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PHYLOGENY OF HALIMEDA (BRYOPSIDALES): LINKING PALEONTOLOGICAL, MORPHOLOGICAL AND MOLECULAR DATA

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Abstract. The green calcareous alga *Halimeda* Lamouroux 1812 (Chlorophyta, Bryopsidales) is an ancient genus which has been traced to the Permian. In the Holocene of the present it is a comparatively species rich alga, colonizing lagoons and festooning forereefs of many of the world's tropical reefs, and after death contributing considerable volumes of calcium carbonate to the reef mass. As part of an investigation of its phylogeny, its long fossil history is reconstructed to show species diversity during successive geological periods and epochs. Peaks of diversity are indicated for Late Cretaceous, Paleocene, Eocene, Miocene and Holocene. The Holocene peak of 33 species, distributed in five taxonomic sections, is more than four times greater than the total number of species reported for any epoch. The genus appears to have survived events associated with the Cretaceous/Tertiary boundary, and to have achieved greatest diversification in the Cenozoic.

Recent cladistic analyses of morphometric traits and molecular sequence data for *Halimeda* have yielded the best model of a phylogeny to date, and provided information about the phylogenetic significance of 23 morphological characters. One of the next steps is to work out time reference points of major events in order to set an evolutionary clock for the genus. Paleontological studies seeking to determine approximate times of origin for one or more of the major lineages (roughly equivalent to taxonomic sections) using phylogenically informative characters could achieve this goal. Lineage diversification, by facilitating colonization across a broad spectrum of reef habitats, broader than has been achieved by many algae, has contributed greatly to *Halimeda* success. Examining fossil specimens from the perspective of determining lineages could lead also to the discovery of extinct lineages and earlier series of lineages.

Developing other time reference points, by estimating ages of extant species from fossil data, seems less productive because of the very considerable difficulties of aligning fossil taxa with extant species. Consequently, the identification of Miocene material as *H. opuntia* should now, perhaps, be considered in the broader context of *H. opuntia* homologues, new species, or the less likely alternatives of other opuntioid or small segmented extant species. At the genus level, age determination is confounded by taxonomic implications of close resemblance to *Arabicodium* and *Boueina* and possibly other halimediform genera. Were some of these taxa placed in synonymy, the genus could date from the Ordovician instead of the Permian. However, without a solid statistical base of morphological characters suitable for comparing fossil and extant samples, the comparisons required are unlikely to be achieved. Continuing to recognize these taxa as separate entities seems the prudent approach until non morphological traits are available.

Paleontologists can make another major contribution to *Halimeda* phylogeny and tropical reef dynamics by seeking field data concerning species diversity and biomass for the approximately 50 million years preceeding the Holocene. The apparent explosion of speciation during the Holocene is most likely an artifact of effort. Conditions appeared to be suitable during some of the Paleogene and Neogene for sizeable populations to develop, but records mostly indicate *Halimeda* sp., or are silent.

Keywords: *Halimeda*, phylogeny, Cenozoic, *Arabicodium*, *Boueina*, Bryopsidales, phylogenetic clock, cladistics.

INTRODUCTION

The algal genus *Halimeda* Lamouroux 1812 (Chlorophyta, Bryopsidales) is a species diverse, biomass rich component of Holocene reefs and, since the early 20th century, has been recognized as a major carbonate contributor in coral reef systems (e.g. Finckh, 1904; Emery et al., 1954; Milliman, 1974, 1993; Hillis, 1980, 1991, 1997; Freile et al., 1995). The fossil literature provides a Permian origin (Poncet, 1989; Bucur 1994), thereby indicating an age of at least 250 million years (Myr). Comparatively little, however, is known about the genus until the Late Cretaceous (e.g. Elliott, 1960; Johnson, 1969) when it appears as a species diverse, relatively abundant component of warm water floras spanning a broad Tethyan area. It is not known, however, whether the Cretaceous genus was complex and subdivided into different categories such as taxonomic sections or lineages, or alternatively, whether the internal anatomy and environmental adaptations of the different species exhibited little or considerable variation.

