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Taxonomy and morphological variation of the genus *Ceramium*
(Rhodophyta, Ceramiales) in Hawaii

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TAXONOMY AND MORPHOLOGICAL VARIATION OF THE
GENUS CERAMIUM (RHODOPHYTA, CERAMIALES)
IN HAWAII

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF
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ABSTRACT

Algal taxonomy is mainly based on vegetative and reproductive characters. Red algae (Rhodophyta) are characterized for having a wide variation of thallus construction types, ultrastructural features, and several and complex life histories that provide abundance of characters on which to base distinction among taxa. Nevertheless, the morphological variability exhibited by most of theses characters often difficults the taxonomic processes. Morphological variability may be correlated to external (environmentally induced) or internal (i.e., life history phase or age) factors.

Species belonging to the genus _Ceramium_ Roth (Ceramiaceae, Ceramiales) are no exception to this morphological variability in diagnostic characters. _Ceramium_ is a worldwide distributed genus of uniaxial construction. In the Hawaiian archipelago it consists of small, delicate species exhibiting cortication restricted to certain portions of the thallus. This research project was developed with the goal of contributing to the taxonomic knowledge of _Ceramium_ species in Oahu, including morphological experimental

studies to dilucidate the significance of the
morphological variability within each of three selected
species.

Eleven species of _Ceramium_ were recorded in
Oahu.   Five of these species: _Ceramium aduncum_, _C._
clarionensis, _C._ _affine_, _C._ _flaccidum_, and _C._ _fimbriatum_
are also recorded in southern North America and Japan
indicating their wide distribution throughout the
tropical and subtropical North Pacific Ocean.   Two other
species represent new undescribed species and three
others gave no conclusive results because of the little
material available.

Growth experiments under controlled conditions
of light intensity, photoperiod, nutrient concentration,
temperature and water movement indicate that most of the
morphological characters are susceptible of variation.
However, while _Ceramium_ sp.1 may change its external
morphology in culture to the extent of being
unrecognizable from field-growing specimens, _C._
flaccidum remains easily identifiable under most growing
conditions.   Differences among tetrasporophytes and
gametophytes (and between male and female gametophytes)

are outstanding in <u>C</u>. <u>clarionensis</u>, and they can be
modified through different culture conditions. In
<u>Ceramium</u> sp.1, on the contrary, no significant
differences are detected among the life history phases
and this fact does not change by modifying the culture
conditions.

Thus, morphological variability in <u>Ceramium</u> has
different degrees of expression depending on the
species, and it is the result of the interaction of
genetic and environmental factors.

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LITERATURE REVIEW

Characteristics of the Division Rhodophyta

Introduction.

The Rhodophyta consist of a very distinctive assemblage of plants which differs markedly from other algal divisions. One of the major characteristics of all of the red algae is the presence of phycobilins in all taxa as accessory pigments, in addition to chlorophyll a. Phycobilins are also present in bluegreen algae (Gantt, 1980), but their absorption spectra are different, with the exception of the Bangiophycidae. The combination of pigments that these plants possess, as well as the occasional photodestruction of phycobilins, produces a wide range of color variation, and thus it is not always easy to recognize them by being red in color. A second major characteristic feature in red algae is the complete absence of all motile cells throughout the stages of their life history. Reproduction in the group is oogamous and the processes of zygote initiation and development are unique as will be discussed later. The

cell wall structure is similar throughout the group;
basically it consists of randomly arranged microfibrils
of polysaccharide, cellulose in most red algae, embedded
in an amorphous matrix of a gelatinous nature. Cell wall
calcification, either calcite or aragonite, is present in
some members of the group. In addition, a predominant
storage substance floridean starch (a branched molecule
with a main chain of D-glucose conected by α-1,4 bonds),
is found in most orders of red algae.

Despite the cellular and reproductive features
in common previously mentioned, the Rhodophyta include
diverse morphologies, reproductive systems and life
histories. These characters have been used to separate
the division into two major classes: the Bangiophyceae
and the Florideophyceae. However, this recognition of
classes or subclasses remains more at the historical
level since most of the features used for this
distinction are not exclusive of either group. A
cladistic analysis of the orders of Rhodophyta
(Gabrielson et al, 1985) did not support the recognition
of the 2 classes, regardless of which order was
designated as the outgroup.

Traditionally, the Bangiophyceae include
unicellular to multicellular pseudoparenchymatous forms
as well as colonial and filamentous forms.

Pit-connections are lacking between cells in all, except for the genus _Rhodochaete_ and the "Conchocelis" life-history phases of _Bangia_ and _Porphyra_. Among those genera in which sexual reproduction has been reported, a diphasic type of life history occurs. Most of the Bangiophyceae have intercalary growth with the exception of _Rhodochaete_ which shows apical growth.

The Florideophyceae, on the other hand includes those species that are filamentous although some may be pseudoparenchymatous derived from a multiaxial or uniaxial organization. Pit-connections, thickened and modified connections between daughter cells, are present in all taxa, although Pueschel & Cole (1982) have documented differences among them. This class is characterized by tipically having apical growth, except for members of the Corallinales and the Delesseriaceae, where intercalary growth also occurs. Sexual reproduction is widespread, most commonly with an alternate free-living asexual phase. Other asexual means (e.g., monospores, fragmentation, propagules, etc.) of reproduction are known. Despite variation in life history patterns, they show at least three cytological phases in two life forms. Taxa may have either heteromophic or isomorphic phases in their life histories.

The following section will introduce a brief account of the features which characterize red algae as an unique assemblage of organisms. Some of these features are commonly used for taxonomic purposes and where these are considered relevant for taxonomy, this will be mentioned with some examples. A discussion summarizes their significance.

Cellular structure and biochemistry.

Being photosynthetic organisms, red algae have adapted to maximize light harvesting from the sun in order to enhance their survival and propagation in an aquatic medium which often does not offer optimum conditions for light absorption. Thus, in addition to the presence of chlorophyll $\underline{a}$, a number of accessory pigments are found in their photosynthetic lamellar structure, extending the range in which the algae absorb visible light (e.g., Dring, 1981). The work of these accessory pigments in conjunction with chlorophyll $\underline{a}$ optimizes light harvesting for photosynthesis (Gantt, 1975; 1980a).

Phycobiliproteins are the major accessory pigments in red, blue-green (Cyanophyta) and cryptophyte (Cryptophyta) algae. In red and blue-green algae,

phycobiliproteins exist in special aggregated structures, the phycobilisomes, which appear to be organized for maximum energy transfer with reaction center chlorophyll $\underline{a}$ as the final acceptor. The involvement of these accessory pigments in photosynthesis of red and blue-green algal groups was established by refined action spectra using whole plants (Haxo and Blinks, 1950). This study showed that photosynthetic rates are high in the spectral regions absorbed by the water-soluble phycobiliproteins, while the light absorbed by chlorophyll is poorly utilized for oxygen production. However, photosynthetic efficiency seems to be variable from one cell type to another in the region of the spectrum utilized by the accessory pigments and constant in the region of the spectrum where chlorophyll absorbs light (Brody & Brody, 1962). In absorption spectra it can be observed that phycobiliproteins (R-phycoerythrin, R-phycocyanin, allophycocyanin) enhances the small amount of light absorption taken up by chlorophyll $\underline{a}$. The absorption peak for R-phycoerythrins is 540 - 565 nm, for R-phycocyanins is 610 - 640 nm and about 650 nm for allophycocyanins (O'hEocha, 1965). The proportion in which these pigments exists relative to chlorophyll $\underline{a}$ varies depending on light intensity (Waaland $\underline{et}$ $\underline{al}$, 1974; Ramus $\underline{et}$ $\underline{al}$, 1976; Dring,

1981). Energy absorbed by phycobiliproteins can be transferred to chlorophyll with a degree approaching 80% - 90% of efficiency (Tomita and Rabinowitch, 1962), and in its transfer sequence, excitation energy moves from phycoerythrin to phycocyanin to allophycocyanin and is finally trapped by reaction center chlorophyll $\underline{a}$ (Gantt, 1975; Larkum & Weyranch, 1976).

Structurally the pigments are composed of proteins and chromophores, which are covalently bonded. These assemblages, called phycobilisomes, are regularly arranged on the stroma side of the photosynthetic lamellae (Gantt and Conti, 1965; 1966; Edwards and Gantt, 1971) and their shape (ranging from disc-like to prolated) may be determined by the predominant phycobiliproteins present (Gantt and Conti, 1966). Since the phycobiliproteins serve as antennae pigments that transfer the energy absorbed primarily to photosystem II (PSII) reaction centers, it can be logically assumed that a PSII structural particle would be in close contact with the phycobilisome (Gantt, 1980). There is circumstantial evidence (Wollman, 1979) that the PSII structural particles may be the small intra-thylakoidal particles that are arranged in parallel rows in 0.5 to 2.0 phycobilisomes per particle (Lichtle & Thomas, 1976).

The fine structural aspects of the chloroplasts in red algae not only include the pigment composition, and the phycobilisomes in which these pigments are arranged, but as defining features of the Rhodophyta. Chloroplasts in red algae are surrounded by an envelope comprised of two membranes, and contain single, nonaggregated thylakoids (Dixon, 1973; Duckett and Peele, 1978). Peripheral thylakoids may encircle the chloroplast (Bisalputra, 1974; Hara and Chihara, 1974). Electron-transparent regions or genophores (apparently DNA-containing regions) are scattered in the stroma (Bisalputra, 1974). Pyrenoids have been observed in some Bangiophyceae and some members of the Florideophyceae (McBride and Cole, 1972; Duckett et al, 1974; Lin et al, 1977; Hawkes, 1978) and different types have been described (Dodge, 1973), although they have not been isolated and their chemical structure has not been characterized yet in red algae (Brawley and Wetherbee, 1981).

The structural changes seen in the Golgi complex or dictyosome during intense activity in the red algae have not been reported in other plant or animal cells (Brawley and Wetherbee, 1981), thus deserving special attention as a distinguishing characteristic of the

Rhodophyta. Golgi bodies typically possess six to ten cisternae separated from one another by a space of approximately 10 nm with an overall dictyosome size of 0.5 um (Alley and Scott, 1977). When the size and activity of the Golgi complex is maximal, the dictyosomes become hypertrophied and the intercisternal space disappears, the adjacent cisternae becoming closely appressed (Duckett and Peele, 1978). The Golgi complex plays an active role in secreting extracellular products during the differentiation of spores in several red algae (Chamberlain and Evans, 1973; Pueschel, 1979; McBride and Cole, 1972) and it is responsible for the production of carpospore wall material in several species (Delivopoulos & Kugrens, 1984, 1985; Kugrens & Delivopoulos, 1986).

Red algal cell walls reveal a layered fibrillar appearance in which the randomly oriented microfibrils of the inner layer are composed of cellulose (Myers et al, 1956) in Florideophyceae and of mannan and xylan (Frei & Preston, 1964) in Bangia and Porphyra, of the Bangiophyceae. The outer mucilaginous layer and the wall matrix of many red algae are made of a sulphated water-soluble polysaccharide (i.e., agar, carrageenan), water soluble and able to form gels and viscous solutions under appropriate conditions (Mackie and Preston, 1974).

These polysaccharides appear to originate from both the cell walls and the intercellular regions. They have a distinctive structure and they are widespread throughout the Rhodophyceae (Rees,1965; Anderson and Rees, 1966). Although variation occurs in the chemical nature of the units in these polysaccharides (Duckworth & Yaphe, 1971a; 1971b; Anderson et al, 1973), the underlying repeating structure is a galactan in which the building units are alternately B-1,4 and α-1,3 linked (Anderson et al, 1965; DiNinno & McCandless, 1978a; 1978b).

Members of the order Corallinales have the capacity of depositing calcium carbonate ($CaCO_3$) in the form of calcite crystals within the cell walls (Borowitzka and Vesk, 1978; Borowitzka, 1982). Crystals are arranged within an organic matrix and are absent from the thin layer of cell wall material adjacent to the plasma membrane (Borowitzka and Vesk, 1979). Secondary deposits of $CaCO_3$ of unknown crystallography are also found in the spaces between the cell walls of Lithothrix aspergillum Gray suggesting two mechanisms of calcification in this species (Borowitzka and Vesk, 1979). In the Nemaliales, calcium carbonate in the form of aragonite crystals have been found in Yamadaella

cenomyce (Decaisne) Abbott, in which calcium deposits are
wholly extracellular (Borowitzka et al, 1974).

Only a few species all in the order Ceramiales
and the bangiophycean alga Porphyridium have been examined
for mitosis. Ultrastructural descriptions of mitosis in
Membranoptera (McDonald, 1972), Polysiphonia (Scott et al,
1980; 1981) and Dasya (Phillips and Scott, 1981) show the
formation of a closed fenestrated spindle, the presence of
a perinuclear endoplasmic reticulum, a metaphasic
arrangement of chromosomes, layered kinetochores,
chromosomal and non-chromosomal microtubules and the
presence of nucleus associated organelles, known as polar
rings, located singly in large ribosome-free zones. In
addition to the few members of the Ceramiales mentioned
above, polar rings have been detected in the freshwater
red alga Batrachospermum ectocarpum Sirodot (Scott, 1983)
of the Batrachospermales. While among the Bangiophyceae
they are reported only in Porphyridium purpureum (Bory)
Drew et Ross (Schornstein and Scott, 1981). In the higher
orders of algae polar rings appear as hollow,
electron-dense cylinders of double-ring structure with
fine filaments or granules within the cylinder center. In
contrast, in Porphyridium they consist of a broad solid
granule topped by a small flattened disc. Further work in

Polysiphonia (Scott et al, 1981) showed polar rings as
persistent organelles during interphase, but a portion of
them is dispersed during prometaphase in Porphyridium
(Schornstein and Scott, 1981). In Dasya as well as in
Polysiphonia these structures apparently play the role of
establishing the division axis by the migration of one of
them along the nuclear envelope, whereas the other remains
in its original position.

Ultrastructural studies in meiosis of red algae
are scarce (Kugrens and West, 1972b; Scott and Thomas,
1975; Pueschel, 1979). However, detailed research on Dasya
baillouviana (Gmelin) Montagne (Broadwater et al, 1986a;
1986b) gives an account of the ultrastructural differences
between the processes of mitosis and meiosis. Among some
of the differences are: i) the presence of large
accumulations of smooth endoplasmic reticulum which are
often found at the division poles during meiosis I and ii)
the occurrence of the apparent fusion of the four nuclei
after centripetal migration to the center of the
tetrasporangium following meiosis II.

The characteristic reserve storage material found
in red algae is floridean starch, first described by
Kuetzing (1843). Floridean starch is granular and
develops in the cytoplasm in intimate association with the

endoplasmic reticulum, which appears to be involved in starch grain formation, and with particles presumed to be ribosomes (Borowitzka, 1978; Pueschel, 1979). The chemical characterization of this starch has been well studied (cf. Craigie, 1974), and place it among amylopectin-type structures rather than glycogen-type substances common in animal cells (Pea et al, 1959a; 1959b; Greenwood and Thomson, 1961; Manners and Wright, 1962). Floridean starch differs from higher plant amylopectins by possessing a different basal chain length (15 glucose units). The reactions to amylolysis also differ between the algal storage product and that of the flowering plant, under the different enzymes tested (Manners and Wright, 1962).

Septum formation is incomplete at cell division in most red algae, leaving a centrally located cytoplasmic connection between the two daughter cells. The contiguous cells remain connected by the cell membrane and the pore becomes plugged by a glycoprotein plug. The conjunction is called a primary pit-connection. Secondary pit-connections are formed when a cell in a filament generates a small cell which acts as a bridge between this 'parental' cell to a cell in an adjacent filament. Primary pit-connections are distinctively present in the

cross walls of adjacent cells of most red algae. They were originally defined as well-marked pits, occupied by broad cytoplasmic strands, occurring in the septa of adjacent cells (Fritsch, 1945). Among the Bangiophyceae, pit-connections have been found in the vegetative cells of the sporophytic, "Conchocelis" phase of Bangia (Fan, 1960) and species of Porphyra (Cole and Conway, 1975; Pueschel and Cole, 1985) as well as in Rhodochaete. Structural differences between the pit-connections of gametophytes and sporophytes have been shown in Rhodochaete (Pueschel and Magne, 1987). Pit connections appear to be present throughout the Florideophyceae. The pit-plug, a structure that occludes the septal pore (Pueschel & Cole, 1982), has a complex organization in Florideophyceae, consisting of a plug core, plug caps of one or two layers and associated cap membranes. Differences in the components of pit-plug structure have been used as a taxonomic feature at the ordinal level (Pueschel and Cole, 1982). In the Bangiales there is no cap membrane and the cap layer is slender (Pueschel, 1987) while in a member of the Rhodochaetales, Rhodochaete parvula Thuret, cap membranes are also absent and plug caps are present; this condition is considered to be an ancestral state of red-algal pit-plugs (Pueschel and Magne, 1987). The Nemaliales and Cryptonemiales seem to

be heterogeneous assemblages with respect to pit structure, and pit-plugs do not aid in distinguishing the Palmariales from the Nemaliales (Pueschel, 1987; Pueschel & Cole, 1972).

No member of the Cryptonemiales, Gigartinales or Ceramiales has two-layered plug caps, which is a characteristic feature of the Corallinales (Pueschel and Cole, 1982). Nevertheless, because of the high variation that can be found in the structure of pit-connections within a single species, more studies need to be done in order to fully evaluate pit-connections as a taxonomic feature. In Griffithsia flosculosa (Ellis) Batters of the Ceramiales there are structural differences in the cap membrane between the phases of the life-history including the complete absence of the membrane (Peryiere, 1977). A similar occurrence is found between the filamentous gametophytic phase and the erect fleshy gametophytic phase in Pseudogloiophloea (Cryptonemiales) (Ramus, 1969c). In Faucheocolax attenuata Setchell (Cryptonemiales), an enlarged, crenulate septal plug occurs between the fusion cell and the auxiliary cell (Kugrens and Delivopoulos, 1985). Broadwater and Scott (1982) studying the pre-fertilization events in the carpogonial branch system of Polysiphonia harveyi Bailey (Ceramiales), found three

types of pit-plugs, depending on the number of
pit-membranes, which had a very specific location within
the branch.

Pit-plug formation has been described, among
others, in _Laurencia spectabilis_ Postels & Ruprecht
(Ceramiales) (Bisalputra _et al_, 1967) and
Pseudogloiophloea confusa (Setchell) Levring
(Cryptonemiales) (Ramus, 1969b). Soon after nuclear
division, centripetal deposition of wall material develops
a septum within the two cells, the septum formation ceases
before the partition is complete and the resulting
aperture is closed by the condensation of flattened
vesicles that become the pit-plug. Thus, the plug
formation completes the process of cytokinesis.

The original theory that pit-connections had
actually a cellular continuity between adjacent cells
acting as a pathway for nutrient translocation in red
algae has been raised a few times in the past 10 years
(Wetherbee, 1979). Wetherbee (1979) suggested that pit
plugs between carposporophyte cells of _Polysiphonia_ are
structurally specialized for nutrient translocation. This
interpretation was not based on evidence of translocation
but on plug ultrastructure, and was later rejected by
Pueschel (1980) because of the lack of direct evidence.

Photosynthates translocation has been demonstrated between
parasitic red algae and their hosts (Goff, 1979a),
although pit-plugs (from secondary pit-connections in this
case) do not seem to be involved in the process since they
are plugged with an electron-dense matrix separated from
the cytoplasm by a membrane (Goff, 1976). Goff (1979b)
proposed a method of translocation between Harveyella
mirabilis (Reinsch) Schmitz & Reinke and its host that
involves the membrane system and plasmalemma extensions of
the rhizoidal cells of Harveyella. A transfer of nuclei
occurs between the parasite and the host during secondary
pit-connection formation in Polysiphonia confusa
Hollenberg and its parasite Choreocolax (Goff & Coleman,
1984), but this happens prior to the formation of the plug
for this pit-connection. In one species of Cryptonemia
(Cryptonemiales), pit-connections were proposed as the
route for transport of solutes towards the deeply buried
layers of living medullary cells (Wetherbee and Kraft,
1981). Because this species has thick stalks which can
reach 2 cm diameter and where the outermost cells are
dead, the question of transport through a system which
theoretically contains totipotent cells remains untested.

Thallus organization.

Among the Rhodophyta habits range from
unicellular forms, where individuals can be isolated or
may form irregular masses of cells, to large foliose
pseudoparenchymatous, filamentous or crustose forms, where
some individuals show a high degree of differentiation
within thalli.

The most simple forms are found among the
Bangiophyceae although some pseudoparenchymatous species
also belong to this subdivision. Several genera consist
of unicells, either single or grouped in colonies
surrounded by mucilage, e.g., Porphyridium (Sommerfield &
Nichols, 1970; Lin et al, 1975), Rhodosorus (West, 1969),
and Chroothece (Kylin, 1956). Other genera have a small
epiphytic thalli which consist of irregularly branched
filaments and are surrounded by mucilaginous envelopes.
This organization can remain uniseriate (i.e., some
species of Erythrotrichia, e.g., E. ceramicola and
Kylinella) in some species but become multiseriate in
others (i.e., Goniotrichum). At this level it is often
difficult to differentiate between one family and another
because frequently uni- or bi-seriate forms interchange
with filamentous forms; this appears to depend on

prevailing environmental conditions (Lewin & Robertson, 1971).

The order Bangiales includes various habits of growth: creeping filaments becoming discoid or polystromatic (several layers) cushions (e.g., Erythrocladia), or heterotrichous filaments, which display both a prostrate and an erect system (e.g., Porphyropsis) (Murray et al, 1972). In Erythrotrichia, the prostrate system consists of one-layered base produced first by the germinating spore, bearing unbranched erect threads (Heerebout, 1968). In Smithora (Hollenberg, 1959), the prostrate system is a cushion-like base from which clusters of blades are produced. The best known bladed genus is Porphyra where the cells of an uniseriate row divide longitudinally to produce a typical multiseriate morphology.

Apparently the typical thallus of most Bangiophyceae lacks a definite growing point (Fritsch, 1945). In filamentous types the filaments grow by intercalary cell division, a meristematic region is not localized to a specific portion of the thallus but cell division takes place throughout the filament. In rare cases (i.e., Compsopogon), an initial uniseriate filament becomes corticated with small cells. A pseudopaenchy-

matous construction by longitudinal divisions of the filament cells results in the expanded fronds of _Porphyra_ and some _Bangia_ species.

The majority of the Florideophyceae exhibit a more complex structure than in Bangiophyceae. A fundamental characteristic of almost all members of this subdivision is apical growth. This is effected by apical cells which cut off a single series of segments parallel to the base (in certain advanced types the apical cells are 2 or 3-sided and give rise to as many series of segments). However, intercalary cell division also occurs in certain genera of Delesseriaceae as well as in all the order Corallinales.

