda, and by Pia (1927). Because Halimeda, Boueina and Arabicodium are characterized by very similar constructional patterns of the central region (medulla) and the peripheral zone (cortex), and because segmentation and branching are common features of all three genera, there is no agreement about the validity of the taxa: Some authors have even felt the genera could not be differentiated (e.g., Johnson 1968: Badve and Nayak 1983). Elliott (1965) thought that Halimeda had arisen by hybridization from Boueina and Arabicodium; therefore Boueina and Arabicodium were regarded as subgenera of Halimeda. However, Elliott reworked this assignment in 1975. By contrast, Conrad and Rioult (1977) pointed out that the evidence available for defining these genera in fossil occurrences was incomplete, and that different morphological patterns found in different species of Halimeda were recognizable in Boueina as well. Bassoullet et al. (1983) consider the taxa distinct because of differences in the stratigraphical occurrence (Boueina: Upper Triassic to Upper Cretaceous; Arabicodium: Middle Jurassic to Early Tertiary; Halimeda: Lower Cretaceous to Recent).

Fossil udoteacean green algae are generically distinguished by the shape and construction of the thallus and by the arrangement and shape of the cortical filaments (utricles) and the medullary filaments (Elliott 1956, 1957, 1970; Konishi 1961). In addition, structures interpreted as reproductive organs may be of taxonomic importance. Some of these criteria – e.g., the filament pattern of the cortical zone – seem to be highly variable even on the specific level if compared with recent species of Halimeda (cortical filament patterns described from various species of Arabicodium and Boueina can also be recognized in different species of Halimeda! Compare Hillis-Colinvaux 1980, Fig. 20). Another reason for apparent morphological differences between Boueina, Arabicodium and Halimeda might depend on differences in the degree of calcification, which also varies between species of Halimeda (Flajs 1977; Wefer 1985). Differentiation of fossil species is made more difficult by selective preservation (cf.
Wright 1981). Taking into account all these problems, the survey described in this paper will give a rather tentative picture of the forerunners of *Halimeda*.

**The paleontological record**

The paleontological record will be discussed in terms of inventory, discussion of fossil taxa, Triassic precursors, and distributional patterns in time.

**Inventory**

*Arabicodium* Elliott is characterized by segmented thalli similar to *Halimeda*, but with simple elongate segments, and with both medullary and cortical filaments being finer and more uniform. Type-species: *A. aegagrapiloides* Elliott.

Species: *A. aegagrapiloides* Elliott, 1957 (Upper Jurassic: Portlandian - Eastern Carpathian Mountains, Romania); *A. cantabricus* Dragastan, 1982 (Lower Cretaceous: Aptian/Albian – Northern Spain); *A. elongatus* Dragastan, 1971 (Lower Cretaceous: Barremian – Eastern Carpathian Mountains, Romania); *A. indica* Pal, 1971 (Maastrichtian to Paleocene - India); *A. jurassieum* Dragastan, 1971 (Upper Jurassic: Portlandian – Eastern Carpathian Mountains, Romania); *A. orientalis* Dragastan, 1971 (Lower Cretaceous: Aptian – Eastern Carpathian Mountains, Romania and Bulgaria); *A. texana* Johnson, 1968 (Lower Cretaceous: Barremian and Aptian – Southern France; Upper Cretaceous: Cenomanian – Texas, India); *A. tibeticum* Yu Jing, 1976 (Early Tertiary: Paleocene to Lower Eocene Southern Tibet). *Arabicodium* sp. is known also from the Middle Jurassic (Bathonian) of England (Elliott 1975).

*Boueina* Toula is characterized by usually irregularly arranged medullar filaments and slender branched cortical filaments decreasing in thickness towards the periphery of the thalli. Type-species: *B. hochstetteri* Toula.

Species: *B. chirakhanensis* Pal, 1971 (Cretaceous: India); *B. globosa* Dragastan, Bucur and Demeter, 1977 (Lower Cretaceous: Barremian and Upper Aptian – France, Romania); *B. hochstetteri* Toula, 1983 (Upper Jurassic: Tithonian – Eastern Carpathian Mountains, Romania and Bulgaria; Lower Cretaceous: Berriasian, Hauterivin, Barremian, Aptian – Spain, Portugal, France, Serbia, Bulgaria, Romania, Western Turkmenia, Iran, Iraq; Upper Cretaceous: Cenomanian, Turonian, Campanian, Maastrichtian: Texas, Brasil, ?Libya). Upper Triassic specimens, described as *B. cf. hochstetteri* by Kemper et al. (1976), are discussed below; *B. hochstetteri liassica* LeMaitre, 1937 (Upper Triassic: Norian – Northern Alps; Lis: Morocco, Iraq, Italy, Yugoslavia); *B. hochstetteri moncharmonti* deCastro, 1963 (Lower Cretaceous: Aptian – Italy); *B. pygmaea* Pia, 1936 (Lower Cretaceous: Aptian – France, Romania, Arizona; Upper Cretaceous: Cenomanian, Turonian, Campanian, Maastrichtian – France, Spain, Libya, Egypt, the Middle East, Cuba; ?Paleocene – India).

*Halimeda* Lamouroux is represented by about 30 recent species and by about 15 fossil species, most of which have been described from the Tertiary.

Species: *H. camenitzae* Dragastan and Bucur, 1979 (Lower Cretaceous: Aptian – Romania); *H. corneloa* Badve and Nayak, 1983 (Cretaceous – India); *H. densituba* Badve and Nayak, 1983 (Cretaceous – India); *H. eliotti* Conrad and Rioul, 1971 (Upper Cretaceous: Turonian – Southern France); *H. entogensis* Yu-Jing, 1976 (Early Tertiary: Paleocene to Lower Eocene – China); *H. eocaenica* Morollet, 1940 (Early Tertiary: Eocene – France); *H. johnsoni* Pal, 1971 (Maastrichtian or Paleocene – India); *H. lingulata* Yu-Jing, 1976 (Early Tertiary and Eocene – China); *H. nana* Pia, 1932 (Early Tertiary: Taranian, Paleocene – Morocco, Iraq, Iran); *H. opuntia* Lamouroux, 1812 (Tertiary: Miocene and Pliocene – Malaysia, Recent); *H. pipaldehlaensis* Badve and Nayak, 1983 (Cretaceous – India); *H. praemonilis* Morell, 1940 (Early Tertiary: Paleocene, Eocene – France, Iraq, Iran); *H. praepuncta* Morollet, 1922 (Tertiary: Miocene – France, Iraq); *H. robusta* Badve and Nayak, 1983 (Cretaceous – India); *H. triradiata* Badve and Nayak (Cretaceous – India).

*Leckhamptonella* Elliott is known by segments only cortically calcified and exhibiting an inner zone with swollen branching utricles each dividing into several thinner outer parallel utricles, which again subdivide peripherally. The only species known is the type-species *L. llewellyae* Elliott, 1982, from the Middle Jurassic (Aalenian) of England.

**Discussion of fossil taxa**

The species described by Pal (1971) have been questioned by Badve and Nayak (1983), who found only echinoderm fragments in some of the type thin sections.