At the end of the 20th century there are more than four times the number of species of the Late Cretaceous. The 33 extant species have been assigned to five sections: Rhipsalis J. Ag. *ex* De Toni 1889 (8 sp.), Opuntia J. Ag. *ex* De Toni 1889 (7 sp.), Halimeda J. Ag. *ex* De Toni 1889 (13 sp.), Micronesicae Hillis-Colinvaux 1980 (3 sp.) and Crypticae Hillis-Colinvaux 1980 (1 sp.) (Hillis, 1980, Hillis et al., 1998). These generic subdivisions are formally defined by the types of fusion patterns of siphons occurring within the node, i.e. the region between abutting segments of the thallus (Hillis,1980). Hillis also pointed out in the 1980 monograph, the association of other distinctive traits such as type of holdfast or general physique, with specific taxonomic sections, and advanced the hypothesis that these groups of species represented natural units within *Halimeda*. The hypothesis is well suited to testing by cladistic analysis of molecular and morphological data, i.e. applying numerical methods to shared derived (versus ancestral) characteristics of component taxa (Veron, 1995). Yet, for a genus with a long fossil record, data from the past also should play a role in reconstructing phylogeny. As a step towards developing a complete phylogeny of the genus, this paper brings together morphological, molecular and

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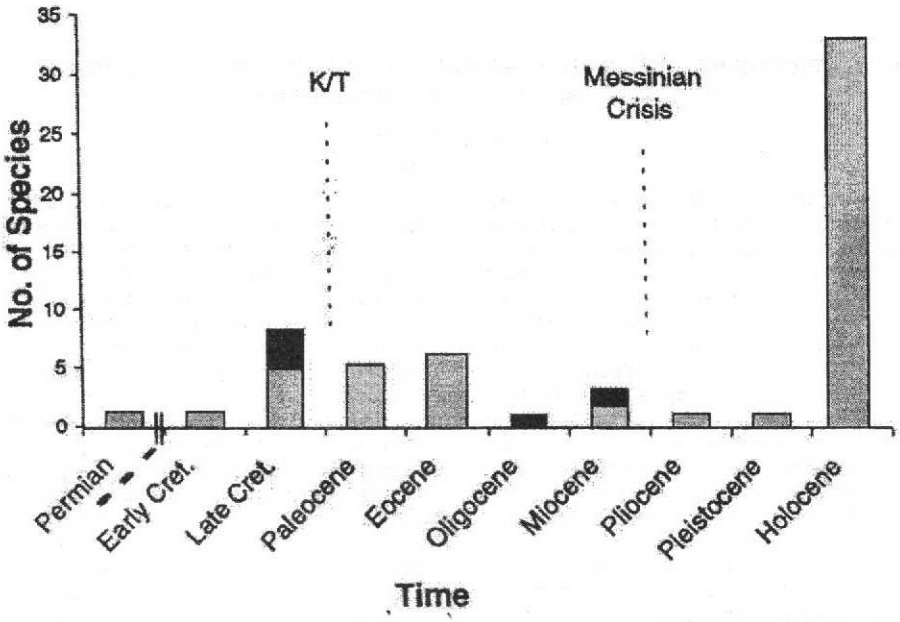

Figure 1 - Diversity of *Halimeda* species in geological time. Darker shading at the top of some of the bars indicates uncertainties with that portion of the stratigraphic record.

paleontological data, and discusses paleontological approaches and problems associated with strengthening the data set and developing reference points for an evolutionary clock.