The resulting segments from apical cell divisions remain connected by conspicuous pit-connections in their septa. Where the close juxtaposition of several filaments obscures the basic construction, the pit-connections are often of great value in tracing the ontogenetic relationships of adjacent cells. Some forms, however, develop secondary pit-connections between unrelated cells. Neighboring filaments or cells may establish contact secondarily and create linkages within the thallus. A small cell is cut off by one of the cells involved, eventually this new-formed cell comes into

contact and fuses with a cell of an adjacent filament. The remaining pit-connection now links the two adjacent cells (Rosenvinge, 1888). Secondary pit-connections are probably very common among the red algae, but they are only used in Laurencia (Rhodomelaceae) (e.g., Saito, 1969) as well as in the crustose members of the order Corallinales for taxonomic purposes (e.g., Adey, 1970).

Because a Florideophycean thallus is formed by the aggregation of filaments, it is essentially pseudoparenchymatous in nature. Thallus organization is either uni- or multiaxial depending upon whether there is one filament or a group of filaments forming the central axis of the thallus. According to Kylin (1956), one of these categories, the "Zentralfadentypus", is formed by a single monosiphonous filament which grows by means of an apical cell. This generates the framework of the thallus by producing many lateral branches. A second category, "Springbrunnentypus", is formed by several to many parallel long filaments, with apical growth. Their lateral branches are attached radially and appear fountain-like shape in longitudinal view.

Dixon (1973) considered that the attempts to apply these two conceptual categories to crustose thalli were totally irrelevant and indicated that, from a

morphogenetic point of view, the two types of basic
construction among Florideophyceae are the encrusting
thallus and the erect foliose thallus, both types being
the result of a differential development of the components
of an heterotrichous organization.

Among those genera that have an obvious
heterotrichous organization, some forms have a vegetative
thallus which consists only of the prostrate portion,
e.g., Peyssonnelia, Petrocelis (Denizot, 1968), the erect
filaments are never formed except in some cases in
connection with the origin of reproductive structures. In
crustose coralline algae, the growth of the upright
filaments, which increases the thickness of the crust, is
attributable to the meristematic activity of subterminal
cells, thus the growth is not apical as in most other
Florideophyceae, but intercalary (Johansen, 1981).

In erect foliose thalli there may be
differentiation at three levels of complexity. The basic
feature of this differentiation involves growth control.
The principal central axial filament presents unlimited
(indeterminate) growth, whereas the lateral surrounding
filaments usually exhibit limited (determinate) growth
(Dixon, 1971). In the simplest heterotrichous
organization, found in some species of Acrochaetium, the

thallus is composed of a prostrate system of filaments from which the upright filaments arise (West, 1968). In most foliose Florideophyceae, there is a clear differentiation between principal axial and lateral filaments, the latter commonly arises in opposite pairs of whorls from the cells of the main axes. These laterals are formed when the segments of the initial uniseriate axis cuts off laterally two or more pericentral cells which either i) undergo no further divisions or ii) continue to divide and to act as the apicals of lateral branches. Thallus growth in length is the result of the number of divisions undergone by the apical cells and the subsequent enlargement of the segments. In certain uniaxial forms (i.e., _Centroceras_ and _Ceramium_), some lateral filaments grow downwardly showing different cell size and shapes than those which have laterally projecting filaments. They may partially or entirely cover the axial filament, referred to as "cortication" (Hommersand, 1963). The ultimate appearance of the thallus is therefore a result of the development of main axes in relation to laterals of limited or unlimited growth as well as the formation of proliferations and dichotomies. The latter can be truly formed only in algae of multiaxial construction in which the orientation of the apical cell

divisions diverges in opposite directions on each half of the cluster of axial filaments. In uniaxial types however, the unequal products of the apical cell division give rise to pseudodichotomies instead of true dichotomies (Dixon, 1973).

In more specialized uniaxial or multiaxial organization, these primary features may be obscured by later developments, and thus an initial axial growth pattern may be difficult to recognize. In algae of uniaxial construction, some Cryptonemiales (i.e., Cryptosiphonia, Endocladia and Gloiopeltis), a portion of the apical cell cuts off two pericentral cells which develop ultimately into a compact cortex (Kylin, 1928; 1930). A similar level of differentiation occurs in some Gigartinales (i.e., Hypnea) in which laterals develop a cortex while the innermost axial cells elongate and differentiate into a medullary region (Fritsch, 1945). In this case the initial central axis can usually be seen. Another member of the Gigartinales, Gracilaria verrucosa (Hudson) Papenfuss exhibits large, highly vacuolate, thick-walled medullary cells such that the initial axial thread is unrecognizable, but cells from a narrow cortical zone remain small (Frederiq & Hommersand, 1989). In Plocamium coccineum (Huds.) Lyngb. the unequal timing and

development of the pericentrals is responsible for the typical flattening of the frond (Kylin, 1923). The central cells elongate markedly and the innermost lateral cells enlarge and function as storage cells.

Among the Ceramiales, an exclusively uniaxial order, one family, the Delesseriaceae, has aggregations of lateral filaments which obscure the axial filament by lateral adhesion to form a flat sheet of tissue (Kylin, 1923; Rosenvinge, 1924). In this order, all traces of heterotrichy are absent, except in cases in which the thallus as a whole may be differentiated secondarily into erect and prostrate axes. Contact with a substrate usually stimulates the development of attachment structures along the length of the thallus (Dixon, 1973). The mature thallus in algae of multiaxial construction can be compressed or markedly flattened, the elements of the thallus are modified and differentiated secondarily. For example, Agardhiella subulata (C.Ag.) Kraft has a mature thallus consisting of a mass of narrow threads surrounded by a fine cortex bounded by a narrow zone of photosynthetic cells (Borgesen, 1919; Kylin, 1928). In Chondrus crispus (L.) Stackh. the medulla comprises elongated cells with thick mucilaginous walls, their narrowed ends bridged by pit-connections (Rosenvinge,

1930). Numerous perpendicular, small-celled laterals form a compact cortex separated from the central threads by cells of intermediate size. **Gigartina stellata** (Stackh.) Batt. has essentially the same structure, but in this species the cells of the inner cortex and medulla produce downgrowing septate hyphae (Fritsch, 1945). Some multiaxial thalli may also be lightly to heavily calcified (i.e., **Galaxaura**, **Liagora**, and Corallinales species. In the articulated Corallines the thalli are composed of calcified segments (intergenicula) separated by flexible, non-calcified joints (genicula). The deposition of $CaCO_3$ takes place particularly between the filaments of limited growth, therefore the joints, which only consist of axial filaments of unlimited growth, remain devoid of calcification (Johansen, 1981).

Life history and reproduction.

One of the most distinctive characteristics of the Rhodophyta is the absence of flagellated stages in any part of their life history. Sexual reproduction is oogamous and involves non-motile male cells called spermatia, and highly specialized female cells, carpogonia. These two gametophytic structures can either

be produced in the same individual (monoecious) or in different (dioecious) plants. The carpogonium bears an emergent portion, more or less elongated, the trichogyne, which acts as a receptive surface to which the spermatium attaches. Sexual recombination takes place with the fusion of a haploid spermatial nucleus and a haploid carpogonial nucleus. The zygote nucleus undergoes successive mitotic divisions which result either in the direct formation of a number of diploid carpospores as in Porphyra, or in the formation of a non-free-living diploid generation, the carposporophyte. This generation produces carposporangia for Florideophycean algae. The carposporophyte is one of the phases in the life history of the alga because, although it is borne on the gametangial (haploid) plant, it is the diploid product of fertilization.

The simplest form of sexual reproduction known in red algae is exhibited by the monotypic order Rhodochaetales (Magne, 1960). The thallus in Rhodochaete is haploid, monoecious, and apparently all the cells, except the most basal ones, may become reproductive. No distinguishing features allow the recognition of the spermatangial mother cell or the cell that will eventually become a carpogonium. A small cell or spermatocyst

(=spermatangium), is formed by mitosis within a vegetative cell and protrudes from the middle part of the latter (Fig.1.1a). The spermatocyst releases a spermatium (Fig.1.1b) which fertilizes the carpogonium (Figs.1.1c,d,e). By means of a mitotic division after nuclear fusion, the cell that acts as carpogonium produces a diploid carpospore (Figs.1.1f,g,h) (Magne, 1960). The fate of the carpospore is not known and no evidence of meiosis has been observed in Rhodochaete. Because gametophytes are by definition haploid, at least two alternatives may be hypothesized as ways in which gametophytes are restored in a life history. In one, meiosis occurs after carpospore germination which may represent the origin of the haploid gametophyte. While in the second the carpospore germinates into a diploid generation bearing the structures (sporangia) in which meiosis will be localized. The origin of a carpospore directly from the fertilized carpogonium or through a number of unknown steps can be interpreted as the formation of an extremely reduced carposporophyte. This event may be significant as a primitive or derived condition within the subdivision Florideophyceae. Although not nearly as complex as the carposporophyte of the latter, the carposporophyte in Rhodochaete resembles

it by showing _in situ_ zygotic development with attendant diploid cells.

Upon germination of spores, morphologies can be either similar to the earlier phase (isomorphic) or completely dissimilar (heteromorphic), and show intergrades between these two. Sexual dimorphism within a species where female and male gametangial plants do not look alike morphologically is also known.

Among the sexually reproducing genera of the Bangiales carpospores can germinate into a filamentous diploid stage, the '_conchocelis_' stage (Figure 1.2). This sporophytic phase gives rise to conchospores, formed in specialized structures, the conchosporangia. The conchospores undergo meiosis at germination and initiate a foliose thallus. The gametophytic thallus of _Porphyra_ and _Bangia_ produces spermatia and carpogonia. The latter, after fertilization, divides mitotically to form packets of 4,8 or 16 carpospores (Cole & Conway, 1980; Richardson, 1970). Apomictic species of _Bangia_ and _Porphyra_ also form a foliose stage bearing spermatia and carpospores and a filamentous stage bearing conchospores in which the chromosome number is not changed (Mumford & Cole, 1977). Asexually, both phases can recycle themselves by the production of monospores (Kurogi, 1972; Conway & Cole,

1977; Richardson, 1972) in the foliose and filamentous
stages respectively. Therefore, instead of a triphasic
life history (typical of the Florideophyceae), the
Bangiophyceae show a diphasic life history which has been
considered as a primitive condition (Richardson & Dixon,
1968).

Because production of conchospores in Japanese
Porphyra is stimulated by short days and inhibited by long
days (Kurogi, 1959), the production of the foliose thallus
is restricted to winter months, while the filamentous
stage recycles and is probably a perennial, persistent
stage in the life history.

In other groups either the tetrasporophytes or
the carposporophytes typical of a triphasic life history
are absent. In Batrachospermales carpospores germinate
into a small filamentous stage (prothallus) which
undergoes a direct transition to an erect gametophyte
(Fig. 1.3), thus the diploid vegetative cells of the
prothallus undergo meiosis without the formation of a
tetrasporophyte (Magne, 1967a; 1967b). In other groups
(Palmariales) the tetrasporophyte apparently develops
directly within the female gametophyte, thus; no
carposporophytic phase is present. In the Palmariales,
two interpretations have been suggested; one is that the

tetraspores segregate large haploid male plants (Fig. 1.4) and small haploid female plants (Van der Meer, 1980). After fertilization the diploid tetrasporophyte blades (morphologically indistinguishable from the male plants), develop directly from the carpogonium without the formation of a carposporophytic stage. The second interpretation of Magne (1987) is that after fertilization a carposporophytic plant develops that is morphologically identically to male plants, but the carpospores are never released and they mature _in situ_, which produces a reduced parasitic tetrasporophyte (Fig. 1.5) (Magne, 1987). Although the life history in the majority of _Liagora_ species involves heteromorphic phases (Von Stosch, 1965), with a filamentous tetrasporophyte (Fig. 1.6), this free-living stage is absent from life-histories of some species of _Liagora_. For _Liagora_ _tetrasporifera_ Borgesen the carposporophyte bears terminal, cruciately divided carpotetrasporangia in which meiosis occurs. These carpotetraspores germinate upon release and are able to continue with the life history (Coute, 1971), producing a filamentous phase.

Among those groups in which a carposporophyte develops, gonimoblast filaments bear carposporangia which release many individual carpospores. Gonimoblast

filaments develop at four possible locations i) the fertilized carpogonium, ii) the cell immediately beneath it, the hypogynous cell, or, iii) the fusion of the carpogonium and the hypogynous cell (i.e., Gelidiales, some Bonnemaisoniales, and some Nemaliales), or, iv) an auxiliary cell which is produced before (Cryptonemiales, Gigartinales, Rhodymeniales, Corallinales) or after fertilization (Ceramiales).   The auxiliary cell receives the zygotic diploid nucleus by means of a direct fusion with the carpogonium, or it is transferred by either a connecting filament or connecting cell formed by the fertilized carpogonium. These post-fertilization events are tightly coupled with the position of the auxiliary cell and the carpogonium.   A number of variations occur and are held as primarily important to the taxonomy of the Florideophyceae.

The tetrasporophytic thalli produces tetrasporangia, the sites of meiosis which produces a tetrad of spores. Germination of a tetraspore generally will result in haploid gametophytes. In summary, a typical Floridophyceae life history includes three phases: a male or female gametophyte (haploid), a carposporophyte (diploid) and a tetrasporophyte (diploid) (Fig. 1.7). The gametophytic and tetrasporophytic phases are free-living

while the carposporophyte develops directly on the gametophyte.

The tetrasporangium is reported as the site of meiosis, with the meiotic process being documented by microphotography and chromosome counting (Austin, 1960; Tozun, 1974). However, it was not until the occurrence of synaptonemal complexes was documented as conclusive evidence for meiosis that this was accepted. Synaptonemal complexes are flattened structures corresponding to the axes of homologous chromosomes and are visible in cells undergoing prophase of the first meiotic division (Krugens & West, 1972a). These have been detected in several red algae (Krugens & West, 1972a; 1972b) during tetrasporogenesis.

Although the previously described life history is characteristic of the red algae and particularly widespread among the Florideophyceae, there are numerous species in which only part of this life cycle is reported or where one or more of the phases is unknown. Most of these deviations from the "normal" life history consist of the occurrence of only tetrasporophytic plants in which apomeiosis apparently bypasses the gametophyte, recycling the tetrasporophyte. Acrochaetium proskaueri West produces tetrasporangia and monosporangia in the same plant, but

both types of reproductive structures initiate
sporangia-producing plants (West, 1971). Tetrasporangia
are produced only under conditions of long day (16:8 h LD)
and apparently, instead of undergoing meiosis, it appears
that all the spores are mitotically divided, although
cytological information is not available. A similar
situation is reported for Rhodochorton concrescens Drew
(West, 1970), where only tetrasporophytes have been
observed. Also, even though Iridaea cordata (Turner) Bory
possesses an isomorphic alternation of generations, a
study in situ of populations in central California
demonstrates that the highest proportion of the population
consists of tetrasporophytic individuals (Hansen, 1977).
These populations are seasonal, with the blades
disappearing at the beginning of the winter. The main
mechanism by which the population is renewed is by the
production of erect blades from the basal crusts that
remain throughout the year (Hansen, 1977). Apparently,
tetrasporangial crusts are more resistant and longer-lived
than gametangial crusts and thus, tetrasporangial plants
persist forming blades simply by mitosis in this species
(Kim, 1976).

The influence of environmental conditions may
play an important role in the timing of the different

phases of a life cycle. Tetraspores released by crustose stages of Gloiosiphonia verticillaris Farlow develop into gametophytes, if they are placed under long day conditions (De Cew et al., 1981). But, under short photoperiods, they germinate into tetrasporophytes. The ploidy levels of these stages have not been studied, but it seems that meiosis can be induced by long day conditions, whereas short day conditions induce apomeiotic tetrasporogenesis for this alga.

A more complex sequence involves apparent meiotic and mitotic processes in the same plants, Mastocarpus papillatus (C.Ag.) Kuetz.. Carposporophytic plants are able to produce crust-like tetrasporophytes as well as typical blade-like female plants. Some of the latter ones undergo normal fertilization and post fertilization events, while the remainder develop new carposporophytes parthenogenetically (Polanshek & West, 1977). A similar sequence of events is present in Gigartina jardinii J.Ag. (=Gigartina agardhii Setchell & Gardner) (West et al, 1978).

The occurrence of supposedly fundamentally different reproductive structures on the same individual has been frequently reported in some of other red algae (Knaggs, 1969; Rueness & Rueness, 1973; 1985; West &

Norris, 1981). The term mixed phases was coined by Van der Meer & Todd (1977) to designate this condition in *Gracilaria tikvahiae* McLachlan. These authors were able to demonstrate that mitotic recombination is the underlying mechanism that leads to gametophytic reproductive structures present on tetrasporophytes of that species.

A variety of other reproductive structures can be found among red algae. One of them is monospores, asexual reproductive cells produced by a differentiated cell or monosporangium, as commonly present in some Nemaliales (Ramus, 1969; Stegenga & van Erp, 1979; West, 1968). Also polysporangia, a term restricted to sporangia homologous to tetrasporangia, are known in *Pleonosporium vancouverianum* (J.Ag.) J.Ag. (Sheath et al, 1987) and only a few other taxa. Parasporangia, or sporangia containing more than 4 spores but in which apparently no meiosis has occurred, can be found in some members of the Ceramiaceae, e.g., *Plumaria elegans* (Bonnem.) Schmitz (Rueness, 1968), and *Ceramium strictum* Harvey (Fritsch, 1945; Rueness, 1973).

Finally it is also common to observe in some species with a normal life cycle, the formation of propagules, fragments or other means of vegetative ways of

propagation. This is particularly noticeable in species

of <u>Polysiphonia</u> (Kapraun, 1977; Koch, 1986), <u>Callithamnion</u>

(Whittick, 1978), <u>Deucalion</u> and <u>Anisoschizus</u> (Huisman &

Kraft, 1982), and <u>Centroceras</u> (Lipkin, 1977).

<u>Morphological Variation in Macroalgae</u>

Introduction.

Morphological characters, the range and limits of

these, are the most used criteria for the discrimination

of species, algae as well as other plants. Because of the

wide range of variability among individuals within taxa,

it is not surprising that the taxonomy of these groups has

a number of difficulties. The taxonomy of many micro and

macroalgae still needs to be resolved. Criteria for

satisfactory discrimination of species in many cases is

not available, and unsatisfactory separation or grouping

of thesex species under different names or even among

higher levels of classification is still in question.

Many entities which formerly seemed quite distinct are now

known to represent morphological variation of the same

genetic entity (Mathieson <u>et</u> <u>al</u>, 1981) one tribe to

another.

Several of the difficulties attributable to algal variability can be identified. First, species recognition is primarily based on the type method (Silva, 1952). This means that a specimen under study is compared to type-specimen(s) air dried and pressed on an herbarium sheet, liquid preserved and/or mounted on a microscope slide. In addition to obvious problems which arise from preservation, one single or even several specimens cannot encompassed the range of forms found in a population of this species. Further, the preserved specimen may well not be representative of the taxon at all, but a rare, or extreme form of the species rather than within the normal distribution of a selected feature. Second, the usual lack of well documented observations on the material. Third, the collection includes only a few individuals which may represent environmentally induced forms or immature stages. The wide range of variation in thallus form and structure under different habitats, seasonal or geographical conditions is one of the major sources of difficulties in algal taxonomy (Dixon, 1970). Yet, there is an increasing awareness of these problems, but their solution is slow.

Morphological variation among algal life-history stages.

Different morphologies in algal life-history stages of some speciesd has negatively influenced early algal classification. The alternation of heteromorphic reproductive sexual and asexual stages led to the recognition of the different phases of the same species as entirely independent taxa. This is well documented in cases in which one of the phases is a crust-like tetrasporophyte, e.g., Ahnfeltia plicata (Huds.) Fries and Ahnfeltia concinna J.Ag. (Chen, 1977; Farnham and Fletcher, 1976; Magruder, 1977). Monospores of upright plants of A. plicata give rise to a tetrasporangial crustose stage previously identifiable as Porphyrodiscus simulans Batt., while carpospores of A. concinna germinate into crustose thalli able to roduce cruciate tetrasporangia which recycle the gametophytes. Similar life histories have been found in Gigartina jadinii J.Ag. (=G. agardhii Setchell & Gardner) (West,1972) where blade-like gametophytes originated from germinating tetraspores of a non-calcified crust, previously known as Petrocelis franciscana Setch. & Gardn.. Polanshek and West (1977) proposed the linkage of Mastocarpus papillatus (C.Ag.) Kuetz. with Petrocelis middendorffii (Ruprecht)

Kjellman on the basis of the infertility of the
Mastocarpus phase gametophytes of _P_. _middendorffii_ with
field collected sexual plants of _M_. _papillatus_.
Carpospores of _Gloiosiphonia capillaris_ (Hudson)
Carmichael gave rise to crustose tetrasporophytes
morphologically indistinguishable from the prostrate ,
holdfast portion of the upright gametophyte (Edelstein and
McLachlan, 1971).
Another example is found in the genus _Farlowia_ J. Ag.
where the erect gametophytes alternate with a crustose
tetrasporophyte that resembles species belonging to the
genera _Haematocelis_ and /or _Cruoriopsis_ (De Cew and West,
1981).

There are also many instances in which the
alternation of generations is between an upright,
macrophyte thallus and an inconspicuous, filamentous
stage. Species of _Bangia_ Lyngb. and _Porphyra_ C. Ag. have
already been mentioned as having a _Conchocelis_-stage, the
microscopic filamentous phase in their life histories
(Drew, 1949; 1954). Carpospores of _Liagora farinosa_
Lamour. germinate into an _Acrochaetium_-like phase which
produces both monospores and tetraspores (von Stosch,
1965). Two life histories involving conspicuous
gametophytes are those of _Asparagopsis armata_ Harv. and
Bonnemaisonia asparagoides (Woodw.) C.Ag. whose

carpospores give rise to filamentous tetrasporophytic stages known as *Falkenbergia rufolanosa* (Harv.) Schmitz and *Hymenoclonium serpens* (P. & H. Crouan) Batt. respectively (Feldmann and Feldmann, 1942).

Among other algal groups with apparent isomorphic life histories, subtle anatomical differences can be found between the sporophytic and the gametophytic generations. In *Acrochaetium pectinatum* (Kylin) Hamel (= *Audouinella pectinata* (Kylin) Papenfuss) variations in the basal system morphology as well as in the disposition of vegetative branches occur during the ontogeny of both gametophytes and tetrasporophytes. The genus *Chromastrum* Papenfuss has also a characteristic alternation of morphological phases in which the gametophyte has a unicellular base and the tetrasporophyte has a multicellular base (Stegenga & Mulder, 1979). The life history of *Acrochaetium pectinatum* (Kylin) Hamel in unialgal culture includes dissimilar gametophytic and tetrasporophytic morphologies which West (1968) concluded, may provide certain adaptive advantages. Presumably both phases occupy different habitats and are subjected to different environmental factors under which they are better suited with a distinct type of basal system.

Differences in internal anatomical structure led to the recognition of its gametophytes and tetrasporophytes as different species. Galaxaura Lamouroux (Nemaliales) shows an essentially isomorphic type of life history, based on observations that both sexual and asexual plants are in field populations at the same time. Yet, when Kjellman monographed the genus (1900) he described the sexual and tetrasporangial phases of the same species as separate, based mainly on differences in the cortex structure (Howe, 1917; 1918). In some cases, all the species of a taxonomic section appeared to represent sexual phases and the counterpart tetrasporangial individuals represented species in another section (Papenfuss and Chiang, 1969). However, Magruder (1974) showed that one of the most common species Galaxaura oblongata (Ellis et Solander) Lamour., as known in the Pacific, had a microscopic, filamentous, terasporangial phase in culture. Thus the field correlations of Galaxaura species presumably having "isomorphic" generations need to be further tested

In addition to the often distinct morphologies expressed between different algal life-history stages, departures from a strict isomorphic life history can be derived as a consequence of reproductive organ formation.

The minor deviations from presumably isomorphic life
history stages can be recognized in branching pattern
differences between cystocarpic and tetrasporangial plants
of *Ceramium rubrum* (Hudson) C.Ag. Cystocarpic plants of
C. rubrum collected in the field of Nova Scotia exhibit a
significantly higher number of first and second order
branches, and trichotomies (without counting involucral or
derivative branches typical cystocarpic thalli of *C.
rubrum* than those observed in tetrasporangial plants,
giving the former a distinctive three dimensional bushy
appearance (Garbary *et al.*, 1980). Seasonal changes tied
to the onset of tetrasporangia formation are observed in
the morphology of *Pterocladia caerulescens* (Kuetzing)
Santelices, where sterile plants are thin and much
branched and throughout the year, but the individuals
within a population changed in appearance towards the end
of the year, becoming shorter and less branched.
Formation and shedding of tetrasporangia modify the
appearance of frond tips because elongation of the main
axis is slowed and lateral branches are lost (Santelices,
1978).

Morphological variation in algae with isomorphic life histories.

In species with isomorphic alternation of generations, variability in vegetative structures is not always well documented between different stages. Moreover, if variation is not expressed in the position of reproductive organs, or as secondary growth patterns generated by the production of these, then an absolute isomorphism is assumed. Nevertheless, variation is commonly observed among individuals belonging to the same phase, within or between populations, either on genetic or environmental basis.

In benthic macroalgae, as well as in any other sexually reproducing organisms, genetic recombination is the basis for character variation the expression of which is phenotypically modified. Among these characters, the ones commonly used as diagnostic features are morphologic, although chemical product composition is becoming increasingly important in algal taxonomy (Fenical & Norris, 1975; Norris & Fenical, 1985, McCandless et al, 1983). If the degree of characters variability between individuals of the same species is sufficiently low, or fairly constant, it is considered taxonomically valuable.

However, frequently the use of a character as a diagnostic feature was initiated before science realized its variability, yet, its use continues to be applied without information of the range of variation it shows within a population, or between populations.

Among 18 species of _Pterocladia_ which were described from Pacific localities, _Pterocladia pyramidale_ (Gardner) Dawson was reported (Dawson, 1953; 1954; 1963) to have morphological similarity to _P. okamurai_ (Setchell & Gardner) Taylor, _P. robusta_ Taylor, _P. mexicana_ Taylor and _P. complanata_ Loomis. Plants identified as _P. pyramidale_ were collected from ten intertidal and subtidal populations in California (Stewart, 1968), and among these populations morphological variability overlapped with these 5 taxa , and on this basis Stewart (1968) considered them conspecific with _P. pyramidale_. The variation of several growth forms in _P. pyramidale_ observed by Stewart (1968), is apparently related to the degree of exposure to light, temperature and surf action.

Phenotypic variability within a species may be the result of at least two processes: a) the result of natural selection promoting genetic divergence of locally adapted populations, enhanced by the possibility of inbreeding or b) the result of environmentally induced

plasticity, the range of possible phenotypic expressions of an individual genotype. In the first case, the phenotypic variation reflects the genotypic variation of the individuals within or between populations. Changes of one particular phenotype to another occur from one generation to the next. The selection of a particular phenotype is made by the differential survival of individuals which carry the corresponding genotype most suited for the prevailing environmental conditions. In the second case the phenotypic variation reflects different stages in a character based on a single genotype. Changes of phenotypic characteristics can occur during the life time of one individual. The alterations in the phenotype (regulated by the same genotype) are produced by the influence of environmental conditions upon each individual of the population.

Phenotypic variability is well documented in benthic red macroalgae (Norris, 1964; Abbott & Norris, 1965; West, 1971; Chapman et al, 1977; King et al, 1988). Often the variations appear to be a result of aging of the plant or seem to be correlated with the environmental characteristics of their habitat. A wide spectrum of phenotypes is observed in Icelandic populations of Halosaccion ramentaceum (L.) J.Ag. A

species with a wide vertical distribution that extends into the upper sublittoral (Munda, 1976). Field observations show that the form and size of the plants are likely to be a function of exposure and depth (Munda, 1981). On exposed slopes, sparsely branched or unbranched individuals prevailed, in places where the exposure was less strong the plants were provided with bushy side branches and in sheltered sites the plants were narrow and vigorously branched (Munda, 1981). Low intertidal and subtidal specimens were up to 40 cm long with the size decreasing upwards until dwarf forms are found in the upper intertidal. Similar variations in thallus consistency, size and form are observed in _Palmaria palmata_ (L.) Kuntze, size and branching pattern of _Ahnfeltia plicata_ (Huds.) Fries and other characters in several red algal species from the Iceland coasts (Munda, 1981).

Several studies have tested the correlation between algal thallus morphology and wave and current exposure, herbivory, light intensity and associated microflora. Furthermore, these studies demonstrated in several cases that the morphological variation is a result of the phenotypic plasticity exhibited by individuals studied by field transplants, and in cultures with

controlled manipulation of the environmental conditions.

The crustose coralline _Lithophyllum congestum_
Foslie is sensitive to microenvironmental changes in
Caribbean algal ridges. Different gross morphologies are
found in nearby areas (Steneck & Adey, 1976). Plants are
able to develop terete protuberances in turbulent areas
with moderately low light conditions, while under moderate
to highly turbulent conditions with reduced light no
protuberances are formed. Finally, in turbulent areas
with high light conditions the tips of the protuberances
broaden as a result of greater lateral than apical growth
rate; they anastomose and form distinctive spherical
heads. Changes of a particular morphology to another
occurred in individuals transplanted from one set of
conditions to the other indicating that these
morphological changes are environmentally induced.

There are many examples of correlations between
environmental factors and algal thallus morphology among
the Phaeophyta (brown algae). Sporophytes of _Saccorhiza_
polyschides (Lightft.) Batt. grow in three localities
under different current exposure and turbulence degrees
and show clear differences in external morphology as well
as in the internal anatomy of blades (Norton, 1969).
Further, plants growing in an area subjected to continuous

strong current are characterized by tough, very digitate, long blades; those plants growing in a small bay under a regime of weak current were fragile, non-digitate and broad-bladed, whereas the plants inhabiting a wave-protected locality, but subjected to continual turbulence were tough, digitate and short-bladed (Norton, 1969). Internally the main difference in the anatomy among the populations was the thickness of the blade cortex. Progeny of morphologically diverse parents became indistinguishable under similar culture conditions. Plants transferred from one habitat to another acquire the typical appearance of the individuals native to that habitat. These experiments clearly showed that the great morphological range in variation exhibited by Saccorhiza can be explained in terms of environmental modification.

Padina jamaicensis (Coll.) Papenfuss, a brown alga common in the Caribbean reefs, shows a clear dimorphism induced by the increased grazing pressure of parrotfishes (Lewis et al, 1987). Padina grows as a slender turf form, forming prostrate entangled clumps of small and irregularly branched, uncalcified, strap-shaped fronds in areas of high density of herbivores, while its frondose form occurs in habitats not subjected to herbivory where they are large, erect plants with

distinctively fan-shaped, calcified foliose blades. Exclusion of herbivores demonstrates that the turf-prostrate habit can be changed from growth by a single apical cell into the "typical" foliose form, with growth by a meristematic row of cells, in approximately 4 days. There is no apparent shift from foliose to prostrate habit, instead constant grazing of the branch apices maintains the fronds in the turf form with growth by a single apical cell. The large, frondose blades are entirely eaten when transplanted to a high herbivory habitat. If these distinct morphologies represent phenotypic responses within a single frond to different levels of grazing pressure, then the expression for one or the other morphology depends on the effects of the environment, i.e., herbivory, upon the early developmental stages of the plant, while the prostrate form retains the potentiality to change to the foliose form under favorable circumstances, i.e., reduced herbivory. The foliose form would be fixed in its phenotype. An alternate explanation would be that the prostrate form unidirectionally leads to the fan-shaped form and that grazers activity is just removing all fan-shaped plants.

There are also noticeable cases of phenotypic plasticity in marine benthic green algae. Morphological

responses to illumination in the genus <u>Caulerpa</u> Lamour.
make the boundaries delimiting species highly uncertain.
<u>Caulerpa</u> consists of a prostrate stolon which bears
branched attaching rhizoids below, and erect branches
named assimilators, above. The assimilators usually bear
numerous determinate branchlets and their shape is
extremely plastic in some species. Species of <u>Caulerpa</u>
can be categorized into a group with bilateral leaf-like
assimilators and another group with radially disposed
assimilators (Borgesen, 1907; Svedelius, 1906). Three
species and five varieties of <u>Caulerpa</u> were studied under
low light intensities (Calvert, 1976). Morphologies
developed in culture in all cases were unlike the field
forms but resemble the morphology of other described taxa.
Most responses were a change in the symmetry of the
assimilators from radial disposition to a bilateral one.
This indicates that the involved <u>Caulerpa</u> forms should not
be considered as separate species or varieties, but as one
single taxonomic entity including a variety of
morphologies.

Phenotypic plasticity may also obscure
intergeneric recognition of taxa. In absolute axenic
culture <u>Ulva</u> and <u>Enteromorpha</u> displayed atypical but
viable morphologies that were restored to their normal

frond shapes when certain bacteria were added (Provasoli, 1972; Provasoli & Pintner, 1964; 1976). Morphologies encompassing those of the two genera were observed from the progeny of a single plant of Ulva lactuca L. Because the variation of morphologies has occurred through several generations of haploid clones reproducing asexually, neither genetic mutation nor sexual recombination is needed to explain variation among progeny (Bonneau, 1977).

In other cases, phenotypic variability is the result of genetic divergence and the variation is expressed between discrete populations inhabiting localities characterized by different interactions of environmental parameters. Experiments testing whether morphological variation is a plastic response or is genetically fixed have been done for many brown algae. Culture of spores from parental plants of a particular morphology under different conditions, as well as transplants of juveniles and adults in the field are the most common approaches in these studies. The genus Laminaria in Nova Scotia consists of two species, Laminaria longicruris de la Pyl. and L. agardhii Kjell., separated on the basis of having a long hollow stipe versus a short, solid stipe respectively. The variability

of these characters shows a clinal differentiation in the
populations on a gradient of wave exposure, making it
impossible to delimit populations of L. longicruris from
L. agardhii (Chapman, 1973). Transplants of adult plants
resulted in no change of their original characteristics of
the type suggesting that the differences represent a
result of natural selection or that they are a result of
phenotypic plasticity in which changes of morphology are
channeled in the early development of the plants (Chapman,
1973).

Differences in life span, habitat preferences and
thallus shape were found among four populations of
Pylaiella littoralis (L.) Kjell. in St. Andrews, Scotland
(Russell, 1963). When specimens of these four populations
were grown in culture under different conditions of
salinity, similar to those of each population, no changes
in form occurred and the plants did not survive the new
conditions. Germlings from the different Pylaiella
populations retained the morphological characteristics of
the parental plants when grown under different conditions
from which the latter came. This suggests that these
distinct morphologies were genetically fixed. Fucus
distichus L. is also a species that exhibits morphological
variation among natural populations. For example,

discrete, morphologically distinct populations were found when comparing individuals from sheltered and open coastal areas (Sideman & Mathieson, 1985). In this species, the characteristics belonging to each population were inherited by the progeny when they were grown in experimental gardens. In addition, no changes were detected in embryos transplanted to field conditions different from the cultures (Pollock, 1969), which indicates that morphological variation is truly ecotypic differentation of _Fucus_.

Morphological variation may be attributable to many mechanisms. A combination of genetic variability in some characters selected by environmental forces and the plastic response expressed by other characters may be exhibited by some taxa. For example _Laminaria_ _digitata_ (Huds.) Lamour. has three interfertile Norwegian forms (Sundene, 1958). The normal progeny and the hybrids do not show differences when grown under the same conditions. When sporophytes 2 to 4 months old were placed in the habitat of one of these three forms, some characters typical of each form were maintained (i.e., bullations in lamina and stipe stiffness), this indicated that they are genetically determined, while others were

modified (e.g., narrow to broad lamina) as a response to
the prevailing environmental conditions (Sundene, 1962).

Another source of morphological variation which
results in intermediate overlapping forms among taxa is
hybridization. Rueness (1978) theorizes that hybrids of
red algae are not commonly reported for two reasons. One,
they may be common but dismissed as phenotypic variants or
two, they may not survive, an expectation if isolating
mechanisms are effective. Testing species boundaries
based on morphological features has been expanded to
include cross-fertilization experiments by several
researchers (Edwards, 1970; Guiry, 1984; Kapraun, 1977;
Larsen, 1971; Rueness, 1973; Rueness & Rueness, 1975;
1982).

Hybrids have been successfully formed in
controlled culture conditions (Rueness, 1973; 1978;
Rueness & Rueness, 1975; 1982) between disjunct
populations of the same species, between varieties and
between species in some red algal genera. Fully fertile
crosses resulted between Ceramium strictum Harvey from
Norway and C. tenuicorne (Kuetzing) Waern from the
Baltic. Hybridization experiments under culture
conditions between Polysiphonia haemispherica Aresch. from
Europe and P. boldii Wynne & Edwards from Gulf of Mexico

resulted in carposporophyte development and release of
viable carpospores (Rueness, 1973); nevertheless,
tetraspores derived from such interspecific crosses, have
failed to germinate. However, in field locations,
successful hybridization between morphologically
differentiated populations necessarily depends on the
potential for gene flow, which in the case of red algae is
based on the dispersal of non-motile unicells.

A small number of studies have examined spore or
propagule dispersal in macroalgae (Dayton, 1973; Guzman
del Proo et al, 1972; Paine, 1979; Sundene, 1962) and
describe fairly short dispersal distances. Further, spore
sinking rates depend on the water motion conditions
prevailing at the time of their release (Okuda & Neushul,
1981). Increasing attention is being given to vegetative
propagation and probable dispersal by fragmentation
(Dixon, 1965; Whittick, 1978). There are no studies
assessing the capability of thallus fragments to disperse,
nor on their survival rates. An evaluation of the
capability of dispersal of each species would help to
estimate the significance of potential hybrid formation
under natural conditions.

Selection of morphological characters.

While morphological variability within species of macroalgae is widely recognized, the mechanisms effecting this variability are not well studied, nor are the implications of the limits of this plasticity to the taxonomy well understood. The question is: How do taxonomists deal with this problem? What are the steps necessary to test criteria in order to characterize and distinguish species with such variable characteristics? A populational analysis is the first step necessary to fully characterize a species vegetative and reproductive morphological variation. A careful selection of a number of adequate characters is mandatory, because some of them will prove to be more stable under different conditions than others, and some may be genetically fixed and not subject to environmental influence. Studying the effect of different conditions upon the characteristics will most accurately define the taxa. First, based on field observations the morphologies are correlated with the habitat characteristics. Next, transplants to different habitats as well as manipulation of environmental parameters in culture are two useful approaches which assess the basis for variation of morphological characters

in a taxon. For certain genera (i.e., _Ceramium_)
qualitative characters with discrete states (e.g.,
presence versus absence of gland cells, alternate versus
opposite branching, prostrate versus erect thallus) appear
to be less variable than quantitative characters (e.g.,
number of pericentral cells, cell dimensions, thallus
height and width). However, quantitative characters may
be helpful in the distinction of taxa in cases where
ranges of variation can be determined.

The use of morphometric characters demonstrates
that statistical analyses can be used to compare their
variation within and between populations of brown algae.
A number of morphometric features was assessed in
populations of _Fucus_ _serratus_ L. and _Fucus_ _vesiculosus_ L.
by discriminant analysis. The results show that from an
initial set of 15 characters (i.e., thallus length,
distance between dichotomies, thallus width, width of last
dichotomies, distance from last dichotomy to apices, etc.)
only five would reliabily produce a high degree of
separation between the two species. Within each species,
despite the character variation within and between
populations, groups cannot be totally separated (Marsden
et al, 1983a). While this method serves to determine how
many of the characters could be used for each individual
taxon, the selection of these characters is often

subjective and without information of how they are affected by environmental variability.

Other studies evaluated the use of ratios of morphometric variables in distinguishing between species in cases where there was correlation between the two variables. Where variables had more than 50% correlation in _Fucus_ species, they were compounded into a ratio (Marsden et al, 1983b), assuming that one character is regarded as indicative of a valuable feature and the other standardizes its variation by providing a measure of absolute size. The comparison between species of _Fucus_ did not show species-related discontinuities in the variation pattern for any of the computed ratios.

Similarly, the correlation observed between characters may be used as a descriptor of a particular species. Attempts to find variation patterns in fronds of _Macrocystis pyrifera_ (L.) C. Ag. were made to estimate morphological relationships of their characteristics. Morphometric relationships were reported between laminar area versus nodal position of the lamina, laminar area versus laminar weight, and total number of nodes versus length of the frond among others (Jackson et al, 1985). Some of these were linear, others were polynomial, but it was possible to produce equations representing the

morphological relationships. However, these equations may not necessarily be valid for the species description of <u>Macrocystis</u> plants from localities other than the one studied, unless these morphometric characters are evaluated from samples of populations from other localities and habitats.

Often in an effort to assess whether or not species distinction is well based, especially in cases of frequent overlap of morphological characteristics as many characters as possible are analyzed. In the process, two or more characters may be correlated (sometimes one more readily observable than the others) and help in the recognition of the species. After examined several characters of <u>Colpomenia</u> <u>peregrina</u> (Sauvageau) Hamel and <u>C</u>. <u>sinuosa</u> (Roth) Derbes & Solier, it was observed that except for two, all of them were highly variable morphologically (Clayton, 1975). These two features, the presence of punctate sori and the presence of a cuticle in plurilocular sporangia, apparently occur together with no exceptions, allowing the distinction between the two Australian <u>Colpomenias</u>.

In summary, the segregation and characterization of species often cannot adequately be done based on only one or few specimens, which will not show the full

morphological variation of the species in the field. The distinctive characters of plants representative within populations, as well as between populations, must be evaluated in order to assess their possible variation range attributable to age, reproductive state or environmental (physical and/or biotic) conditions. Ideally, diagnostic characters should be stable throughout the growth, life-history and maturation to reproductive activity, all of these processes under different environmental parameters. The use of both qualitative and quantitative characters as well as possible morphometric equations, which summarize relationships among characters, by studying different populations. is necessary to access the variation presumed for species of macroalgae.

Morphological variation of the genus Ceramium.

Ceramium species are generally small, delicate plants occurring along most coasts of the world. Some of theses species are well defined, but many of them are regarded as variable or difficult to identify (Womersley, 1978). An account of specific features that have been as diagnostic was discussed by Dixon (1960a) who believed that the taxonomy of the genus is in a state of chaos as a

result of the "failure of phycologists to recognize and interpret seasonal and environmental modifications of the external form of the thallus".

In fact, in varying degrees, all the morphological features used for the discrimination of species and varieties within the genus are subject to variation. Among those characteristics are: (1) the number of pericentral cells; (2) the dimendions of the axial cells; (3) an index of cortication; (4) the development of adventitious branches; (5)the occurrence of gland cells; (6) the distance between pseudodichotomies; (7) the curvature of the apices; (8) presence or absence of spines and their characteristics; (9) the presence or absence of hairs and their characteristics; (10) the branching pattern, (11) morphological pattern of nodal development and (12) the position of the tetrasporangia. Most of these are vegetative features, because the morphology and pattern of development of female and male reproductive structures appears to be fairly uniform within the genus (Dixon, 1960a, Hommersand, 1963). A brief discussion of the utility of each of these features as specific diagnostic characters is given in the following paragraphs (for explanation of pertinent terminology see section on the genus Ceramium).

(1) The number of pericentral (or periaxial) cells formed from each segment cut off from the apical cell, varies from species to species, but is relatively constant for each species (Feldmann-Mazoyer, 1940; Womersley, 1978). However, slight variation can occur within plants, e.g. the weakly developed branches of *Ceramium poeppigianum* Grunow have 6 to 8 pericentral cells while the main axis usually has 9 to 10 cells (Hommersand, 1963). Thus, this character is useful to differentiate species only in cases in which the variation (or lack of variation) within the species is known (Dixon, 1960a).

(2) The ultimate dimensions of an axial cell are determined by its position in the thallus. Measurements of axial cell dimensions made of every axial cell in various species growing in different environments in the British Isles (Dixon, 1960a) indicate that the rate of increase of the average length of the axial cells and their maximum value per sector (defined as the portion of the thallus between successive pseudodichotomies) varies and is probably affected by environmental conditions. Furthermore, rates of axial cell enlargement of *C. rubrum* (Huds.) C. Ag. are

temperature dependent. Mean lengths of axial cell were greatest at 10°and 15°C, and declined at 20°and 25°C (Garbary et al, 1978). In spite of these variations in the overall average dimensions, a somewhat regular pattern of variation in cell size occurs within each sector. In any sector of the thallus except those immediately behind the principal apical cells, the axial cells show considerable variation in length, the smallest axial cell occurring at the basal end of the sector (immediately after the pseudodichotomy), while the largest is located at the middle of the sector (Dixon, 1960a). At the same time, the average axial cell length in each sector increases towards the basal portion of the axis. Consequently, any measurement of axial cell size must be cited by noting its location in which part of the thallus.

(3) Cortication indices have been defined differently depending on the author, although they are always a relative measurement of the degree of cortication of the thallus. Dixon (1960a) refers to it as the ratio of the length of the cortical band to the length of the adjacent non-corticated portion of the axial cell, the non-corticated portion of the axial cell actually being the difference between the length of the

axial cell and the portion covered by the cortical band.
Because of the complexity of the factors involved,
elongation rate of axial cells, elongation rate of
cortical cells and division rate of cortical cells,
significant differences in this index of cortication
might be found according to the position on the thallus
where measurements are taken. These differences can be
overcome if position on the thallus is standardized for
each plant being measured. Environmental factors can
cause severe changes in degree of cortication within
species. Garbary et al.(1978) suggested that a "crossover
point" may be used as an index of cortication. This is
the point in the thallus where axial cell length equals
cell diameter, expressed as the percentage of the total
length of the main axis where the length:diameter ratio
of axial cells is 1 or greater. However, although this
is a good indicator of the axial cell growth, it does not
seem to be related to the extent of node development.