HALIMEDA SPECIES DIVERSITY AND HALIMEDIFORM ALGAE, AS RECORDED BY FOSSILS

Approximately 250 years of *Halimeda* history, based on species lists in the fossil literature (incl. Morellet and Morellet, 1922, 1941; Pia, 1932; Elliott, 1960, 1965, 1978, 1981, 1982; Conrad and Rioult, 1997; Dragastan and Bucur, 1979; Badve and Nayak, 1983; Bassoullet et al., 1983; Flügel, 1988, 1991; Poncet, 1989; Bucur, 1994), were analyzed from the perspective of species diversity (Figure 1). Relative abundances, a general indicator of overall generic success, were not analyzed since data are too few. Maximum species diversity is indicated for: Cretaceous (6-8 sp.), Paleocene (5 sp.), Eocene (6 sp.), Miocene (2-3 sp.) and Holocene (33 sp.). Additional analyses of the data (not shown) indicated maximum speciation events for the Cretaceous (6-8 sp.), Paleocene (3-5), Miocene (2) and Holocene (32); and periods of extinction during or at the end of the Cretaceous (6 sp.), Paleocene to Eocene (5-6 sp.), Eocene to Oligocene (5-6 sp.), Oligocene to Miocene (?1 sp.), and Miocene to Pliocene (?2 sp.). The first record of an extant species of *Halimeda* is of *H. opuntia* (Linneaus) Lamouroux 1812 for the Miocene (Bassoullet et al., 1983). This reading of fossil literature suggests that the greatest diversification of *Halimeda* species occurred in the Cenozoic. The era is also associated with the development of modern tropical reefs and scleractinian corals, an ecosystem and community of which *Halimeda* is very much a part.

Morphologically very similar (halimediform) genera, *Arabicodium* Elliott 1957 and *Boueina* Toula 1883, occurred during the Cretaceous (Bassoullet et al., 1983; Flügel, 1988, 1991) as well as earlier, with these two taxa apparently more abundant than *Halimeda* for much of their existence. However, *Halimeda* was the only halimediform alga to survive, successfully, the major extinction events associated with the Cretaceous-Tertiary (K/T) boundary and continue beyond the early Eocene. Other halimediform algae, e.g. *Dimorphosiphon diadromum* Gnilovskaja 1972, are reported from the Ordovician (Bassoullet et al., 1983), indicating 1) that the order Bryopsidales, which is distinguished from other green algal orders by a thallus constructed of coenocytic siphons, has a history of at least ca. 450 Myrs, and 2) that species with some of the most complex architectures found in all of Chlorophyta (e.g. *Dimorphosiphon diadromum* Gnilovskaja 1972,) appeared very early in the order's history. It thus appears that these two traits which might be considered advanced: coenocytic construction, and complex architectures, have a long history. Additional information pertaining to halimediform taxa is provided by Elliott (1982) and Flügel (1988).

PHYLOGENETIC INSIGHTS FROM MORPHOLOGICAL AND MOLECULAR DATA OF EXTANT SPECIES

Morphological and molecular data of modern *Halimeda* species have recently been examined cladistically in the papers by Hillis et al., 1998 and Kooistra et al. 1999, to which readers are referred for detailed analyses of the resulting phylogenetic trees. The first paper is a pioneer study applying cladistic approaches to morphological and molecular data obtained from a small, but representative sampling of the genus; in the second paper species diversity is increased and only molecular data are used. Ten species (approximately one-third of the genus) from four taxonomic sections were analyzed in the first paper. Morphometric data were obtained for 23 characters (each with two or more states) by examining hundreds of specimens; molecular data were based on the last 723 nucleotides of the 3' end of the nuclear rDNA 18S gene which included an insertion of ~102 base pairs.

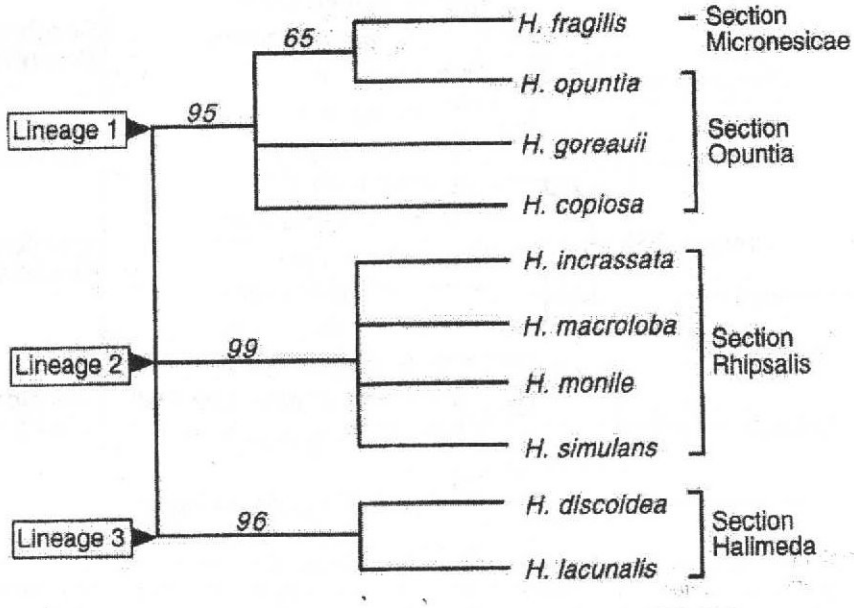

Figure 2 - Strict consensus tree of eight most parsimonious trees inferred from 23 macroscopic and microscopic morphometric characters and their states. The consensus characters were generated by examining numerous samples selected from a broad range of the taxon's distribution. In contrast the molecular samples of Fig. 4 were acquired from one to a very few segments of a collection, and from a single geographic location. The species were selected to match those of the molecular analysis (Fig. 3). Bootstrap values ≥ 50% appear in italics above the internodes. (Modified from Fig. 2, Hillis et al., 1998, by permission of the Journal of Phycology).

Two of the phylogenetic trees obtained are shown in Figs. 2 and 3 (Hillis et al. 1998). Results specifically germaine to paleontological studies of *Halimeda* are: 1) three major lineages are inferred for the genus, and they are essentially congruent in both the morphological and molecular trees; the lineages also closely fit the formal taxonomic sections of Hillis (1980); 2) phylogenetically informative morphological characters are identified.

The more complex tree of Figure 4 is based on 18S rDNA sequences from approximately 50% of all recognized species (n=15), plus four taxa not readily conforming to species descriptions (Kooistra et al. 1999). All five sections are represented. Three major lineages, taxonomic sections Opuntia, Rhipsalis and possibly most of Halimeda, (=the same lineages as in Figs. 2 and 3), provide most of the tree's basic organization. New aspects include at least one other lineage, the *H. gracilis-H. lacrimosa* lineage, and a subdivision of the rhipsalian lineage into Atlantic and Indo-west Pacific clades. A similar geographic separation was hinted at in Figure 3, but with the increased diversity of Pacific species it becomes very apparent in Figure 4. The results also suggest that the amphi-Atlantic and Pacific clades of *H. discoidea* are distinct, but do not resolve their phylogenetic status.

A PROTO PHYLOGENY OF HALIMEDA

If Figure 4 is rotated counterclockwise 90 degrees a proto model of *Halimeda* phylogeny can be discerned somewhat more readily. The basic pattern consists of a few major branches (lineages), the subbranches of which eventually terminate in extant species. Major lineages are differentiated comparatively early in the scheme. Species grouped within them possess similar macroscopic and microscopic morphological features such as erect mien and large holdfasts suitable for anchoring in unconsolidated substrata (Rhipsalis), or multiple thread-like holdfasts and sprawling or pendant thalli (many Opuntia) which drape over rocks or fill many of a reef's crevices (Hillis, 1980, 1988,1991). Lineage diversification facilitated colonization into very different habitats such as lagoons and rocks, contributing to the very considerable success of *Halimeda* in reefs since it now grows in a greater array of habitats than is usual for most algae. This form of niche partitioning may have occurred more than once during the history of *Halimeda*.