The degree to which nodal cortication is
developed, separates the genus Ceramium into two major
groups of species: those which exhibit a continuous layer
of cortical cells throughout the entire thallus; and
those in which nodes are reduced to a few number of
cortical rows leaving part of the axial cells

(internodes) uncorticated and exposed (see section III
for taxonomic implications). The length and the
proportion of the internodal space is often variable in
species where it occurs (Womersley, 1978). Garbary et al
(1978) demonstrated under cultural conditions that the
extent of cortication depends on daylength in C. rubrum.
Ceramium rubrum is a species characterized in nature by
having continuous cortication. It develops discontinuous
nodal bands under long day photoperiod, morphologically
resembling other species, i.e., C. rubriforme Kylin, C.
pedicellatum Decaisne (=C. rubrum var. pedicellatum Duby)
and C. areschougii Kylin. Plants of C. paniculatum
Okamura in culture also showed a decrease in the height
of their cortical bands by producing a reduced number of
transverse cell rows per cortical band (Suh and Lee,
1984).

(4) Adventitious lateral branches of unlimited
growth occur frequently in all species of Ceramium
(Dixon, 1960a; Hommersand, 1963; Itono, 1977). Most
frequently formed in cystocarpic specimens, in groups
subtending the gonimolobes of the carposporophyte they
may also be found in damaged plants replacing apical axes
that have been lost. In some species they adopt the main
pattern of branching (Ceramium serpens Setchell &

Gardner, C. codii (Richards) Mazoyer, C. procumbens

Gardner, C. codii (Richards) Mazoyer, C. procumbens
Setchell & Gardner -Setchell & Gardner, 1930;
Feldmann-Mazoyer, 1940; Dawson, 1950 - among others).
Dixon (1960a) considers them of very little taxonomic
significance because of their environmentally induced
nature and their occurrence in most species.
Nevertheless, the position of the adventitious branches
which form the loose involucrum around the cystocarp
possibly has taxonomic value in some species (Hommersand,
1963).

(5) Gland cells may be rare and variable in some
species others abundant and well developed in others
(e.g., Feldmann-Mazoyer, 1940). They are ephemeral,
normally found in the younger parts of the thallus and
are recognizable by their refractant and colorless
contents. Womersley (1978) regarded them with caution as
diagnostic features because certain species include
specimens with and without them. They are probably
correlated with environmental conditions abundant in
field specimens of C. aduncum Nakamura, but decreased in
number in plants grown under laboratory culture
conditions (Suh and Lee, 1984).

(6) Certain members of the Ceramiaceae
(Chadefaud, 1954) exhibit with some regularity the

formation of branches of non-determinate growth by
unequal oblique divisions of the apical cell, a feature
which shows considerable variation in Ceramium (Dixon,
1960a). Thus, the distance between consecutive branches
or the distance between the origin of the
pseudodichotomies are not reliable characters. In
addition, the distinction has to be made between lateral
branches of non-determinate growth of adventitious origin
and those arising from the apical pseudodichotomy.
Unfortunately this distinction is almost impossible to
make in old specimens.

(7) In some species of Ceramium the apical
portion of the axes is incurved, while in others the axes
are straight throughout. Although the degree of
curvature of the apical parts of the axes is considered
by Dixon (1960a) as a stable taxonomic feature, later
culture studies have shown that, at least in one species,
C. aduncum, the degree of curvature is fairly variable
(Suh and Lee, 1984). Both forcipate and straight apices
are seen within the same plant, but an evaluation of the
proportion of each form of apices within a population may
give information of the prevailing tendency and this may
be used as an additional character.

(8) Some of the most easily recognized species of _Ceramium_ are those which form spines or comparable outgrowths from the cortical cells (Womersley, 1978). In the European species (Feldmann-Mazoyer, 1940), the patterns of development of the different types of spines and their morphology are constant and a useful and reliable taxonomic criterion (Dixon, 1960a; 1960b). The frequency of formation is, however, subject to variation in _C.paniculatum_, where the subulate spines disappear when the plants are grown in culture under illumination of 800 to 1,500 lux, 16^a-18^a C and a photoperiod of 16:8 LD hours (Suh and Lee, 1984).

(9) Hairs may be occasionally present in some of the _Ceramium_ species, but their position can be variable and their presence appears to be subject to environmental conditions. In _C. rubrum_ (Huds.) C. Ag. the abundance and length of unicellular and hyaline hairs is correlated with external nitrogen concentration (DeBoer & Whoriskey, 1983) and consequently they are not a diagnostic character for this species. In other species, the presence and appearance of hairs is responsible for the distinctiveness of the species (e.g. _C. fimbriatum_ Setchell & Gardner) although studies on the variation of

the character under different conditions are necessary to assay their constancy.

(10) The branching pattern of _Ceramium_ is uniformly dichotomous (technically, pseudodichotomous), although formation of adventitious branches of unlimited growth may obscure the original pattern in old or damaged specimens. Most species consist of upright axes that branch pseudodichotomously and become attached to the substrate by rhizoids that originate on the basal portions of the main axis. A few other species, however consist of a prostrate main axis from which adventitious erect branches arise unilaterally forming the upright portions of the plant in which branching may or may not be in this typical pattern (e.g. _C. codii_ (Richards) Mazoyer, _C.procumbens_ Setchell & Gardner, _C.serpens_ Setchell & Gardner). Because of the clear distinction between these two groups, the branching pattern in _Ceramium_ does not appear valuable as a specific diagnostic feature but only to discriminate between these two major groups. Interestingly, consistent differences in the branching pattern between gametophytes and sporophytes of _C. rubrum_ (Huds.) C. Ag. were reported (Garbary _et al._, 1980), this indicates the possible

limitations to the value of this as a taxonomic character for that species.

(11) The use of nodal development was introduced earlier with a discussion of the use of cortication indices. The appearance of a cortical band, which has been considered the principal diagnostic feature in the genus (Dawson, 1950; Dixon, 1960a; Womersley, 1978) is under culture conditions variable and dependent upon those factors that affect the division and elongation rates of axial and cortical cells as well as the division rate of cortical cells (Garbary et al,1978; Suh and Lee, 1984). Nevertheless, despite the culture studies which sometimes may represent conditions of stress, field collections do not show such extreme variations in nodal structure. The sequence of events by which the nodes are formed, i.e., the way in which cortical cells are cut off from the pericentral cells and the successive divisions that the cortical cells undergo to build the node, is characteristic of each species (Womersley, 1978).

(12) Tetrasporangia offer useful taxonomic characters in many species (e.g., Dawson, 1944; 1950; 1953; 1954a; 1962; Nakamura, 1965; Setchell & Gardner, 1930; Womersley, 1978). The degree of involucral protection by the cortical filaments varies from very

slight to almost a complete cover. The sporangial
position (in unilateral abaxial rows, in adventitious
branches, opposite in the plane of branching,
verticillate, etc.) appears to be a stable character in
some species. In others, the position may vary depending
upon the age of the plant or the degree of development of
the reproductive structures and culture conditions
(Rueness, 1973a). The tetrasporangial origin can also be
used as a diagnostic character, because in most species,
they are borne from the pericentral cells, except in C.
aduncum Nakamura where they originate from cortical
cells (Nakamura, 1965).

As with other taxa in the Ceramiaceae, it is
evident that no single character alone will serve to
discriminate all the species. The use of combined
characters, however, should accomplish the task of
separating specific taxa. It is possible that the
variation of some of the characters will correlate with
one or more environmental parameters and thus, the
variation of the character can be utilized at a
subspecific level (e.g., varieties) representing locally
adapted populations.

The genus Ceramium

Anatomy of the family Ceramiaceae.

Members of the family Ceramiaceae (Ceramiales, Rhodophyta), are basically filamentous and uniaxial, where the primary axis consists of one column of cells from which all other axes or branches are derived. Among genera, the ontogeny and organization of the filaments can be traced from the simplest monosiphonous thallus with a verticillate pattern of branching i.e. the Crouaniae (Wollaston, 1968) to the most complex corticated thallus with the production of modified laterals as in Spyridia.

The female reproductive system is fairly uniform within the whole family and the entire order, with a 4-celled carpogonial branch borne on a supporting cell (the fertile pericentral cell) which cuts off an auxiliary cell after fertilization of the carpogonial nucleus. The position of the supporting cell varies from one tribe to another. In addition to the carpogonial branch, the supporting cell cuts off a single sterile group which consists either of a single cell or a short

branch. The distinctive characteristic of the family is a gonimoblast which is either naked or loosely surrounded with involucral branches that do not form a compact enclosure. Spermatangia are produced in clusters consisting of the male reproductive system. The shape of the clusters is also fairly uniform in species, genera and tribes. The formation of monosporangia, bisporangia, tetrasporangia, polysporangia and parasporangia, or a combination of these depending on the group has also been reported (e.g. Wollaston, 1968).

The backbone of the vegetative structure in Ceramiaceae is a single apical cell that controls a primary axis capable of continued production of axial cells in an axis of indeterminate growth. A term used as equivalent of axis of indeterminate growth is "cladome" (L'Hardy-Halos, 1966). Elongation of the primary axis, as well as all other branches of the thallus, is achieved by apical cells which divide to form cells basipetally. In the most basic thallus organization of the Ceramiaceae, each cell of the indeterminate axes bears one to four (or more) lateral determinate branches arranged in a whorl. Several different terms are used referring to determinate lateral branches arranged in a verticillate pattern: "pleuridia" was used by Chadefaud

(1954) and accepted by Hommersand (1963), although the term has been discussed by later authors (Wollaston, 1968). Whorl-branchlets is the term used by Wollaston (1968) and Gordon (1972), lateral branches of limited growth or determinate branches, whorl-branches or pleuridia are all terms utilized by Hommersand (1963) as well as by Itono (1977). The order of formation and the number of lateral determinate branches are of taxonomic value because the sequence of occurrence of pericentral cells which form the basal cells of these branches is genetically fixed. The axial cells cut off the pericentral cells in two different manners: one is in opposite pairs (Carpoblepharis, Herpochondria, Reinboldiella), i.e., the second cell formed lies opposite the first, then the third cell is cut off on either at the left or the right of the first, and the fourth is cut off opposite the third and so on. The other way of basal cell formation is by alternate sequence (Microcladia, Ceramium, Campylaephora, Centroceras), where the second cell is formed at one side of the first and then the third is formed at the other side, etc. so that the last cell formed is opposite the first. This second pattern is referred to as "rhodomelacean sequence" (Hommersand, 1963), because of

its similarity with the pericentral cell formation in the family Rhodomelaceae also in the Ceramiales.

The determinate branches can be produced in two manners according to their position. In a clockwise manner with a divergence of 1/8 or 3/8 in successive axial cells in which case alternate axial cells have superimposed branches (Fig. 1.8). Or, they can be arranged with a divergence of 1/4 to 1/2 in successive axial cells thus, successive axial cells have superimposed branches (orthostichous branches) (Fig. 1.9). Thus, the position in which the determinate branches or pleuridia are formed in consecutive axial cells affects the symmetry of the entire thallus. Five possible modifications by the determinate branches in different genera are known: (1) changes in symmetry of their arrangement, (originating a bilaterally branched thallus as in Platythamnion, in which the lateral filaments of the whorl are developed more extensively than the transverse ones), (2) elimination of the basic number in the whorl (as in Antithamnionella sarniensis Lyle where each whorl consists of 3 determinate branches), (3) increase of the same number (Carpoblepharis, Reinboldiella), (4) condensation of determinate branches derived during the formation of a

cortex (_Ceramium_, _Centroceras_), and (5) abortion of the cells in the branch except for the basal one (_Spyridia_).

The origin of indeterminate branches varies with the tribe (see Table I of Itono, 1977:176) but can be one of five possible alternatives: (1) replacing a determinate branch in its same position, (2) borne on the basal cell of a determinate branch, (3) produced by the apical cell of an indeterminate axis, (4) cut off from the axial segment of an indeterminate axis, following a regular arrangement or (5) adventitious, irregularly produced.

Although most members of the family are uniseriate simple filaments, some species show axial cortication. Cortex formation from condensation of original determinate laterals (Hommersand, 1963) and are thought to originate from i) the periaxial cells, ii) cells of branchlets on the determinate branches, or iii) proximal ends of axial cells of indeterminate axes (Gordon, 1972).

The general characteristics of the reproductive structures in the Ceramiaceae are fairly uniform throughout the family, but they show a certain degree of variation in structural details which is often helpful in

the taxonomy of the tribes, genera and even species.
Monosporangia, bisporangia, tetrasporangia and
polysporangia are generally produced on determinate
lateral branches (pleuridia) and not on the axial cells
of indeterminate axes. An exception is Spyridia for
which sporangia are borne on axial cells of branches of
limited growth (brachyblasts) which are initiated by the
longitudinal division through the entire length of a
secondary segment. Each brachyblast consists of a file
of axial cells, each of these cells produces a band of
condensed determinate branches. Most of the species
produce naked sporangia which lack a cortical layer.
However, in Ceramieae, Wrangelieae and Griffithsieae,
cortical and involucral processes are formed. These
consist of short, non-branched filaments borne on the
same cell from which the sporangia are produced, or the
sporangium develops after the cortex has been formed and
remains embedded within it in those genera (e.g.
Carpoblepharis) with axial cortication.

Spermatangia are often produced in clusters
which can be formed i) on modified determinate branches,
ii) on the surface of cortical cells or iii) on
subterminal or terminal segments of determinate
branches. Spermatangial clusters mostly lack any

covering branchlets except for some species of Wrangelia and Griffithsia, where they are provided with involucra. Spermatangia have gelatinous outer walls, and are covered individually, or in groups.

For most genera the the concept of a procarp, defined by Schmitz (1883) as the structural unit containing both the carpogonial branch and auxiliary cell or auxiliary mother cell, also includes the supporting cell and one group of sterile cells. In certain genera (Spyridia, Sphondylothamnion) one or two additional auxiliary cells may be formed. The supporting cell is one of the pericentral cells from a fertile branch. The position of the fertile branch varies from one group to another, but the supporting cell is always borne on the penultimate axial cell of this branch. The fertile branch can be determinate or indeterminate and the three ultimate cells receive specific names to distinguish them from cells in the same position in a vegetative branch. The ultimate distal cell is the apical cell (Baldock & Womersley, 1968; Gordon & Womersley, 1966), the penultimate cell of the branch is either called the subapical cell (Baldock & Womersley, 1968) or the central cell (Gordon & Womersley, 1966) and the proximal cell has been called the hypogenous cell (Baldock & Womersley,

1968), basal cell (Gordon & Womersley, 1966) or subhypogenous cell (Gordon, 1972) because it is not a "true basal cell", a term that refers specifically to the most proximal cell of the carpogonial branch. Unfortunately, the use of the terms hypogenous and subhypogenous adds confusion, because the spelling is too similar to the term hypogynous, which refers to the cell located immediately underneath the carpogonium in the carpogonial branch.

The supporting cell first cuts off an initial of the sterile group, consisting either of a single cell or a short branch, or it can be completely absent (e.g. tribes Crouanieae, Spyridieae, and some members of Wrangelieae and Callithamnieae). A single sterile group, when present, is characteristic of the whole family. The sterile group is homologous to a vegetative branch produced on a pericentral cell, which is reduced to a single cell or a few cells. The carpogonial branch initial is cut off laterally at right angles from the sterile group initial.

Following fertilization of the carpogonial nucleus the supporting cell enlarges and cuts off an auxiliary cell. The practical difficulties in this interpretation of this process have drawn attention to

other possible mechanisms by which the initial
post-fertilization events occur. Although one of the
diagnostic features of the entire order is the formation
of an auxiliary cell after fertilization, observations on
some species indicate that the supporting cell may play
the role of auxiliary cell (Lewis, 1909; Dixon, 1964;
Brauner, 1979;). The auxiliary cell may act as a
gonimoblast initial in some groups (Compsothamnieae,
Sphondylothamnieae) or divide into a foot cell and a
gonimoblast initial in others (Ceramieae, Antithamnieae,
Callithamnieae). A fusion cell involving the foot cell
and the supporting cell is formed in some members
(Seirospora occidentalis Boergesen) of the tribe
Callithamnieae (Itono, 1977), while the same fusion cell
includes the foot cell, the supporting cell, the fertile
axial cell and in some cases the gonimoblast initial in
members of Antithamnieae and Ceramieae (Hommersand,
1968). In the recently established tribe Radiathamnieae
(Gordon & Kraft, 1981), the fusion of the auxiliary cell
and the fertile axial cell fails to include the
supporting cell. The gonimoblast initial can branch
repeatedly in dichotomous or ternate manner forming
several gonimolobes which are transformed completely into
carposporangia (except for the basal cell) in certain

genera (e.g. *Spyridia*, *Carpoblepharis*, *Microcladia*, *Ceramium*), or only about half of the gonimolobe cells mature into carposporangia in other genera (*Wrangelia*, *Lejolisia*, *Tiffaniella*, *Spermothamnion*).

In fully developed carposporophytes, some species produce special filaments around the cystocarp, which appear as a loose involucrum. The involucral filaments are highly variable in their origin, as they may be formed: i) on the hypogenous cell in the tribe Compsothamnieae, or ii) on the segment below the fertile one in the Ceramieae, or iii) may involve the sterile cell on the fertile periaxial cell, the sterile periaxial cells and the apical cell of the fertile axis in their formation in Sphondylothamnieae (Gordon, 1972; Itono, 1977).

Classification within the family Ceramiaceae.

In 1851, J. Agardh divided the Ceramiaceae into two tribes: Callithamnieae and Ceramieae. The former included the genus *Callithamnion* and an heterogenous assemblage of other genera which are now recognized as belonging to other tribes, plus some which are now in orders other than Ceramiales (Feldmann-Mazoyer, 1940).

Years later, after the establishment of several new genera, Schmitz (1889) subdivided the Ceramiaceae into 15 sub-familial groups giving them the ending "-eae" which denotes the rank of tribe (Hommersand, 1963). The classification of these 15 tribes is based on the thallus morphology and the location and structure of the gonimoblast. They were recognized by Feldmann-Mazoyer (1940) who modified them giving primary importance to the procarp structure and keeping the previous diagnostic characteristics as secondary. The main changes of Feldmann-Mazoyer were to split Schmitz's tribe Spermothamnieae into Spermothamnieae, Lejolisieae and Sphondylothamnieae. Kylin (1956) referred to the tribes as "groups" and recognized 11 such groups, including a number of genera of uncertain position, and united the three tribes of Feldmann-Mazoyer (1940) as the Spermothamnion-group. Gordon (1972) included the Lejolisieae in the Spermothamnieae due to the lack of sufficient differences between its members. Kylin (1956) did not recognize any of the three tribes of Feldmann-Mazoyer and reunited them under his Spermothamnion-group.

Kylin (1930) earlier divided the Ceramiaceae into two developmental lines depending on whether the

procarps are borne on an indeterminate or a determinate
axis. Hommersand (1963) considered the position of the
procarp as a highly variable character and divided the
Ceramiaceae into two subfamilies, describing the
Crouanioideae and Ceramioideae. The Crouanioideae
included thalli in which the successive whorls of
pleuridia are not superimposed (not orthostichous), the
procarps lack sterile groups, the carpogonial branch is
recurved, the initial of the carpogonial branch enlarges
between divisions, and the connecting cell nucleus is
evident after the former has fused with the auxiliary
cell. The subfamily Ceramioideae has characters in
contrast to those of the Crouanioideae, especially in
having sterile groups and straight carpogonial branches.
Hommersand (1963) recognized 12 tribes, basically on the
grounds of their vegetative organization and established
a new one, Antithamnieae and amended the previous
circumscription of the Crouanieae by Kylin (1956).

Wollaston (1968) observed that the rotation of
the whorls of pleuridia varied in different genera such
as Heterothamnion, and that some species of
Antithamnionella as interpreted by Hommersand (1963)
belong to a different subfamily according to his
definitions. She also observed that within the

Antithamnieae sterile groups can range from being single-celled to having a large number of cells, thus indicating that this character related the two subfamilies. In addition, Australian species of the tribe Antithamnieae, of the subfamily Ceramioideae, have a fully formed carpogonial branch that curves upwardly around the supporting cell and does not lie in a straight line, the characteristic of the subfamily (Hommersand, 1963). Finally, in all southern Australian species studied, the connecting cell, if recognizable at all, does not remain distinct for long, a permanent nucleated cell has not been observed. The tribe Heterothamnieae was added by Wollaston (1968) to include those genera in which the carpogonial branches are borne on basal cells of the pleuridia, as opposed to those where a carpogonial branch replaces a pleuridium, and in which the pleuridium sharing the supporting cell with the carpogonial branch, is reduced to 2 to 4 cells.

The tribe Delesseriopsieae was later established by Itono and Tanaka (1973) to include the genera Delesseriopsis Okamura and Balliella Itono & Tanaka whic are characterized by carpogonial branches borne on basal (not apical) cells of lateral branches (or pleuridia) at the upper to middle portions of the thallus. In addition

to this distribution of the carpogonial branch, the
Delesseriopsieae differs (Itono & Tanaka, 1973) from the
Antithamnieae in the absence of a fusion cell, a peculiar
form and position of gland cells, and the presence of
rhizoidal cortications of indeterminate axes in the lower
portions of the thallus. Members of the Delesseriopsieae
are similar to the tribe Heterothamnieae (Wollaston,
1968) in this last characteristic, but differ from it in
having only 2 pleuridia per segment, a sterile group that
is a well developed vegetative branch, absence of
prostrate indeterminate axes, and presence of cruciate
tetrasporangia (Itono, 1977). At the same time Itono
(1977), studying the southern Japanese species of
Ceramiaceae, disagreed with the classification of
Hommersand (1963) and subdivided the family into three
new subfamilies: Antithamnieae, Callithamnioideae and
Compsothamnioideae, based on the position of the procarp
and ontogeny of the cystocarp.

Recently, the tribe Radiathamnieae was added to
the family (Gordon & Kraft, 1981) based on
characteristics of their new genus and species
Radiathamnion speleotis Gordon & Kraft described from
southern Australia. The distinctiveness of the tribe is
based on its peculiar vegetative growth pattern as well

as the probable function of the supporting cell as
auxiliary cell.   In addition, the formation of a fusion
cell in this tribe is derived from the union of the first
post-fertilization cell cut off from the supporting cell
with the fertile axial cell on which the supporting cell
is borne, not including the latter.

Currently the Ceramiaceae include 17 tribes
defined on the basis of a combination of vegetative and
reproductive characters which may be subjected to
revision as new genera and species are described from
different regions of the world. Additional information
of members of sub-familial taxa contributes to further
evaluation of the diagnostic characters of the tribal and
sub-familial groups.

Description of the genus Ceramium.