Two things are needed to complete the evolutionary model. First: all described species, sampled broadly from Atlantic, Pacific and Indian Oceans as well as the Mediterranean need to be included. This will produce adjustments in the terminal branching patterns to accommodate additional species, and probably will resolve some of the ambiguity at the base of the scheme. The basic pattern, showing the importance of a few major lineages, is likely to persist however. Second: a time scale for major phylogenetic events needs to be developed. An appropriate event for initiating this process is the subdivision of the Rhipsalian lineage into Atlantic and Indo-west Pacific species clades (Fig. 4). The most likely explanation is a major vicariant event such as the cessation of the circumtropical Tethys current (Rögl & Steininger, 1984), one of the possibilities suggested by Kooistra et al. (1999), which would isolate Atlantic and western Pacific populations. Applying the time estimates of this event, bifurcation of the Rhipsalis clade would have occurred sometime from between early Oligocene (ca. 35 Myr), when the eastern Tethys flow was reduced to a narrow southwestern passage, and the estimated final cessation of flow of the western Tethys arm through the Mediterranean and into the Atlantic, by ca. 17-16 Myr or early Miocene (Haq, 1984).

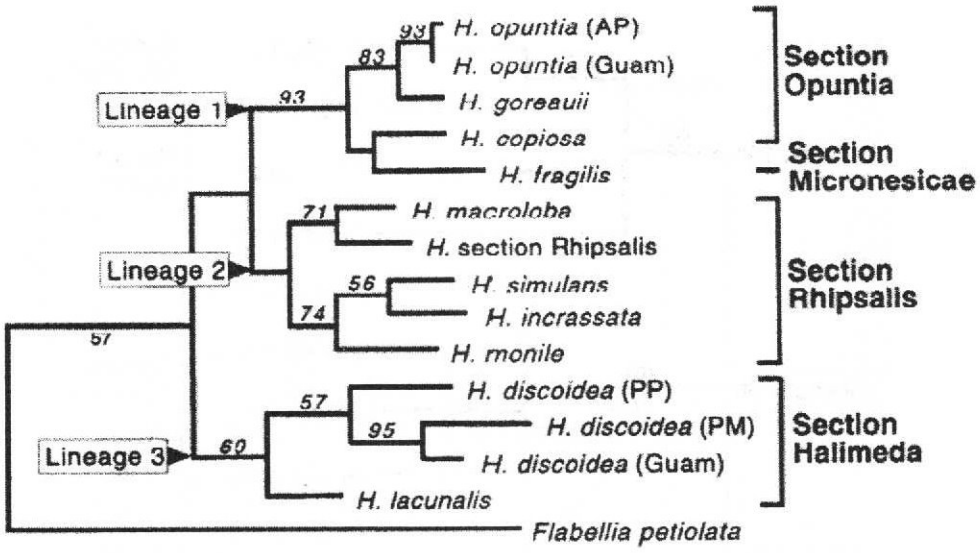

Figure 3 - Maximum parsimony tree based on partial 18S rDNA sequences with insertion. Ten species (14 samples) from 4 of the 5 taxonomic sections are represented; sample *H.* sect. Rhipsalis does not conform readily to species circumscriptions. *Flabellia petiolata* (Turra) Nizamuddin serves as outgroup. Bootstrap values ≥ 50% are in italics above the internodes. Distribution: AP= Atlantic Panama; PM= Pacific Mexico; PP= Pacific Panama. *Halimeda copiosa* is from San Andres I., Colombia; *H. fragilis*, *H. macroloba*, and *H. lacunalis* (f. *lata*) are from Guam; the remainding *Halimeda* samples are from Atlantic Panama; *Flabellia petiolata* is from Malta. Collection sites are listed in the source paper. (Modified from Fig. 5, Hillis et al., 1998, by permission of the Journal of Phycology).

APPLICATION OF PALEONTOLOGICAL DATA TO DATING PHYLOGENETIC EVENTS

Ages of Extant Species

The preceeding time estimate for a phylogenetic event suggests that, in the context of the ca. 250 Myr of *Halimeda* history, extant species have appeared relatively recently. For the one extant species identified in fossil deposits, *H. opuntia*, a suggested age of Miocene or conceivably older, based on the deposits, appears theoretically reasonable. The caveat is the very considerable difficulty of establishing continuity between fossil and extant species. Small sample sizes and less than perfect preservation make species determination of most fossil specimens even more difficult than extant material. Given the few morphological details usually available or provided, and the amount of intraspecific variation encountered in extant material, it is timely to reevaluate the identification. The putative Miocene *H. opuntia* might be a homologue of the species, or one of several small segmented species in section Opuntia, some of which had not been described when the determination was made; assignment to small segmented species of other sections, or conceivably to a new species are other possible interpretations.

A second extant species, *H. cuneata*, also might be a guide for determining ages of *Halimeda* species. Its known distribution, as presently understood, is unusual in that it is the sole strictly subtropical species of the genus. Its distribution in the southern hemisphere is confirmed only for a subtropical band extending from the southern tip of Africa to southeastern Australia. In the northern hemisphere distribution appears to be restricted to the Gulf of Kutch (Hillis, 1980). *Halimeda cuneata* has been cited frequently as occurring in Japan and elsewhere in the northern tropical-subtropical hemisphere, but all specimens I have examined have proved to be other species, most frequently *H. discoidea*.

One hypothesis to explain its distribution is that the species was transported towards Asia from sites such as the southern tip of Africa and Madagascar with the northward tectonic movement of the proto Indian continent. This implies at least an age of Late Cretaceous, and that it survived K/T events. The age certainly falls within the estimate for the genus, but, as for *H. opuntia*, establishing relationships between fossil and extant species is very difficult. For the present, a late Mesozoic age for *H. cuneata* is best considered but a provocative concept.

From these two examples it appears that at the level of species, paleontology will serve mainly as a general guide in age determinations of extant species. To develop a time scale for species origination, the most substantial insights will probably come from cladistic-based inferences derived from molecular and morphological data. For *H. cuneata* the data should be based on two types of geographically diverse collections: rigorously identified *H. cuneata* from the subtropics, and *H. cuneata*-like specimens from the tropics.

Development of Major Lineages

Major lineages in *Halimeda* taxonomy signal significant evolutionary developments, as indicated earlier. Paleontological data could be used to estimate the time of their first appearance, and eventually to develop an evolutionary clock which would be independant of molecular data. Examining fossils from a perspective of determining the lineages to which they belong, could lead also to discovering one or more lineages which possibly had been associated with extant lineages but now are extinct. Awaiting discovery also might be a series of earlier ones, with their component species possibly exhibiting parallelism with extant species and lineages.