The genus Ceramium Roth, 1797 (nom. cons.)
together with Campylaephora J. Agardh., Carpoblepharis
Kuetzing, Centroceras Kuetzing, Corallophila Weber
van-Bosse, Herpochondria Falkenberg, Microcladia
Greville, Reinboldiella De Toni, and Syringocolax
Reinsch belongs to the tribe Ceramieae. The tribe is
characterized (Hommersand, 1963) by the condensation of

the pleuridia to form a pseudoparenchymatous cortex,
which in some genera extended throughout the axis, and in
others reduced to the nodes forming conspicuous nodal
bands. The sequence of initiation of the pericentral
cells in a segment can be either in opposite pairs as in
Reinboldiella schmitziana (Reinbold) De Toni,
Herpochondria dentata (Okamura) Itono), or alternate
(=rhodomelacean sequence sensu e.g. Hommersand, 1963),
Campylaephora crassa (Okamura) Nakamura, and Centroceras
clavulatum (C. Ag.) Montagne). The ordinary production
of indeterminate branches is also unique within the
tribe, as they neither replace pleuridia nor are borne on
pericentral cells. Instead, the apical cell divides
obliquely, giving rise to a new apical initial and
subterminal cell which undergoes a second oblique
division perpendicular to the first in which the daughter
cell becomes the initial of a lateral branch. Hommersand
(1963) regarded this mechanism as "holoblastic
branching". Adventitious branches in genera with
holoblastic branching (i.e. Campylaephora, Ceramium,
Centroceras), are frequently produced from pericentral
cells. Furthermore, in most species of Ceramiaceae, the
asexual sporangia are corticated partially or entirely by
cortical filaments. Some members produce stichidia or

branchlets bearing-tetrasporangia. Spermatangia are produced on cortical cells (except in _Centroceras_) and the position of the procarps depends on the genera or species.

Ceramium is comprised of those species with a filamentous thallus, erect or prostrate, 0.1 to 30.0 cm in length, 0.1 to 1.5 mm in diameter, pseudodichotomously branched, and diferentiated into axial cells and cortex. The axial cells cut off in an alternate sequence a number of cells that have a different shape and that never attain the same height than the axial ones. These are referred to as periaxial cells (Womersley & Cartledge, 1975; Womersley, 1978) and differ from the pericentral cells which are cut off from the axial cells in the same form but eventually attain the same height and shape of the axial cells. Each periaxial cell gives rise to four apical cells, two of which are directed acropetally and two basipetally. These apical cells form the segments of the lateral determinate branches (pleuridia) which are condensed branch systems. The relative growth of either descending or ascending filaments as a result of transverse divisions of apical cells varies, depending on the species and on environmental conditions. The growth of these branches results in a clearly delimited cortical

band that envelops the lower part of the axial cell above, in addition to the upper part of the parent axial cell. When adjacent cortical bands remain distinct, the portion covered by the cortical cells is called a node, while the bare portions are the internodes. The genus shows holoblastic branching formation, i.e., the initial of an indeterminate branch is formed by the oblique unequal division of the apical cell (Fig. 1.10). In certain species one of the branches overtops the other, and the dichotomous appearance is lost resulting in an alternate, subsecund or pinnate branching pattern.

The thallus is attached to the substrate by unicellular and multicellular rhizoids, that originate from cortical cells. In some species these are formed only at the base of the plant, in others, adventitious rhizoids develop from all parts of the plant. Occasionally, the apex of a rhizoid gives rise to a multicellular attachment structure.

Spine-like structures occur in a number of species of Ceramium. They may be formed primarily by the modification of one or two acropetal primordia of lateral branches of limited growth. Spines originate from the apical cell of determinate branches, or secondarily, from cortical cells of such determinate branches.

Tetrasporangia can be cut off from periaxial cells in some species, or in others from cortical cells of different orders of branching. In the latter, the tetrasporangia become scattered, extending to the internodes. In some species the periaxial cells also cut off the initials of 2 or 3 corticating filaments from their distal ends, surrounding the tetrasporangium while this develops.

Most species are dioecious, however Rosenvinge (1924) reported the occurrence of spermatangia on female plants of C. fruticulosum (Kuetzing) J. Ag. Plants with mixed phases, i.e. tetrasporangial and carpogonia or spermatangia in the same plant have also been observed (Davis, 1905; 1910).

The cortical cells cut off spermatangium-mother cells from which spermatangia develop as protuberances on the external surface of the spermatangium-mother cell. Each spermatangium-mother cell may form one to three spermatangia (Nakamura, 1954).

In all investigated species of Ceramium, a periaxial cell functions as the supporting cell of the carpogonial branch (Dixon, 1960a). The supporting cell, apparently is always derived from the first-formed periaxial cell of a segment. The carpogonial branch is

four-celled. The conversion of the first-formed periaxial cell into the supporting cell and the formation of one or more carpogonial branches disrupts the regular pattern of development of the cortical band, thus the position of a carpogonial branch can be detected relatively easily. After fertilization, either the auxiliary cell is cut off from the supporting cell as in Ceramium poeppigianum Grunow (Hommersand, 1963), or the carpogonium fuses directly with the enlarged supporting cell before an auxiliary cell is cut off as in Ceramium paniculatum Okamura (Nakamura, 1954). In Ceramium rubrum (Hudson) C. Ag. the auxiliary cell itself acts as the gonimoblast initial and produces one to several gonimolobes (Kylin, 1923) while in other species the auxiliary cell divides approximately in half to form an inner cell, the foot cell, and an outer cell, the gonimoblast initial (Hommersand, 1963). Each gonimolobe is attached to the primary gonimoblast cell by a short stalk. The filaments of the gonimolobes are dichotomously or ternately branched. Almost all cells, excepting the primary gonimolobe cells are transformed into carposporangia at maturity.

While the gonimoblast is developing, branchlets formed from outgrowths of cortical cells in the segment

next to the fertile segment continue to grow actively and
develop nto the involucral ramuli of the cystocarp
(Nakamura, 1954). When fully mature, the carposporophyte
is encircled by these axes which form a loose, incomplete
involucrum. One of these branches is the primary
indeterminate axis.

There are two types of accessory reproductive
organs in species of Ceramium, they differ in structure,
position and development (Dixon, 1960a). Lateral
sporangia containing from five to twelve spores and which
bear a close resemblance to tetrasporangia have been
detected in a number of species such as Ceramium
deslongchampsii Chauvin and C. vertebrale Petersen
(Rosenvinge, 1924). The one difference between lateral
sporangia and tetrasporangia is that tetrasporangia are
embedded in the cortical band, while lateral sporangia
are formed superficially. No information is available on
the significance of these structures in relation to the
life-histories of the species in which they occur.
The second type of structure consists of an irregularly
shaped mass of spores and is formed only in an apical
position. Feldmann-Mazoyer (1940) reported the
occurrence of these structures in Ceramium diaphanum
(Roth) Harvey. Nothing is known of their cytology or the

implications of their occurrence in the life-history of the plant.

Classification of the genus <u>Ceramium</u>.

Diverse species of algae were attributed to <u>Ceramium</u> by early phycologists (for a review see Dixon, 1960a). Among these, <u>C</u>. <u>virgatum</u> Roth is a member of the genus as now defined (Roth, 1797 cited by Dixon, 1960a). Silva (1952) in a thorough investigation of the nomenclature of the genus favored the conservation of <u>Ceramium</u> Roth, and his proposal was accepted. No type species of the genus was designated by Roth, and Silva (1952) proposed <u>C</u>. <u>virgatum</u> as the lectotype. Roth's herbarium was deposited in the Botanisches Museum of Berlin which was destroyed during World War II. Following the International Code of Botanical Nomenclature the figure of <u>Ceramium virgatum</u> given by Roth (1797) was designated as the type (Dixon, 1960a). Thus the lectotype species of the genus <u>Ceramium</u> is: <u>Ceramium virgatum</u> Roth (1797, p. 148, pl. 8 fig. 1) = <u>Ceramium rubrum</u> (Huds.) C. Agardh (1811, p. 17).

Kuetzing (1841, 1847, 1849) suggested a division of <u>Ceramium</u> into 9 genera namely: <u>Hormoceras</u>,

Gongroceras, Echinoceras, Acanthoceras, Chaetoceras, Trichoceras, Celeceras, Pteroceras and Centroceras, based largely upon the gross structure of the cortex, the location of the tetrasporangia and the presence or absence of hairs and spines. Of these, only Centroceras is still considered distinctive, the rest being considered synonyms of Ceramium. The major difference listed by Mazoyer (1938) between Ceramium and Centroceras was the regular disposition of the cortical cells in longitudinal series and the large number of periaxial cells in Centroceras. Later, the spermatangial structures of Centroceras clavulatum (C. Ag.) Montagne were studied by Hommersand (1963) and Alveal and Joly (1968) who observed the spermatangia in Centroceras are not produced by ordinary cortical filaments, as in Ceramium, but by special filaments originating from upper ends of periaxial cells, thus furnished a sharp distinction between the two genera.

The genus Campylaephora J. Ag. was established by J. Agardh (1851) and distinguished from Ceramium by a thicker cortex and sickle-shaped terminal portions of the branches. Later, Schmitz and Hauptfleish (1897) distinguished Campylaephora from Ceramium by the occurrence of rhizoidal cells in the cortex. Okamura

(1927) united both genera under the assumption that these rhizoidal cells were elongated filamentous cortical cells. The two genera were again separated by Nakamura (1950, 1954) based on evidence that rhizoidal cells in Campylaephora are truly secondarily formed from cortical cells and that the genus has a distinct conical disc composed of rhizoidal cells at its base as well as sickle-shaped portions in the frond.

In addition to Centroceras and Campylaephora, Boergesen (1953) proposed Ceramiella based upon Ceramium huysmansii Weber van-Bosse. According to Boergesen, Ceramiella is distinguished from Ceramium by the formation of endogenous branches cut off from central cells and not by unequal divisions of the apical cell. Later, Joly and Ugadim (1963) and Díaz-Piferrer (1968) added the presence of tetrasporangia-bearing stichidia to the characteristics of Ceramiella. However, the genus was not accepted by Hommersand (1963) who interprets the endogenous branches as adventitious branches, formed from periaxial cells, based on observations of material collected in Nha Trang, Vietnam (Dawson, 1954b). The formation of tetrasporangia in stichidia-like structures is a characteristic observed in several Australian species of Ceramium (Womersley, 1978) and consequently

none of the characteristics attributed to Ceramiella justifies the retention of this genus, according to Ballantine and Wynne (1986).

Finally, the genus Ceramothamnion, proposed by Richards (1901) for his new species Ceramium codii Richards is not different from Ceramium in any essential feature (Dixon, 1960a). The diagnostic characters of Ceramothamnion, the emergent tetrasporangia, extreme reduction in nodal cells and a prostrate thallus were evaluated as not being sufficient for maintenance of a separate genus by Mazoyer (1938).

Despite the careful anatomical and developmental studies on Ceramium, the inclusion of new species reported from different geographical areas leads to a continuous reformulation of the limits of its definition. According to Kylin (1956) there are approximately 60 species of Ceramium. As a result of the scarcity of studies on the effects of the physical and biotic environment on taxonomic characteristics used in the genus, these numbers may not have real significance (Dixon, 1960a). Second, few studies have been based on comparative examination of type specimens, thus contributing to taxonomic and nomenclatural confusion. This has resulted in misapplication of names, incorrect

or dubious synonyms, and descriptions of new taxa that may not be 'new' but rather within morphological variability of poorly known taxa.

Conclusions

Taxonomy of a vast majority, if not all, red algal species is based on vegetative and reproductive morphological features, and is complicated by morphological variability. Detailes studies must address the variability of these characters in order to resolve their taxonomy. Morphological variability in red algae is not an exceptional fact, but a common characteristic, thus taxonomists are faced with the necessity of exploring the range of variability in order to clearly delimit a taxon. There are several approaches to the problem and all are expected to provide a functional definition for taxa. If a specimen or specimens show deviation from the diagnostic characters as described for the type specimen should be considered as the same species or not? Characters at the species level can be assessed by large sampling within and between populations. Sampling within populations show differences among individuals as a result of their

phenotypic expression. Variations among individuals of different reproductive stages can be defined by sampling the population, as well as the probable variation among individuals of different developmental stages and ages. This last point assumes that all reproductive and developmental stages are expressed synchronously, otherwise it may require extended collecting throughout the year (or that period that covers the entire life history of the plant) to obtain all the possible stages. The collection of specimens from different localities (assuming that they are sufficiently far apart to be considered as belonging to different populations) should show variable responses to those environmental conditions characteristic of the locality, either through phenotypic plasticity or natural selection.

A second approach to observe phenotypic variability in algal species is their culture under controlled conditions, either from spores or from fragments of adult plants. The morphologies that may be obtained by this method do not necessarily correspond to those present in the field, because of endless numbers of factors and interactions among those factors. Results of culture studies under controlled conditions show the

potential morphological variability under a defined set
of controlled physical conditions. Nevertheless, culture
studies may contribute to the identification of field
material that originally showed a deviation from
described morphology. Furthermore, artificial culture
techniques permit correlation with factors and changes in
thallus morphology.

Sometimes, the range of variability within a
species, based on the characters which were initially
chosen to distinguish taxa are too variable to alone be
of diagnostic value. New and more reliable characters
should be selected only after obtaining a thorough
information of their variation in nature as well as
testing the variability of the formerly used features
under culture conditions.

Ceramium is no exception to the morphological
variability widely expressed among red algae. In fact,
it has been pointed out by several authors (Dixon, 1960a;
Garbary et al, 1978; Womersley, 1978; Suh et al, 1984) as
being a highly plastic genus. The genus is cosmopolitan
and it has been monographed or treated in floristic
accounts from several regions of the world: the
Mediterranean (Feldmann-Mazoyer, 1940), the Caribbean
(Taylor, 1960), the British Isles (Dixon, 1960a), the

southern coasts of Japan (Itono, 1977), the Gulf of
California (Dawson, 1944, 1962) and Australia (Womersley,
1978). Very little information is available on _Ceramium_
from the Hawaiian Archipelago. Seven species were
reported in dredged samples between 25 and 55m, five of
them for the first time in the Hawaiian Islands (Doty _et_
_al_, 1974). A revision of specimens collected around 1866
shed light upon the presence of many undetermined (or
unknown) species or varieties of _Ceramium_ (Abbott,
1980). Though some of these were mentioned previously
(MacCaughey, 1918), they were accompanied by a poor
description of the vegetative thallus. Two undetermined
taxa were reported as _Ceramium_ by Abbott (1947), one of
them, Ceramium #2 with a detailed description of its
nodal structure. Only two identified specimens, _Ceramium_
paniculatum Okamura and _C_. _amatispinum_ Dawson, have been
reported for the island of Oahu (Hollenberg, 1968). It
is expected that collections of _Ceramium_ from the island
of Oahu will contribute to the overall knowledge of the
genus, especially regarding the taxonomy, morphology and
distribution of subtropical species.

Research Proposal

Hypotheses.

This study proposes to identify and describe the species of _Ceramium_ (Ceramiales, Rhodophyta) from the island of Oahu and to evaluate the morphological variation of specific diagnostic characters shown by some of these species.

The following hypotheses will be tested:

H1. The species of _Ceramium_ present in the Hawaiian islands are of common occurrence in other subtropical locations.

H2. Different species of _Ceramium_ have different degrees of variability of the morphological attributes used as diagnostic characters.

H3. The knowledge of the morphological variability of these species will result in a reevaluation of the taxonomic limits in several species.

H4. The degree of variability of morphological characters can be correlated with the degree of environmental variability.

Methods.

1. Study sites:

Preliminary collections made in several
localities around the island of Oahu, resulted in the
selection of three different habitats: 1) reef flat areas
constantly immersed, 2) flat coral reef benches subject
to tidal fluctuations and 3) rocky intertidal zones.
Morphological data on species present and their
distribution in the places sampled will be gathered from
examination of these collected specimens. The selection
of study sites will be made based up on presence and
abundance of the species, accessibility to these sites,
and logistic difficulties in collecting the material.

The study sites can be divided into three
categories:(1) Those which are easily accessible and show
frequent occurrence of at least one Ceramium species.
These sites will be visited at least once a month in
order to obtain material for cultures and specimens for
taxonomic study, or to make a more extensive study of the
species distribution in the area, (2) sites which will be
occasionally visited in order to collect a representative
sample of the population with the purpose of analyzing

morphological variability, and (3) localities which will
be visited only once during the course of the research to
record species present for distributional studies.

A general characterization at each visit of the
habitat will be provided for each of the sampling
localities including substrate characteristics, salinity
and temperature of the seawater and the light intensity
range under which the plants are growing.

2. Sample handling for observations:

Collections of specimens will be made in the
field by taking clumps of algal material since Hawaiian
Ceramium species are too small to reliably identify
individuals in the field. The algae will be transported
to the laboratory in plastic bags filled with seawater
and specimens will be separated using a dissecting
microscope. Prepared microscope slides of specimens of
Ceramium will be made by staining the material either
with Aniline blue or Methylene blue. Both dyes
differentially stain cell types in Ceramium accentuating
the arrangement of nodal cells and the pit-connections
among them. Other slides will not be stained allowing
the mounted specimens to keep their natural coloration.

Slides will be mounted in clear Karo (trademark of Best
Foods CPC International Inc.) corn syrup, concentrated at
25% Karo/distilled water with phenol added as a
preservative (which is later replaced by Karo corn syrup
at 50%) and covering it with a 22 x 22 mm cover slip.
Embedded paraffin or plastic sections will be made
(Johansen, 1940) in order to observe the number of
periaxial cells, one of the diagnostic features of the
species. Taxonomic characters will be measured for
quantitative studies on the specimens using a Zeiss
microscope. Additional material will be liquid preserved
in a solution of alcohol-Formalin (Feldmann-Mazoyer,
1940) to keep specimens for their eventual preparation of
more microscope slides and as duplicates of voucher
specimens. Dried herbarium specimens will be prepared as
voucher specimens. A set will be deposited in the
Herbarium of the B.P. Bishop Museum (BISH), Honolulu.
Photographic records of the material will be taken using
a Zeiss photomicroscope II.

3. Identification of the material:

Identification of the species will be made by
comparing the material with descriptions of Ceramium

species in the literature (e.g., Setchell & Gardner,
1930, Dawson, 1950, 1962; Hollenberg, 1968; Itono,
1972). The verification of the identifications will
require the observation of type material and collections,
when available, from other herbaria.

4. Analysis of the characters:

The list of characters (Table 1) that will be
measured in each specimen examined, was chosen based on
previous descriptions of _Ceramium_ species from other
regions and according to my observations made on Hawaiian
material, and includes diagnostic features. Hawaiian
specimens will be grouped according to their overall
morphological similarity and a temporary name will be
assigned to each group. This can be the name of a
described species which show resemblances to the Hawaiian
material. Otherwise arbitrary temporary names or numbers
will be used. These groups will be separated into
subgroups according to the place where they were
collected so that they may be analyzed and treated as
separate populations.

Qualitative and quantitative characters will be
statistically analyzed and compared within and between

populations collected from different habitats.
Comparisons will also be made between plants that are in
different reproductive stages within the same population.

5. Handling of material for cultures:

To test whether there is selection of
morphologies at early stages of development spore or if
also mature plants are able to change their morphology
cultures will be started from carpospores, tetraspores
and branches of three species of <u>Ceramium</u>. Plants will
be collected the same way as those for morphological
observations on field specimens, but reproductive plants
will be individually separated into plastic Petri dishes
filled with filtered seawater. Branches bearing
reproductive structures will be isolated from mature
cystocarpic or tetrasporangial individuals and placed in
Petri dishes with sterilized seawater overnight for spore
release. Each Petri dish will have branches from a
single individual, in order to maintain the progeny of
each plant separately. The following day, spores will be
collected with a micropipette and transferred to Petri
dishes with enriched seawater (Table 2) using Grund
medium (McLachlan, 1979), allowed to settle for 24 hours,

then placed under controlled conditions of temperature,
light intensity and photoperiod in a Psycotherm
controlled environment incubator. Controls will be of
two types: 1) mature plants collected in the field at the
time that experiments begin, and, 2) plants grown from
spores and branches of the same plants and subjected to
the same conditions except for one single factor that
will be changed.

Culture medium will be replaced weekly,
antibiotics (to inhibit bacteria and blue-green algal
growth) and GeO_2 (to avoid contamination by diatoms)
will be added when considered necessary. The experiment
will be finished when plants either become reproductively
mature or when they attain the size of adult plants
encountered in the field. Morphometric characters will
be recorded for each plant mounted on a prepared
microscope slide.

Table 1.

Characters to be studied in the Hawaiian species of *Ceramium*.

Vegetative Features

1. Cortication degree
2. Nodal structure
3. Number of cell rows per node
4. Branching pattern
5. Thallus habit
6. Nodal dimensions
7. Internodal dimensions
8. Node/internode ratios
9. Presence/absence of hairs
10. Hair shape & characteristics (origin,position,etc.)
11. Rhizoid shape & characteristics (uni-or multicellular)
12. Number of dichotomies in relation to plant length
13. Presence/absence of spines
14. Spine characteristics (origin,position,size)
15. Abundance & characteristics of adventitious branches
16. Apex characteristics (straight,forcipate,etc.)
17. Presence/absence of gland cells
18. Location & characteristics of gland cells
19. Number of periaxial cells

Reproductive Features

1. Tetrasporangial size
2. Location of tetrasporangia in the thallus
3. Location of tetrasporangia in the node
4. Presence/absence of involucrum
5. Location of spermatangia in the thallus
6. Location of spermatangia in the node
7. Location of cystocarps in the thallus
8. Cystocarp size
9. Number of gonimolobes
10. Number of subtending branches

Table 2.   Growth media: Enriched seawater Grund medium
                     (from McLachlan, 1979).

Additive to sterilized seawater	Concentration/liter
$NaNO_3$	0.5 mM
Na_2HPO_4	30.0 uM
$Fe_2(SO_4)_3$	1.0 uM
Na_2EDTA	10.0 uM
$MnCl_2$	0.1 uM
Cyanocobalamin	1.0 ug
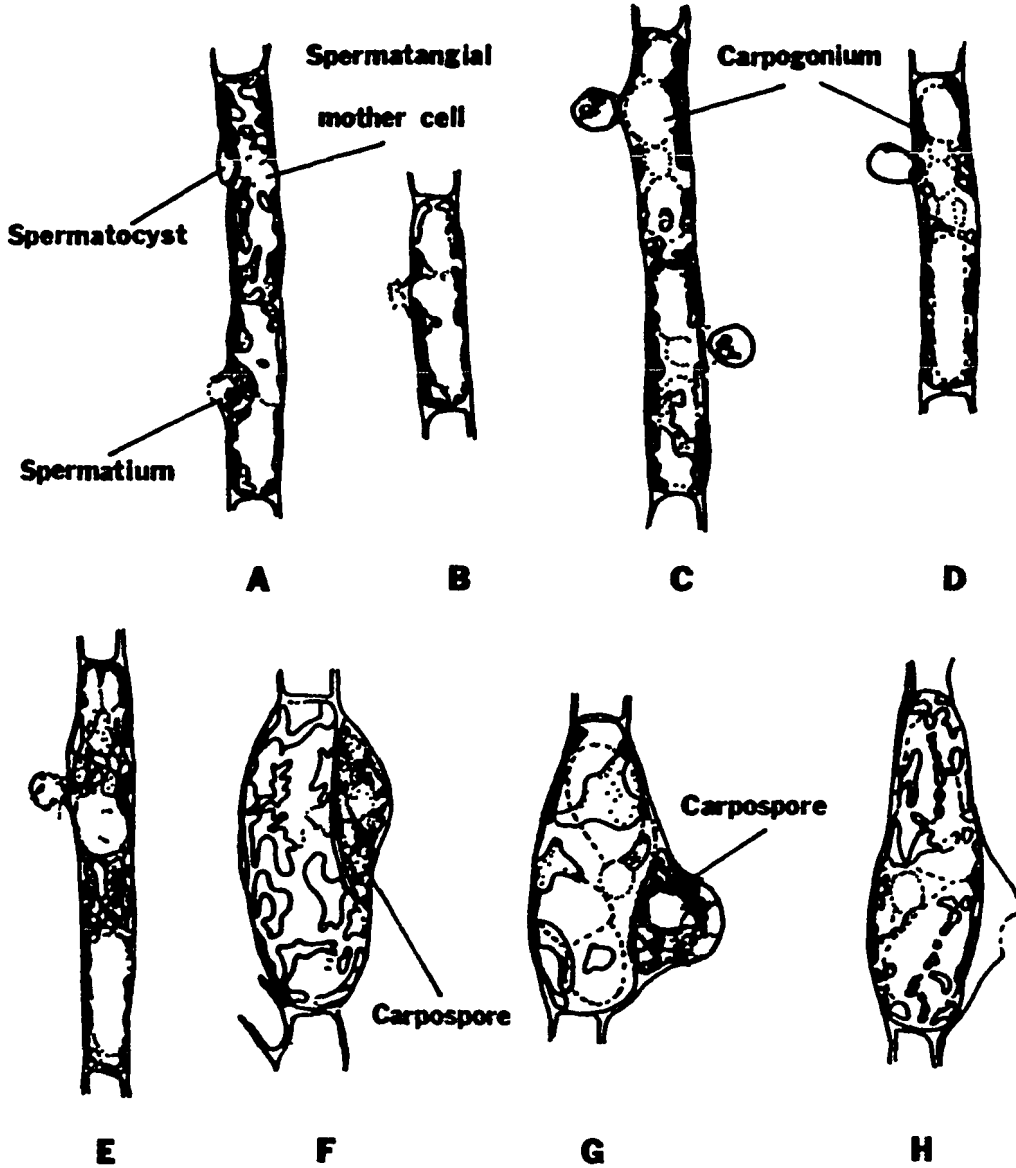
Fig. 1.1 A-h. Sexual reproduction in _Rhodochaete_ _parvula_ (modified from Magne, 1960).

spermatia

aplanospore

carpogonia

carpospores

adult
thallus

unipolar
sporeling

Gametophyte
(n)

bipolar
sporeling

Sporophyte
(2n)

'plantlet'

conchospore

monospore

conchosporangium

Meiosis
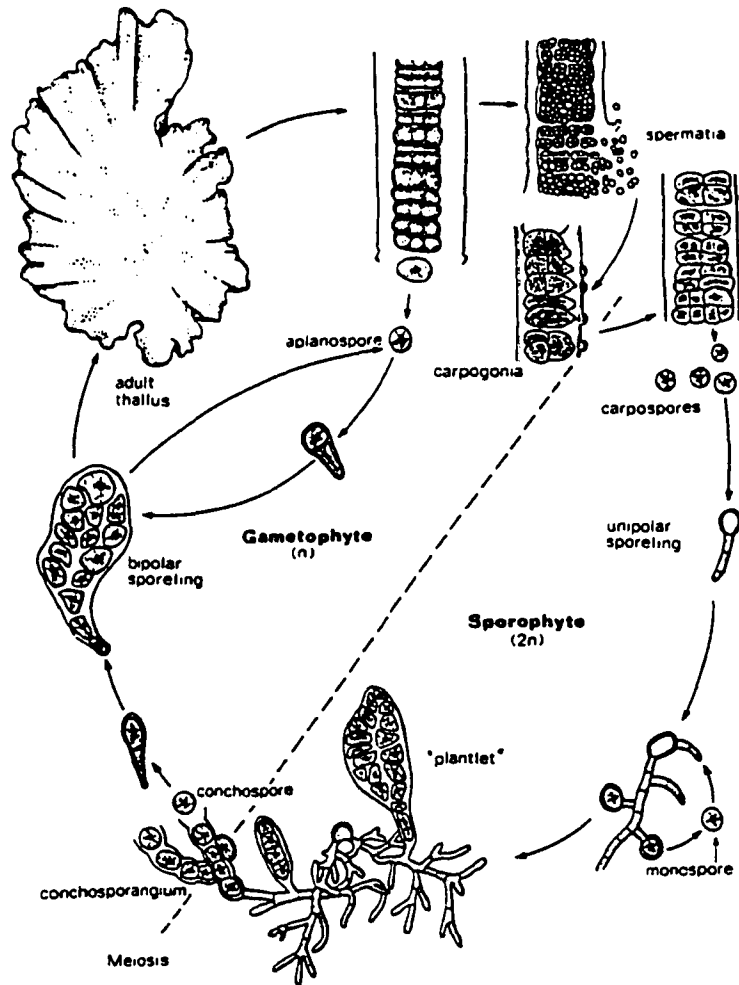
Fig.1.2   Life history of Porphyra (based on West &
Hommersand, 1981).

developing gonimoblast

carpogonial branch

carposporophyte

gametophyte

FERTILIZATION

carpospores

spermatangia

differentiation
into Batrachospermum
phase (meiosis)

monosporangia

development of
gametophyte

"Pseudochantransia"
phase

monospores

sporophyte
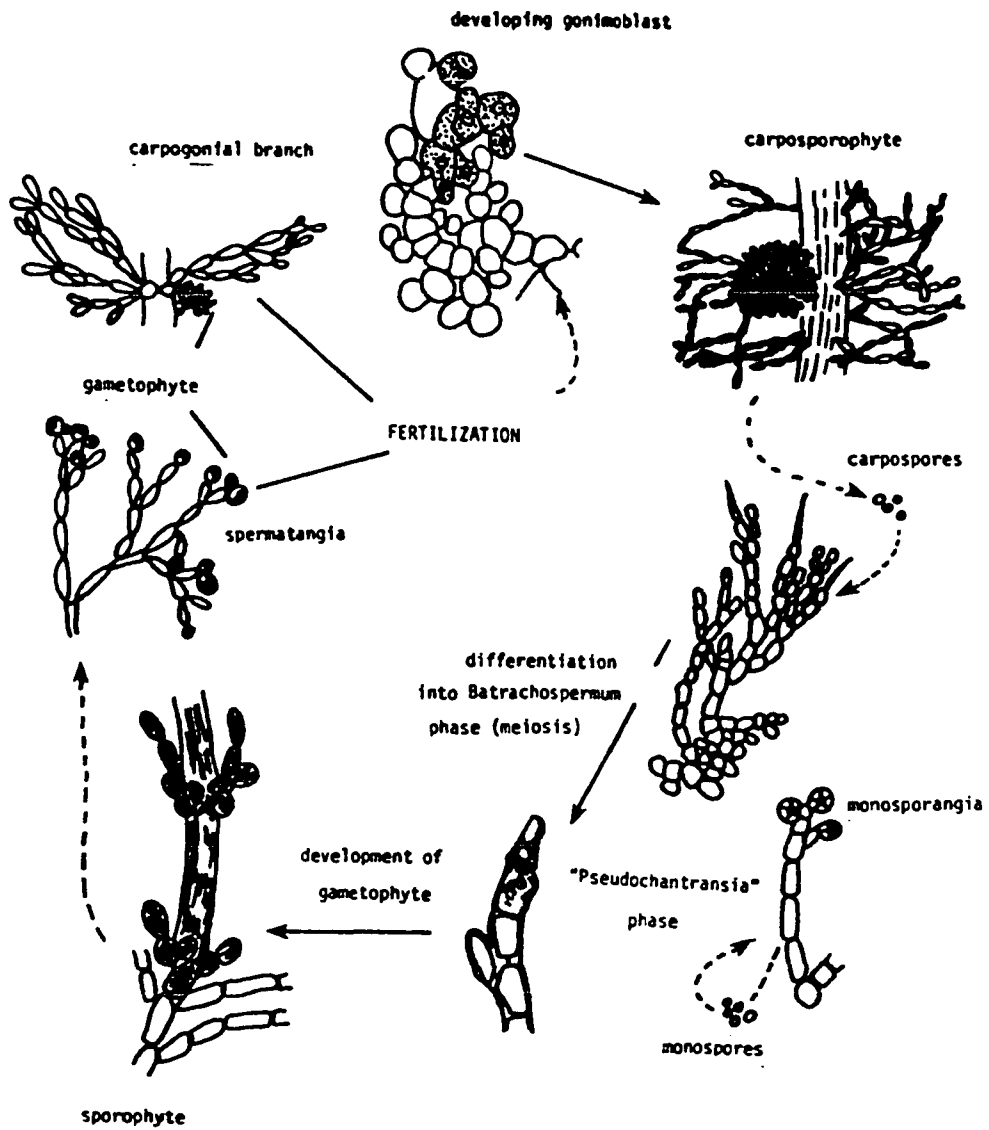
Fig.1.3   Life history of Batrachospermum
mahabaleshwarensis (modified from
Balakrishnan & Chaugule, 1980)
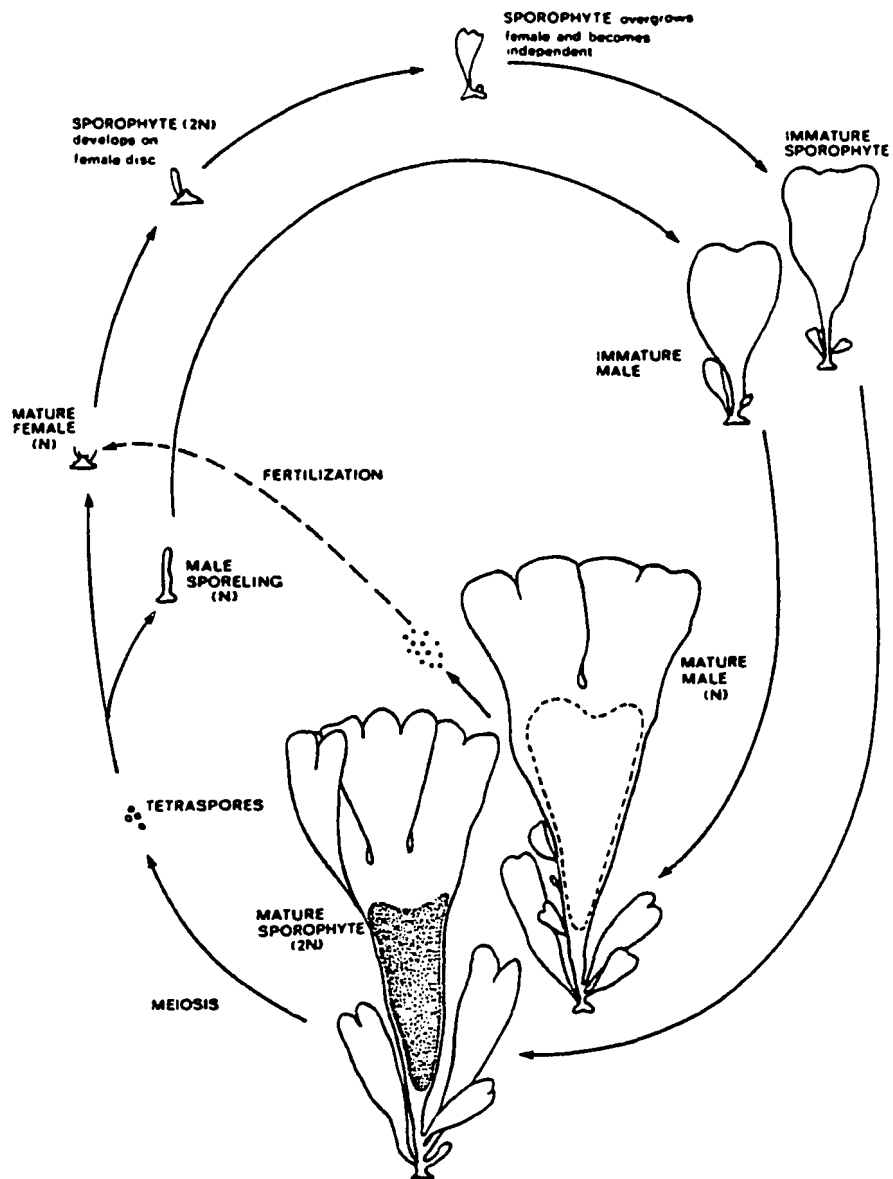
Fig.1.4   Life history of _Palmaria palmata_
(reproduced from van der Meer & Todd,
1980)
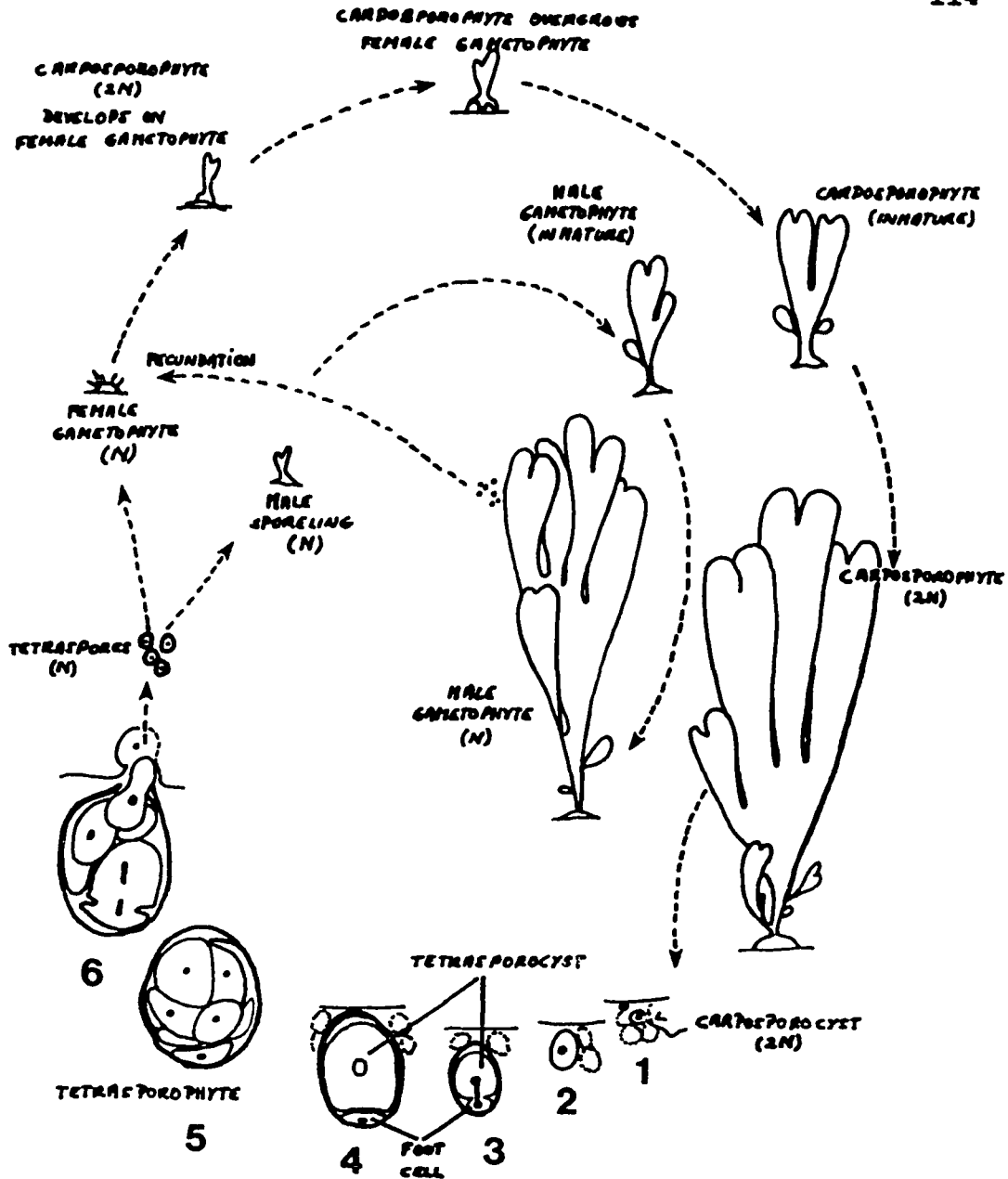
Fig. 1.5 Life history of __Palmaria__ __palmata__ (modified
from Magne, 1987). 1. Carpospocyst
formation. 2. Cell wall modification of
the carposporocyst. 3 & 4. Carposporocyst
contents divide into a foot cell and
a tetrasporocyst. 5. Tetrasporophyte
formed. 6. Tetraspores release and
regeneration of a new tetrasporocyst from
the foot cell.
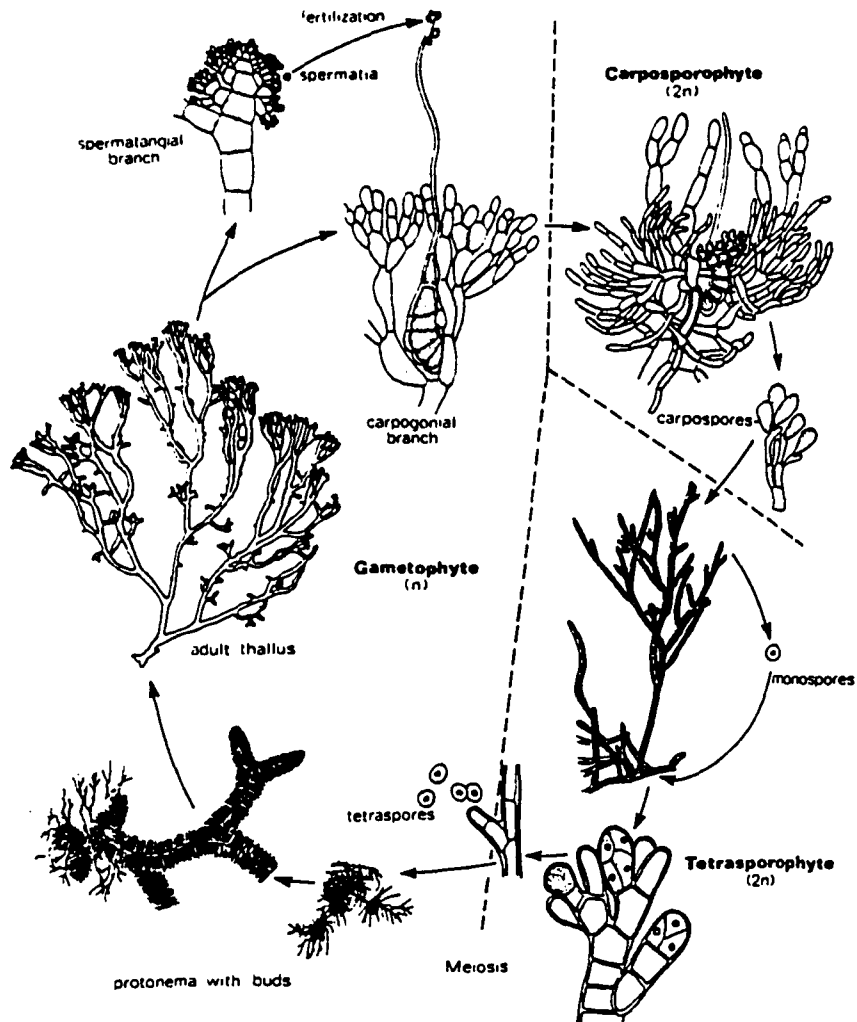
Fig.1.6   Life history of Liagora (reproduced from
Bold & Wynne, 1985).
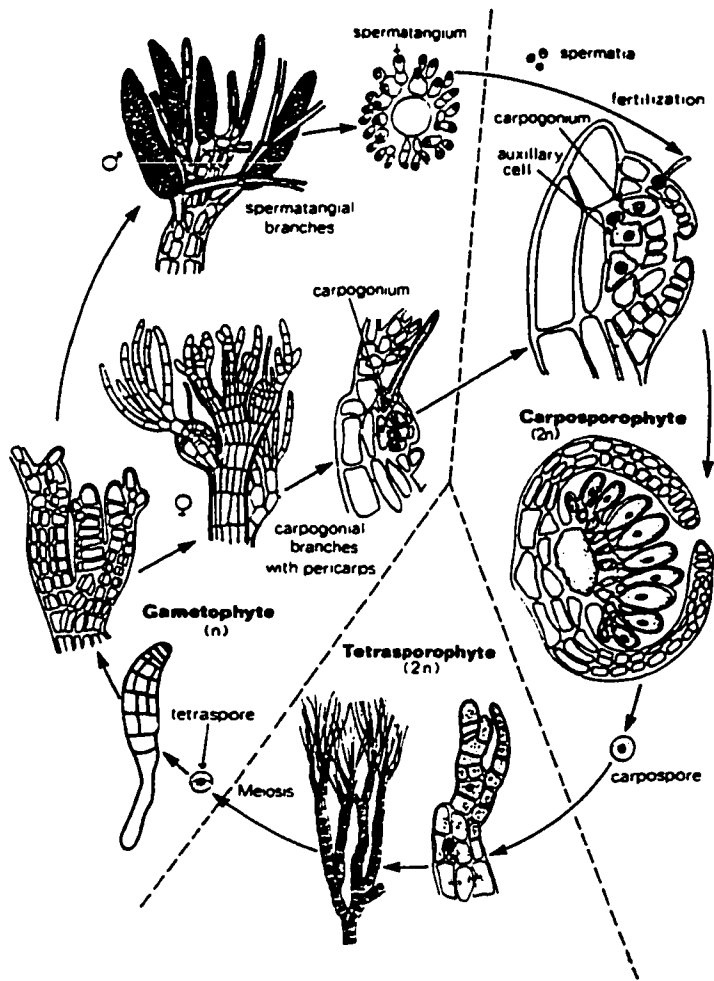
Fig.1.7 **A typical florideophycean life history exemplified by the life history of _Polysiphonia_ (reproduced from West & Hommersand, 1981).**
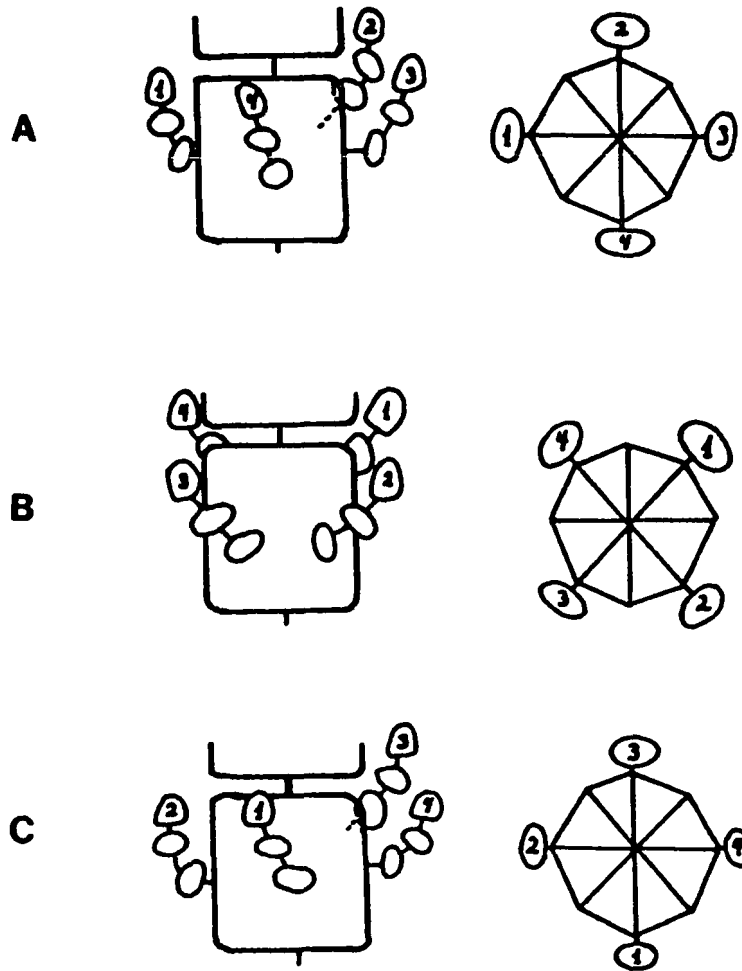
Fig.1.8   Formation of alternately superimposed
            determinate branches in Ceramiaceae. A-C,
            the position of four branches in each of
            three consecutive axial segments is
            depicted in frontal view. Adjacent
            schemes are a cross section of the
            corresponding segment. In cross sectional
            view the axial cell is represented by a
            circle divided into 8 portions. A.
            Branches arranged in the oldest of three
            segments. B. Branches in the next segment.
            Notice rotation of position with respect
            to the first segment. C. Branches in the
            uppermost segment show their positions
            superimposed on branches of the lower-
            most (oldest) segment.
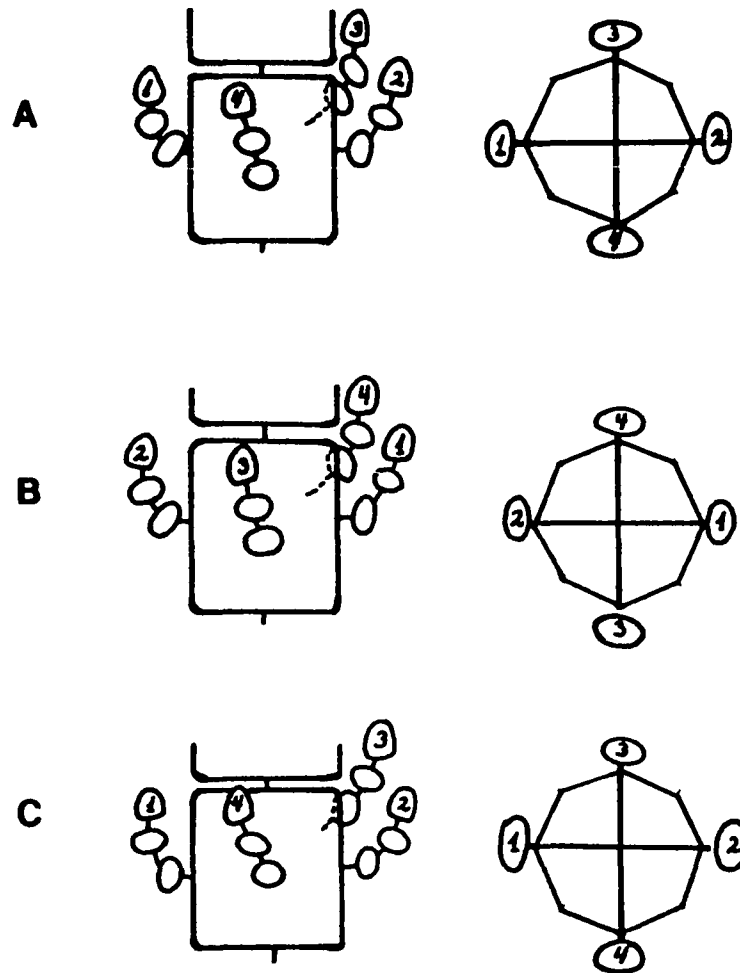
Fig.1.9   Formation of orthostichous determinate
           branches in Ceramiaceae. A-C, the position
           of four branches in each of three
           consecutive axial cell segments is
           depicted in frontal view. Adjacent schemes
           area cross section of the corresponding
           segment. In cross sectional view the axial
           cell is represented by a circle divided
           into 4 portions. A. Branches arranged in
           the oldest of three segments. B. Branches
           in the second segment superimposed to the
           branches of the first one. C. Branches in
           the uppermost segment superimposed to the
           two lower (older) ones. Although the
           original position of the branches has
           changed in consecutive segments, the
           overall arrangement of the branches
           remains the same.