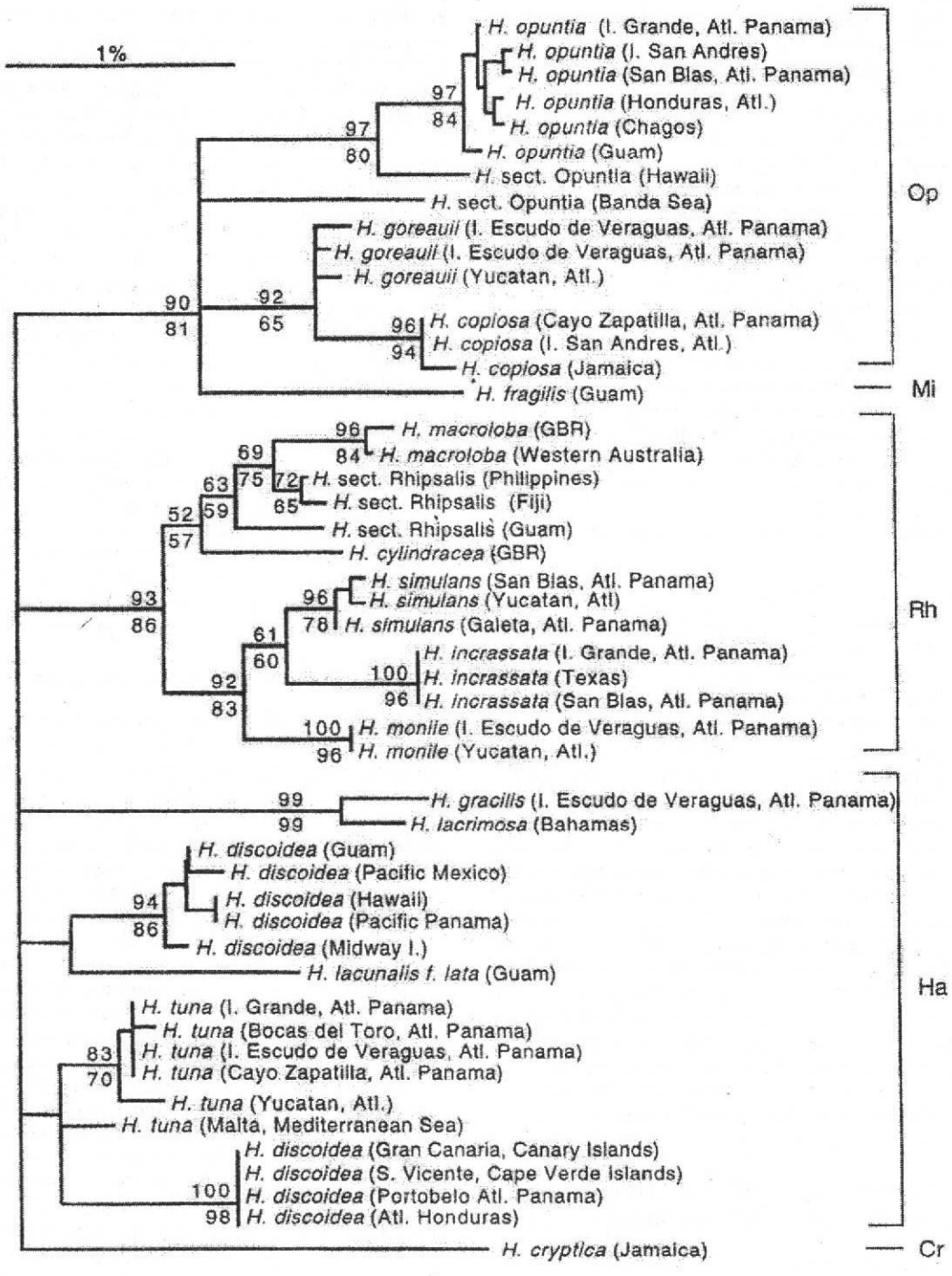

Figure 4 - Neighbor joining phylogeny of partial 18S rDNA sequences with insertion, inferred from Kimura 2-parameter corrected distances. Almost half the genus, fifteen species (48 samples) of *Halimeda*, and all 5 sections are represented. Five samples (4 taxa) do not readily conform to species circumscriptions. Species representation of the most complex and diverse section, Halimeda, has been increased 2.5 times. Neighbor joining bootstrap values (1000 replicates) of >50%, associated with a clade, are mapped above the internode leading to it; maximum parsimony bootstrap values of >50% are presented underneath internodes. Dichotomies without sufficient bootstrap support and without a decay index, or those not recovered in the consensus of the equally most parsimonious trees appear as polytomies. Scale bar above the tree indicates branch length. Abbreviations represent the 5 sections: Opuntia, Micronesicae, Rhipsalis, Halimeda, and Crypticae. Collection sites are listed in the source paper. (Modified from Fig. 1, Kooistra et al., 1999, with permission from Kluwer Academic Publishers).

The task of assigning well preserved *Halimeda* fossils to major lineages, although not without pitfalls, is probably more within the realm of possibility than aligning fossil and extant species. Members of section Opuntia, for example, are set apart from sections Rhipsalis and Halimeda by phylogenetically informative characters such as 1) absence of siphonal constrictions in the cortex except for those at the bases of peripheral (primary) utricles, and 2) cortical branching primarily dichotomous except when associated with peripheral utricles (characters 15 and 23 respectively, Hillis et al., 1998). Statistically significant data pertaining to phylogenetically informative traits are necessary to assign membership confidently to specific lineages.

The extent of extinction implied for the end of the Cretaceous, and the occurrence of paleo-environmental conditions favorable for speciation and diversification in the early Cenozoic are two of the reasons favoring, to some extent, the hypothesis that the major lineages associated with extant species developed early in the Cenozoic, and that similar or entirely different lineages may have appeared earlier in *Halimeda*'s phylogeny. The topic needs to be explored when additional data are available.