Literature Cited

Abbott, I.A. 1974. Brackish-water algae from the Hawaiian
Islands. Pac. Sci. 1: 193-214.

----- 1980. Early collections of Hawaiian marine algae.
Pac. Sci. 34: 101-107.

----- & Norris, R.E. 1965. Studies on Callophyllis
(Rhodophyceae) from the Pacific coast of North
America. Nova Hedwigia 10: 67-84.

Adey, W.H. 1970. A Revision of the Foslie Crustose
Coralline Herbarium. D.K.N.V.S., Skrifter I: 1-45.

Agardh, C.A. 1811. Dispositio algarum sueciae. Fasc. 2.
Lund (Berlin), pp.17-26.

Agardh, J.G. 1851. Species genera et ordines algarum.
vol.2(1). Lund pp. ii-iii, i-xii, 1-351.

Alley, C.D. & Scott, J.L. 1977. Unusual dictyosome
morphology and vesicle formation in tetrasporangia
of the marine red alga Polysiphonia denudata. J.
Ultrastruct. Res. 58: 289-298.

Alveal, K. & Joly, A.B. 1968. The sexual male plants of
Centroceras clavulatum (C. Agardh) Montagne. Rickia
3: 111-115.

Anderson, N.S. & Rees, D.A. 1966. The repeating structure of some polysaccharide sulphates from red seaweeds. Proc. Int. Seaweed Symp. 5: pp. 243-249.

----- Dolan, T.C.S. & Rees, D.A. 1965. Evidence for a common structural pattern in the polysaccharide sulphates of the Rhodophyceae. Nature (London), 205: 1060-1062.

----- 1973. Carrageenans. Part VII. Polysaccharides from Eucheuma spinosum and Eucheuma cottonii. The covalent structure of i-carrageenan. J. Chem. Soc. Perkin Trans. I: 2173-2176.

Austin, A.P. 1960. Life history and reproduction of Furcellaria fastigiata (L.) Lam. 2. The tetrasporophyte and reduction division in the tetrasporangium. Ann. Bot., N.S. 24: 296-312.

Balakrishnan, M.S. & Chaugule, B.B. 1980. Cytology and life history of Batrachospermum mahabaleshwarensis. Cryptogam. Algol. 2: 83-97.

Baldock, R.N. & Womersley, H.B.S. 1968. The genus Bornetia (Rhodophyta, Ceramiaceae) and its southern Australian representatives, with description of Involucrana gen. nov. Aust. J. Bot. 16: 197-216.

Ballantine, D.L. & Wynne, M.J. 1986. Notes on the marine algae of Puerto Rico, II: Additions of Ceramiaceae (Rhodophyta) including, Ceramium verongiae sp. nov. Bot. Mar. 29: 497-502.

Bisalputra, T. 1974. Plastids. In W.D.P. Stewart (ed.), Algal Phisiology and Biochemistry. Blackwell Sci. Publ. Oxford, pp. 124-160.

----- Rusanowski, C. & Walker, W.S. 1967. Surface activity, cell wall, and fine structure of pit-connection in the red alga Laurencia spectabilis. J. Ultrastruct. Res. 20: 277-289.

Bold, H.C. & Wynne, M.J. 1985. Introduction to the Algae. Structure and Reproduction. Prentice-Hall Inc., New Jersey. 720 pp.

Bonneau, E.R. 1977. Polymorphic behavior of Ulva lactuca (Chlorophyta) in axenic culture, I: Occurrence of Enteromorpha-like plants in haploid clones. J. Phycol. 13: 133-140.

Boergesen, F. 1907. An ecological and systematic account of the Caulerpas of the Danish West Indies. K. Dan. Vidensk. Selsk. Skr., Ser. VII, Naturvi. og Math., 4: 337-392.

----- 1920. The marine algae of the Danish West Indies. Vol.2 Rhodophyceae. Dan. Bot. Ark. Bd.3: 498 pp.

Borowitzka, M.A. 1978. Plastid development and floridean starch grain formation during carposporogenesis in the coralline red alga Lithothrix aspergillum Gray. Protoplasma 95: 217-228.

----- 1982. Morphological and cytological aspects of algal calcification. Int. Rev. Cytol. 74: 127-162.

----- Larkum, A.W.D. & Nochodls, C.E. 1974. A scanning electron microscope study of the structure and organization of the calcium carbonate deposits of algae. Phycologia 13: 195-203.

----- Vesk, M. 1978. Ultrastructure of the Corallinaceae. I. The vegetative cells of Corallina officinalis and C. cuvieri. Mar. Biol. 46: 295-304.

----- 1979. Ultrastructure of the Corallinaceae (Rhodophyta) II. Vegetative cells of Lithothrix aspergillum. J. Phycol. 15: 146-153.Brauner, J.F. 1979. Developmental morphology and taxonomy of Medeiothamnion flaccidum (Hooker f. & Harvey) comb. nov. (Ceramiaceae, Rhodophyta) from South America. Phycologia 18: 338-346.

Brawley, S.H. & Wetherbee, R. 1981. Cytology and ultrastructure. In: C.S. Lobban & M.J. Wynne (eds.), The Biology of Seaweeds. Univ. Calif. Press, Berkeley,. Pp. 248-299.

Broadwater, S.T. & Scott, J. 1982. Ultrastructure of early

development in the female reproductive system of

Polysiphonia harveyi Bailey (Ceramiales, Rhodophyta).

J. Phycol. 18: 427-441.

----- & Pobiner, B. 1986a. Ultrastructure of meiosis in

Dasya baillowiana (Rhodophyta) I. Prophase I. J.

Phycol. 22: 490-500.

----- 1986b. Ultrastructure of meiosis in Dasya baillowiana

(Rhodophyta) II. Prometaphase I - Telophase II and

post-division nuclear behavior. J. Phycol. 22:

501-512.

Brody, M. & Brody, S.S. 1962. Induced changes in the

photosynthetic efficiency of Porphyridium cruentum

II. Archiv. Biochem. Biophys. 96: 354-359.

Calvert, H.E. 1976. Culture studies on some Florida

species of Caulerpa: morphological responses to

reduced illumination. Br. phycol. J. 11: 203-214.

Chadefaud, M. 1954. Sur la morphologie de quelques

Ceramiacees de la Mediterranee. Rev. Algol. 1: 71-87.

Chamberlain, A.H. & Evans, L. 1973. Aspects of spore

production in the red alga Ceramium. Protoplasma 76:

139-159.

Chapmann, A.R.O. 1973. Phenetic variability of stipe

morphology in relation to season, exposure, depth in

the non-digitate complex of <u>Laminaria</u> Lamour.
(Phaeophyta, Laminariales) in Nova Scotia.
<u>Phycologia</u> 12: 53-57.

----- Edelstein, T. & Power, P.J. 1977. Studies on
<u>Gracilaria</u> I. Morphological and anatomical variation
in samples from lower Gulf of St. Lawrence and New
England. <u>Bot</u>. <u>Mar</u>. 20: 149-153.

Chen, L. C-M. 1977. The sporophyte of <u>Ahnfeltia</u> <u>plicata</u>
(Huds.) Fries (Rhodophyceae, Gigartinales) in
culture. <u>Phycologia</u> 16: 163-168.

Clayton, M.N. 1975. A study of variation in Australian
species of <u>Colpomenia</u> (Phaeophyta, Scytosiphonales).
<u>Phycologia</u> 14: 187-196.

Conway, E. & Cole, K. 1977. Studies in the Bangiaceae:
structure and reproduction of the conchocelis of
<u>Porphyra</u> and <u>Bangia</u> in culture (Bangiales,
Rhodophyceae). <u>Phycologia</u> 16: 205-216.

Cole, K. & Conway, E. 1975. Phenetic implications of
structural features of the apprehending phase in the
life history of <u>Porphyra</u> and <u>Bangia</u> (Bangiophyceae,
Rhodophyta). <u>Phycologia</u> 14: 239-245.

----- 1980. Studies in the Bangiaceae: reproductive modes.
<u>Bot</u>. <u>Mar</u>. 23: 545-553.

Coute, A. 1971. Sur le cycle morphologique du _Liagora_
     tetrasporifera compare a celui du _Liagora_ _distenta_
     (Rhodophycees, Nemalionales, Helminthocladiacees). C.
     R. Acad. Sci. Paris 273: 626-629.

Craigie, J.S. 1974. Storage products. In: W.D.P. Stewart
     (ed.), Algal Physiology and Biochemistry. Univ.
     Calif. Press, Berkeley, Pp.

Davis, B.M. 1905. Studies on the plant cell. VI. Section
     V. Cell activities at critical periods of ontogeny in
     plants. Am. Nat. 39: 449-499.

----- 1910. Nuclear phenomena of sexual reproduction in
     algae. Amer. Nat. 44: 513-522.

Dawson, E.Y. 1944. The marine algae of the Gulf of
     California. A. Hancock Pac. Exped. 3: 189-453.

----- 1950. A review of _Ceramium_ along the Pacific coast
     of North America with special reference to its
     Mexican representatives. Farlowia 4: 113-138.

----- 1953. Marine red algae of Pacific Mexico. Part I.
     Bangiales to Corallinaceae subf. Corallinoideae. A.
     Hancock Pac. Exped. 17: 1-239.

----- 1954a. The marine flora of Isla San Benedicto
     following the volcanic eruption of 1952 - 1953. A.
     Hancock Found. Publ. Occas. Pap. 16: 1-25.

----- 1954b. Marine plants in the vicinity of the
Institute Oceanographique de Nha Trang, Viet Nam.
Pac. Sci. 8: 373-469.

----- 1962. Marine red algae of Pacific Mexico. Part 7.
Ceramiales: Ceramiaceae, Delesseriaceae. A. Hancock
Pac. Exped. 26: 1-207.

----- 1963. New records of marine algae from the Galapagos
Islands. Pac. Nat. 4: 1-23.

Dayton, P.K. 1973. Dispersion, dispersal and persistence
of the annual intertidal alga Postelsia palmaeformis.
Ecology 54: 433-438.

De Boer, J.A. & Whoriskey, F.G. 1983. Production and role
of hyaline hairs in Ceramium rubrum. Mar. Biol. 77:
229-234.

De Cew, T.C. & West, J.A. 1981. Investigations on the life
histories of three species of Farlowia (Rhodophyta,
Cryptonemiales, Dumontiaceae) from the Pacific coast
of North America. Phycologia 20: 342-351.

----- West, J.A. & Ganesan, E.K. 1981. The life histories
and developmental morphology of two species of
Gloiosiphonia (Rhodophyta: Cryptonemiales,
Gloiosiphoniaceae) from the Pacific coast of North
America. Phycologia 20: 415-423.

Delivopoulos, S.G. & Kugrens, P. 1984. Ultrastructure of
carposporogenesis in the parasitic red alga
Faucheocolax attenuata Setch. (Rhodymeniales,
Rhodymeniaceae). Am. J. Bot. 71: 1245-1259.

----- 1985. Ultrastructure of carposporophyte development
in the red alga Gloiosiphonia verticillaris
(Cryptonemiales, Gloiosiphoniaceae). Am. J. Bot. 72:
1926-1938.

Denizot, M. 1968. Les algues floridees encroutantes (a
l'exclusion des Corallinacees). Laboratoire de
Cryptogamie. Museum National d' Histoire Naturelle,
Paris. 310 pp.

Díaz-Piferrer, M. 1968. Ceramiella joly, a new species of
Rhodophyta from Puerto Rico. Carib. J. Sci. 8:
199-205.

DiNinno, V. & McCandless, E.L. 1978a. The inmunochemistry
of α- type carrageenans from certain red algae.
Carbohydr. Res. 66: 85-93.

----- 1978b. The inmunochemistry of   - type carrageenans
from certain red algae. Carbohydr. Res. 67: 235-241.

Dixon, P.S. 1960a. Studies on marine algae of the British
Isles: the genus Ceramium. J. Mar. Biol. Assoc. U.K.
39: 331-374.

----- 1960b. Studies on marine algae of the British Isles: *Ceramium shuttleworthianum* (Kuetzing) Silva. J. Mar. Biol. Assoc. U.K. 39: 375-390.

----- 1964. Auxiliary cells in the Ceramiales. Nature (London), 201: 519-520.

----- 1965. Perennation, vegetative propagation and algal life histories, with special reference to *Asparagopsis* and other Rhodophyta. Proc. Mar. Biol. Symp., Goteborg, 5: 67-73.

----- 1970. The Rhodophyta: some aspects of their biology. II. Oceanogr. Mar. Biol. Annu. Rev. 8: 307-352.

----- 1971. Cell enlargement in relation to the development of thallus form in Florideophyceae. Br. phycol. J. 6: 195-205.

----- 1973. *Biology of the Rhodophyta*. Hafner Press, New York. 285 pp.

Dodge, J.D. 1973. *The Fine Structure of Algal Cells*. Academic Press, London. 261 pp.

Doty, M.S., Gilbert, W.J. & Abbott, I.A. 1974. Hawaiian marine algae from seaward of the algal ridge. Phycologia 13: 345-357.

Drew, K.M. 1949. Conchocelis-phase in the life history of *Porphyra umbilicalis* (L.) Kuetz. Nature (London) 164: 748-749.

----- 1954. Studies in the Bangiophycidae III. The life
history of Porphyra umbilicalis (L.) Kuetz.
var.laciniata (Lightf.) J.Ag. Ann. Bot., N.S. 18:
183-211.

Dring, M.J. 1981. Chromatic adaptation of photosynthesis
in benthic marine algae: An examination of its
ecological significance using a theoretical model.
Limnol. & Oceanogr. 26: 271-284.

Duckett, J.G., Buchanan, J.S., Peel, M.C. & Martin, M.T.
1974. An ultrastructural study of pit-connections and
percurrent proliferations in the red alga Nemalion
helminthoides (Vell.) Batt. New Phytol. 7: 497-507.

Duckworth, M. & Yaphe, W. 1971a. The structure of agar.
Part I. Fractionation of a complex mixture of
polysaccharides. Carbohyd. Res. 16: 189-197.

----- 1971b. The structure of agar. Part II. The use of a
bacterial agarase to elucidate structural features of
the charged polysaccharides in agar. Carbohyd. Res.
16: 435-445.

----- & Peel, M.C. 1978. The role of transmission electron
microscopy in elucidating the taxonomy and phylogeny
of the Rhodophyta. In: D.E.G. Irvine & J.H. Price
(eds.), Modern Approaches to the Taxonomy of Red and
Brown Algae. Academic Press, London, pp. 157-204.

Edelstein, T. & McLachlan, J. 1971. Further observations on _Gloiosiphonia capillaris_ (Hudson) Carmichael in culture. _Phycologia_ 10: 215-219.

Edwards, P. 1970. Attempted hybridization in the red algal genus _Polysiphonia_. _Nature_ 226: 467-468.

Edwards, M.R. & Gantt, E. 1971. Phycobilisomes of the thermophilic blue-green alga _Synechococcus lividus_. _J. Cell Biol_. 50: 896-900.

Fan, K-C. 1960. On pit-connections in Bangiophycidae. _Nova Hedwigia_ 1: 305-307.

Farnham, W.F. & Fletcher, R.L. 1976. The occurrence of a _Porphyrodiscus simulans_ Batt. phase in the life history of _Ahnfeltia plicata_ (Huds.) Fries. _Br. phycol. J_. 11: 183-190.

Feldmann, J. & Feldmann, G. 1942. Recherches sur les Bonnemaisoniacees et leur alternance de generations. _Ann.Sci. Nat. Bot. Ser_., 11: 75-175.

Feldmann-Mazoyer, G. 1940. _Recherches sur les Ceramiacees de la Mediterranee occidentale._ Imprimerie Minerva, Alger, 510 pp.

Fenical, W. & Norris, J.N. 1975. Chmotaxonomy in marine algae: chemical separation of some _Laurencia_ species (Rhodophyta) from the Gulf of California. _J. Phycol_. 11: 104-108.

Frederiq, S. & Hommersand, M.H. 1989. Proposal of the
Gracilariales ord. nov. (Rhodophyta) based on an
analysis of the reproductive development of
Gracilaria verrucosa. J. Phycol. 25: 213-227.

Frei, E. & Preston, R.D. 1964. Non-cellulosic structural
polysaccharides in algal cell walls. II. Association
of xylan and mannan in Porphyra umbilicalis. Proc. R.
Soc. Lond. B Biol. Sci. 160: 314-327.

Fritsch, F.E. 1945. The Structure and Reproduction of the
Algae. Vol.II. Cambridge Univ. Press, Cambridge. 939
pp.

Gabrielson, P.W., Garbary, D.J. & Scagel, R.F. 1985. The
nature of the ancestral red alga: inferences from a
cladistic analysis. ByoSystems 18:335-346.

Gantt, E. 1975. Phycobilisomes: light harvesting pigment
complexes. Bioscience 25: 781-787.

----- 1980. Structure and function of phycobilisomes:
light harvesting pigment complexes in red and
blue-green algae. Int. Rev. Cytol.66: 45-80.

----- & Conti, S.F. 1965. The ultrastructure of
Porphyridium cruentum. J. Cell Biol. 26: 305-338.

----- 1966. Granules associated with chloroplast lamellae
of Porphyridium cruentum. J. Cell. Biol. 29: 423-434.

Garbary, D.J., Grund, D.W. & McLachlan, J. 1978. The taxonomic status of _Ceraminum rubrum_ (Huds.) C.Ag. (Ceramiales, Rhodophyceae) based on culture experiments. _Phycologia_ 17: 85-94.

----- 1980. Branching patterns and life history stages in _Ceramium rubrum_ (Huds.) C.Ag. _Nova Hedwigia_ 33: 249-260.

Goff, L.J. 1976. The biology of _Harveyella mirabilis_ (Cryptonemiales, Rhodophyceae). V: Host responses to parasite infection. _J. Phycol._ 12: 313-328.

----- 1979a. The biology of _Harveyella mirabilis_ (Cryptonemiales, Rhodophyceae). VI: Translocation of photoassimilated ^{14}C. _J. Phycol._ 15: 82-87.

----- 1979b. The biology of _Harveyella mirabilis_ (Cryptonemiales, Rhodophyceae). VII: Structure and proposed function of host-penetrating cells. _J. Phycol._ 15: 87-100.

Goff, L.J. & Coleman, A.W. 1984. Transfer of nuclei from a parasite to its host. _Proc. Natl. Acad. Sci. U.S.A._ 81: 5420-5424.

Gordon, E.M. 1972. Comparative morphology and taxonomy of the Wrangeliae, Sphondylothamnieae, and Spermothamnieae (Ceramiaceae, Rhodophyta). _Aust. J. Bot._ (suppl.) ser. No. 4: 1-180.