Age of the Genus Halimeda

The time when the genus originated, whether Permian as indicated above or earlier, is obscured by taxonomy. Paleontologists have drawn attention to the close similarity of *Halimeda*, *Arabicodium* and *Boueina* (incl. Elliott, 1965; Johnson, 1969; Bucur, oral communication, 1999), some tentatively suggesting that all should be considered members of the genus *Halimeda*. Although the closeness of all three taxa, and possibly other serial-segmented halimediforms is unquestioned, resolving the question of synonymy presents the usual problems encountered when working with fossils, including the very difficult initial one of locating sufficient well preserved samples to provide statistically significant data bases. Until that can be done, it seems prudent to maintain the *status quo* of the taxa. Nonetheless, one can ponder the changes that would be incurred in our concept of the earliest chapters of *Halimeda* history were future taxonomic changes to include species such as *Dichotomosiphon diadromum*, a halimediform alga of the Ordovician and Silurian, and reflect on the considerable impact of taxonomy on all studies involving organisms.

OTHER CONTRIBUTIONS OF PALEONTOLOGY TO PHYLOGENETIC STUDIES OF *HALIMEDA*

The apparent explosion of speciation in the Cenozoic (Fig. 1), resulting principally from the combination of critical taxonomic studies (e.g. Barton, 1901; Howe, 1905; Taylor, 1950; Hillis, 1959), and field work beginning with the Siboga Expedition (e.g. Barton, 1901) is most likely an artifact of effort. Because of poorly understood interactions between *Halimeda* and scleractinian coral populations, and their impacts on the increasing complexity of reef systems, it is especially unfortunate that epochs when considerable *Halimeda* diversification was likely to have occurred, such as the Miocene and Oligocene, have been so poorly sampled for *Halimeda*. What results there are have too often been recorded only as *H.* sp., making analyses of species diversity meaningless.

Field parties could remedy the situation significantly if sites similar to those now supporting *Halimeda* meadows and draperies, reefal lagoons and fore-reef slopes for example, were the goal of study, instead of the traditional reef ridges and coral sites; the latter is hardly known for substantial *Halimeda* populations, yet so much of reef biology concentrates on this location. The Pleistocene tropics, as well as portions at least of preceeding epochs, are likely to have supported sizeable populations of *Halimeda* species. However, we do not know the impact global lowering of atmospheric carbon dioxide concentrations, with associated changes in carbonate solution equilibria in the oceans, would have on *Halimeda* growth. It is likely that some of most interesting aspects of *Halimeda* speciation and biomass increase occurred during this time frame. Discovering them would be a significant paleontological venture, and important contribution to tropical reef research.

DEDICATION AND ACKNOWLEDGMENTS

This paper was written to honor the 60th anniversary of Professor Ovidiu Dragastan, an internationally respected and dedicated scholar of fossil algae, and an esteemed colleague and friend.

My thinking on the origins of *Halimeda* has developed over a long professional lifetime, being guided by many colleagues, from William Randolph Taylor who first set me on the trail at the University of Michigan and the Marine Biological Laboratory, Woods Hole, J. Harlan Johnson of the Colorado School of Mines, Graham Elliott at the British Museum (Natural History), Max Doty of the University of Hawaii, through Paul Silva of the University of California, Berkeley, and Robert Riding, University of Wales College of Cardiff, to their successors in phycological research. The recent molecular analyses on which much of this paper is based, were carried out when I was an affiliated staff scientist at the Smithsonian Tropical Research Institute in Panama. I thank W. H. C. F. Kooistra and J. A. Engman for collaboration with the molecular trees, P. D. Zamore for technical assistance with paleohistory diagrams and M. Calderón for laboratory assistance. Financial support for the molecular work was provided by the National Science Foundation (9296094), the Smithsonian Institution's Scholarly Studies Program, and the Andrew W.Mellon Foundation.

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