----- & Womersley, H.B.S. 1966. The morphology and
    reproduction of Sphondylothamnion multifidum (Hudson)
    Nageli (Ceramiaceae). Br. phycol. Bull. 3: 23-30.

----- & Kraft, G.T. 1981. The morphology of Radiathamnion
    speleotis gen. et sp. nov., representing a new tribe
    in the Ceramiaceae (Rhodophyta) from southern
    Australia. Phycologia 20: 122-130.

Guiry, M.D. 1984. Structure, life history and
    hybridization of Atlantic Gigartina teedii
    (Rhodophyta) in culture. Br. phycol. J. 19: 37-55.

Greenwood, C.T. & Thomson, J. 1961. Physicochemical
    studies on starches Part XXIII. Some physical
    properties of floridean starch and the
    characterization of structure-type of branched
    -1,4-glucans. J. Chem. Soc. (Lond.) Part II:
    1534-1537.

Guzman del Proo, S.A., de la Campa-De Guzman, S. &
    Pineda-Barrera, J. 1972. Shedding rythm and
    germination of spores in Gelidium robustum. Proc.
    Int. Seaweed Symp. 7: 221-228.

Halos, M-Th. 1966. Remarques sur la morphologie des
    Céramiacées: la notion de brachycladome. C.r. Seanc.
    Acad. Sci., Paris 262: 64-67.

Hansen, J.E. 1977. Ecology and natural·history of _Iridaea cordata_ (Gigartinales, Rhodophyta) growth. _J. Phycol_. 13: 395-402.

Hara, Y. & Chihara, M. 1974. Comparative studies on the chloroplast ultrastructure in the Rhodophyta, with special reference to their taxonomic significance. _Sci. Rep. Tokyo Kyoiku Daiguku, Sect. B_. 15: 209-235.

Hawkes, M.W. 1978. Sexual reproduction in _Porphyra gardneri_ (Smith et Hollenberg) Hawkes (Bangiales, Rhodophyta). _Phycologia_ 17: 329-353.

Haxo, F.T. & Blinks, L.R. 1950. Photosynthetic action spectra of marine algae. _J. Gen. Physiol_. 33: 389-422.

Heerebout, G.R. 1968. Studies on the Erythropeltidaceae (Rhodophyceae, Bangiophycidae). _Blumea_ 16: 139-157.

Hollenberg, G.J. 1959. _Smithora_, an interesting new algal genus in the Erythropeltidaceae. _Pac. Nat_. 1: 3-11.

----- 1968. Phycological notes III. New records of marine algae from the central tropical Pacific ocean. _Brittonia_ 20: 74-82.

Hommersand, M.H. 1963. The morphology and classification of some Ceramiaceae and Rhodomelaceae. _Univ. Calif. Publ. Bot_. 35: 165-366.

Hooker, J.D. & Harvey, W.H. 1848. Algae Novae Zelandiae
(supplementum primum). _London_ _J_. _Bot_. 7: 443-445.

Howe, M.A. 1917. A note on the structural dimorphism of
sexual and tetrasporic plants of _Galaxaura_ _obtusata_.
Bull. _Torrey_ _Bot_. _Club_ 43: 621-624.

----- 1918. Further notes on the structural dimorphism of
sexual and tetrasporic plants in the genus _Galaxaura_.
Brooklyn _Bot_. _Gard_. _Mem_. 1: 121-197.

Huisman, J.M. & Kraft, G.T. 1982. _Deucalion_ gen. nov. and
Anisoschizus gen. nov. (Ceramiaceae, Ceramiales), two
new propagule-forming red algae from Southern
Australia. _J_. _Phycol_. 18: 177-192.

Itono, H. 1977. Studies on the Ceramiaceaous algae
(Rhodophyta) from southern parts of Japan. _Nova_
Hedwigia _Bibl_. _Phycol_. 35: 1-499.

----- & Tanaka, T. 1973. _Balliella_, a new genus of
Ceramiaceae (Rhodophyta). _Bot_. _Mag_. _Tokyo_ 86:
241-252.

Jackson, G.A., James, D.E. & North, W.J. 1985.
Morphological relationships among fronds of giant
kelp _Macrocystis_ _pyrifera_ off La Jolla, California.
Mar. _Ecol_. _Prog_. _Ser_. 26: 261-270.

Johansen, D.A. 1940. _Plant_ _Microtechnique_. McGraw-Hill
Book Co. New York. 523 pp.

Johansen, H.W. 1981. Coralline Algae, a First Synthesis. CRC Press, Inc., Florida. 237 pp.

Joly, A.B. & Ugadim, Y. 1963. Notes on the occurrence of one species of Ceramiella (Rhodophyta) in American South Atlantic. Fac. Fil., Cienc. & Letr. Univ. Sao Paulo, 288 (Botanica 20): 41-53.

Kapraun, D.F. 1977. Asexual propagules in the life history of Polysiphonia ferulacea (Rhodophyta, Ceramiales). Phycologia 16: 417-426.

Kim, D. 1976. A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae. Nova Hedwigia 27: 1-146.

King, R.J., Puttock C.F. & Vickery, R.S. 1988. A taxonomic study of Bostrychia tenella complex (Rhodomelaceae, Rhodophyta). Phycologia 27: 10-19.

Knaggs, F.W. 1969. A review of florideophycidean life histories and of the culture techniques employed in their investigation. Nova Hedwigia 18: 293-330.

Koch, C. 1986. Attempted hybridization between Polysiphonia fibrillosa and Polysiphonia violacea (Bangiophyceae) from Denmark; with culture studies primarily on P. fibrillosa. Nord. J. Bot. 6: 123-128.

Kugrens, P. & Delivopoulos, S.G. 1985. Ultrastructure of auxiliary and gonimoblast cells during

carposporophyte development in Faucheocolax attenuata
(Rhodophyta). J. Phycol. 21: 240-249.

----- 1986. Ultrastructure of the carposporophyte and
carposporogenesis in the parasitic red alga
Plocamiocolax pulvinata Setch. (Gigartinales,
Plocamiaceae). J. Phycol. 22: 8-21.

----- & West, J.A. 1972a. Synaptonemal complexes in red
algae. J. Phycol. 8: 187-191.

----- 1972b. Ultrastructure of tetrasporogenesis in the
parasitic red alga Levringiella gardneri (Setchell)
Kylin. J. Phycol. 8: 370-383.

Kurogi, M. 1959. Influence of light on the growth and
maturation of conchocelis-thallus of Porphyra. I.
Effects of photoperiod on the formation of
monosporangia and liberation of monospores.
Bull. Tohoku Reg. Fish. Res. Lab., 15: 33-42.

----- 1972. Systematics of Porphyra in Japan. In: I.A.
Abbott & M. Kurogi (eds.), Contributions to the
Systematics of Benthic Marine Algae of the North
Pacific. Jap. Soc. Phycol., Kobe, Japan. pp. 167-191.

Kuetzing, F.T. 1841. Ueber Ceramium Ag. Linnaea 15:
727-746.

----- 1843. Phycologia generalis. (F.A. Brockhaus),
Leipzig. 458 pp.

----- 1847. Diagnosen und Bemerkungen zu neuen oder
kritischen Algen. Bot. Ztg., 5: 1-5, 22-25, 33-38,
52-55, 164-167, 177-180, 193-198, 219-223.

----- 1849. Species algarum...Leipzig, vi + 922 pp.

Kylin, H. 1923. Studien ueber die Entwicklungsgeschichte
der Florideen. K. Svensk. Vet. Akad. Handl. 63:
1-139.

----- 1928. Entwicklungsgeschichtliche Florideenstudien.
Lunds Univ. Arsskr. N.F. Avd. 2, 24: 1-127.

----- 1930. Ueber die Entwicklungsgeschichte der
Florideen. Lunds Univ. Arsskr. N.F. Avd.2, 26: 1-104.

----- 1956. Die Gattungen der Rhodophyceen. CWK Gleerups
Foerlag, Lund. xv + 673 pp.

Larkum, A.W.D. & Weyranch, S. K. 1977. Photosynthetic
action spectra and light-harvesting in Griffithsia
monilis (Rhodophyta). Photochem. Photobiol. 25:
65-72.

Larsen, J. 1981. Crossing experiments with Enteromorpha
intestinalis and Enteromorpha compressa from
different European localities. Nord. J. Bot. 1:
128-136.

Lewin, R.A. & Robertson, J.A. 1971. Influence of salinity
on the form of Asterocystis in pure culture. J.
Phycol. 7: 236-238.

Lewis, I.F. 1909. The life history of <u>Griffithsia</u> <u>bornetiana</u>. <u>Ann</u>. <u>Bot</u>. 23: 639-690. Plates 49-53.

Lewis, S.M., Norris, J.N. & Searles, R.B. 1987. The regulation of morphological plasticity in tropical reef algae by herbivory. <u>Ecology</u> 68: 636-641.

Lichtle, C. & Thomas, J.C. 1976. Etude ultrastructurale des thylacoides des algues a phycobiliproteines, comparaison des resultats obtenus par fixation classique et cryodecapage. <u>Phycologia</u> 15: 393-404.

Lin, H-P., Sommerfeld, M.R. & Swafford, J.R. 1975. Light and electron microscope observations on motile cells of <u>Porphyridium</u> <u>purpureum</u> (Rhodophyta). <u>J</u>. <u>Phycol</u>. 11: 452-457.

----- J.R. Swafford & Sommerfeld, M.R. 1977. Comparative ultrastructure of the alternating vegetative phases of <u>Bangia</u> <u>fuscopurpurea</u> (Bangiophycidae, Rhodophyta). <u>Bot</u>. <u>Mar</u>. 20: 339-444.

Lipkin, Y. 1977. <u>Centroceras</u>, the "missile"-launching marine red alga. <u>Nature</u> 270: 48-49.

MacCaughey, V. 1918. Algae of the Hawaiian archipelago. I and II. <u>Bot</u> <u>Gaz</u>. 65: 42-57; 121-149.

Mackie, M. & Preston, R.D. 1974. Cell wall and intercellular region polysaccharides. <u>In</u>: W.D.P.

Stewart (ed.), <u>Algal Physiology</u> and <u>Biochemistry</u>.
Blackwell Sci. Publ. Oxford, pp. 40-85.

Magne, F. 1960. Le <u>Rhodochaete</u> <u>parvula</u> Thuret (Bangioidee)
et sa reproduction sexuee. <u>Cah</u>. <u>Biol</u>. <u>Mar</u>. 1:
407-420.

----- 1967a. Sur l'existence, chez les <u>Lemanea</u>
(Rhodophycees, Nemalionales) d'un type de cycle de
developpement encore inconnu chez les algues rouges.
<u>C</u>.<u>R</u>. <u>Acad</u>. <u>Sci</u>. (<u>Paris</u>) 264 D: 2632-2633.

----- 1967b. Sur le deroulement et le lieu de la meiose
chez Lemaneacees (Rhodophycees, Nemalionales). <u>C</u>.<u>R</u>.
<u>Acad</u>. <u>Sci</u>. (<u>Paris</u>) 265 D: 670-673.

----- 1987. La tetrasporogenese et le cycle de
developpment des Palmariales (Rhodophyta): une
nouvelle interpretation. <u>Cryptogam</u>. <u>Algol</u>. 8:
273-280.

Magruder, W.H. 1977. The life history of the red alga
<u>Ahnfeltia</u> <u>concinna</u> (Rhodophyta, Gigartinales).
<u>Phycologia</u> 16: 197-203.

----- 1984. Reproduction and life history of the red alga
<u>Galaxaura</u> <u>oblongata</u> (Nemaliales, Galaxauraceae). <u>J</u>.
<u>Phycol</u>. 20: 402-409.

Manners, D.J. & Wright, A. 1962. -1,4-glucosans Part XIV.
The interaction of concanavalin A with glycogens. <u>J</u>.
<u>Chem</u>. <u>Soc</u>., <u>Part</u> IV: 4592-4595.

Marsden, W.J.N., Evans, L.V. & Callow, J.A. 1983a.
Analysis of character variation in <u>Fucus</u> L. I.
Discriminant analysis of morphometric estimates. <u>Bot</u>.
<u>Mar</u>. 26: 383-392.

------ 1983b. Analysis of character variation in <u>Fucus</u> L.
II. Use of ratios of morphometric estimates. <u>Bot</u>.
<u>Mar</u>. 26: 527-531.

Mathieson, A.C., Norton, T.A. & Neushul, M. 1981. The
taxonomic implications of genetic and environmentally
induced variations in seaweed morphology. <u>Bot</u>. <u>Rev</u>.
47: 313-347.

McBride, M.D. & Cole, K. 1972. Ultrastructural
observations on germinating monospores in <u>Smithora</u>
<u>naiadum</u> (Rhodophyceae, Bangiophycidae). <u>Phycologia</u>
11: 181-191.

McCandless, E.L., West, J.A. & Guiry, M.D. 1983.
Carrageenan patterns in the Gigartinaceae. <u>Biochem</u>.
<u>Syst</u>. <u>Ecol</u>. 11: 175-182.

McDonald, K. 1972. The ultrastructure of mitosis in the
marine red alga <u>Membranoptera platyphylla</u>. <u>J</u>. <u>Phycol</u>.
8: 156-166.

McLachlan, J. 1979. Growth media-marine. In: J.R. Stein (ed.), Handbook of Phycological Methods. Vol. Culture Methods and Growth Measurements. Cambridge Univ. Press, Cambridge, pp. 25-51.

Meeks, J.C. 1974. Chlorophylls. In: W.D.P. Stewart (ed.), Algal Physiology and Biochemistry. Univ. Calif. Press, Berkeley, pp. 161-175.

Mumford Jr., T.F. & Cole, K. 1977. Chromosome numbers for fifteen species in the genus Porphyra (Bangiales, Rhodophyta) from the west coast of North America. Phycologia 16: 373-377.

Munda, I.M. 1976. The distribution of Halosaccion ramentaceum (L.)J.Ag. in associations in the Icelandic coastal area and their hydrographically conditioned variations. Bot. Mar. 19: 161-179.

----- 1981. Some examples of polymorphism in benthic algae from Icelandic waters. Nova Hedwigia 35: 377-406.

Murray, S., Scott, J.L. & Dixon, P.S. 1972. The life history of Porphyropsis coccinea var. dawsonii in culture. Br. phycol. J. 7: 323-333.

Myers, A., Preston, R.D. & Ripley, G.W. 1956. Fine structure in the red algae. I. X-ray and electron microscope investigation of Griffithsia flosculosa.

Proc. Roy. Soc. Lond., Sect. B. Biol. Sci. 144:
450-459.

Nakamura, Y. 1950. New Ceramiums and Campylaephoras from
Japan. Sci. Pap. Inst. Algol. Res., Hokkaido Univ. 3:
155-172.

----- 1954. The structure and reproduction of the genera
Ceramium and Campylaephora in Japan with special
reference to criteria of classification. Sci. Pap.
Inst. Algol. Res., Fac. Sci. Hokkaido Univ. 4:
15-62.

----- 1965. Species of the genera Ceramium and
Campylaephora especially those of northern Japan.
Sci. Pap. Inst. Algol. Res., Fac. Sci. Hokkaido Univ.
14: 52-71.

Norris, J.N. & Fenical, W.H. 1985. Natural products
chemistry: uses in ecology and systematics. In:
Littler, M.M. & Littler, D.S. (eds.). Handbook of
Phycological Methods, Vol. 4. Ecological Field
Methods: Macroalgae. Cambridge Univ. Press,
Cambridge, pp. 121-145.

Norris, R.E. 1964. The morphology and taxonomy of South
African Kallymeniaceae. Bot. Mar. 7: 90-129.

Norton, T.A. 1969. Growth, form and environment in
    Saccorhiza polyschides. J. Mar. Biol. Assoc. U.K. 49:
    1025-1045.

O'hEocha, C. 1965. Biliproteins of algae. Ann. Rev. Plant
    Physiol. 16: 415-434.

O'hEocha, C. 1971. Pigments of the red algae. Oceanogr.
    Mar. Biol. Ann. Rev. 9: 61-82.

Okamura, K. 1927. On Campylaephora hypnaeoides J. Ag. Bot.
    Mag. Tokyo 41: 365-368.

Okuda, T. & Neushul, M. 1981. Sedimentation studies of red
    algal spores. J. Phycol. 17: 113-118.

Paine, R.T. 1979. Disater, catastrophe and local
    persistence of the sea palm, Postelsia palmaeformis.
    Science 205: 685-687.

Papenfuss, G.F. & Chiang, Y-M. 1969. Remarks on the
    taxonomy of Galaxaura (Nemaliales, Chaetangiaceae).
    Proc. Int. Seaweed Symp. 6: 303-314.

Peat, S., Turvey, J.R. & Evans, J.M. 1959a. The structure
    of floridean starch. Part I. Linkage analysis by
    partial acid hydrolysis. J. Chem. Soc. (Lond) Part
    IV: 3223-3227.

----- 1959b. The structure of floridean starch. Part II.
    Enzymic hydrolysis and other studies. J.Chem. Soc.
    (Lond) Part IV: 3341- 3344.

Peyriere, M. 1977. Infrastructure des synapses du
    Griffithsia _flosculosa_ (Ellis) Batters et de quelques
    autres Rhodophycees Floridees. _Rev_. _Algol_. _N_._S_. 12:
    31-43.

Phillips, D.J. & Scott, J. 1981. Ultrastructure of cell
    division and reproductive differentiation of male
    plants in the Florideophyceae (Rhodophyta). Mitosis
    in _Dasya_ _baillouviana_. _Protoplasma_ 106: 329-341.

Polanshek, A.R. & West, J.A. 1977. Culture and
    hybridization studies on _Gigartina_ _papillata_
    (Rhodophyta). _J_. _Phycol_. 13: 141-149.

Pollock, E.G. 1969. Interzonal transplantation of embryos
    and mature plants of _Fucus_. _Proc_. _Int_. _Seaweed_ _Symp_.
    6: 345-356.

Provasoli, L. 1972. Effects of bacteria on seaweed
    morphology. _J_. _Phycol_. 8 (suppl.):10.

----- Pintner, I.J. 1964. Symbiotic relationships between
    microorganisms and seaweeds. _Am_. _J_. _Bot_. 51: 681.

----- 1964. Bacteria-induced polymorphism in an axenic
    laboratory strain of _Ulva_ _lactuca_. _Proc_. _Int_. _Seaweed_
    Symp. 8: 231.

----- 1976. Bacteria-induced polymorphism in an axenic
    culture. I. Occurrence of _Enteromorpha_-like plants in
    haploid clones. _J_. _Phycol_. 13: 133-140.

Pueschel, C.M. 1979. Ultrastructure of tetrasporogenesis
in Palmaria palmata (Rhodophyta). J. Phycol. 15:
409-424.

----- 1980. Pit-connections and translocations in red
algae. Science 209: 422-423.

----- 1987. Absence of cap membranes as a characteristic
of some red algal orders. J. Phycol. 23: 150-156.

----- & Cole, K.M. 1982. Rhodophycean pit-plugs: an
ultrastructural survey with taxonomic implications.
Am. J. Bot. 69: 703-720.

----- 1985. Ultrastructure of germinating carpospores of
Porphyra variegata (Kjellm.) Hus. (Bangiales,
Rhodophyta). J. Phycol. 21: 146-154.

----- & Magne, F. 1987. Pit-plugs and other
ultrastructural features of systematic value in
Rhodochaete parvula (Rhodophyta, Rhodochaetales).
Cryptogam. Algol. 8: 201-209.

Ramus, J. 1969a. The development sequence of the marine
red alga Pseudogloiophloea in culture. Univ. Calif.
Publ. Bot. 52: 1-42.

----- 1969b. Pit-connection formation in the red alga
Pseudogloiophloea. J. Phycol. 5: 57-63.

----- 1969c. Dimorphic pit-connections in the red alga
Pseudogloiophloea. J. Cell Biol. 41: 340-345.

----- Beale, S.I., Manzerall, D. & Howard, K.L. 1976.
Changes in photosynthetic pigment concentration in
seaweeds as a function of water depth. Mar. Biol.
37: 223-229.

Rees, D.A. 1965. Carbohydrate sulphates. Ann. Rep. Chem.
Soc. 62: 257-273.

Richards, H.H. 1901. Ceramothamnion codii, a new
rhodophyceous alga. Bull. Torrey Bot. Club. 28:
257-265.

Richardson, N. 1970. Studies on the photobiology of Bangia
fuscopurpurea. J. Phycol. 6: 215-219.

----- 1972. Spore classification in the genera Bangia and
Porphyra. Br. phycol. J. 7: 49-51.

----- & Dixon, P.S. 1968. Life history of Bangia
fuscopurpurea (Dillw.) Lyngb. in culture. Nature 218:
496-497.

Rosenvinge, L.K. 1888. Sur la formation de spores
secondaires chez les Polysiphonia. Bot. Tidsskr. 17:
10-19.

----- 1924. The marine algae of Denmark. Contributions to
their natural history... Part III. Rhodophyceae
(Ceramiales). K. Dan. Vidensk. Selsk. Skr. 7. Raekke,
Naturvidensk. og Mathem., Afd. VII. 3: 285-487, 3
pls.

----- 1930. The marine algae of Denmark. Contributions to their natural history. Part IV. Rhodophyceae (Gigartinales, Rhodymeniales, Nemastomatales). K. Dan. Vidensk. Selsk. Skr. 7. Raekke, Naturvidensk. og Mathem., Afd. VII, 4: 487-637, 1 pl.

Rueness, J. 1968. Paraspores from Plumaria elegans (Bonnem.) Schmitz in culture. Norw. J. Bot. 15: 220-224.

----- 1973a. Culture and field observations on growth and reproduction of Ceramium strictum Harv. from the Oslofjord, Norway. Norw. J. Bot. 20: 61-65.

----- 1973b. Speciation in Polysiphonia (Rhodophyceae, Ceramiales) in view of hybridization experiments: P.hemisphaerica and P.boldii. Phycologia 12: 107-109.

----- 1978. Hybridization in red algae. In: D.E.G. Irvine & J.H. Price (eds.), Modern Approaches to the Taxonomy of Red and Brown Algae. Academic Press, New York. Pp. 247-262.

----- & Rueness, M. 1973. Life history and nuclear phases of Anthithamnion tenuissinum, with special reference to plants bearing both tetrasporangia and spermatangia. Norw. J. Bot. 20: 205-210.

----- 1975. Genetic control of morphogenesis in two varieties of <u>Antithamnion</u> <u>plumula</u> (Rhodophyceae, Ceramiales). <u>Phycologia</u> 14: 81-85.

----- 1982. Hybridization and morphogenesis in <u>Callithamnion</u> <u>hookeri</u> (Dillw.) S.F.Gray (Rhodophyceae, Ceramiales) from disjunct north-eastern Atlantic populations. <u>Phycologia</u> 21: 137-144.

----- 1985. Regular and irregular sequences in the life history of <u>Callithamniom</u> <u>tetragonum</u> (Rhodophyta, Ceramiales). <u>Br</u>. <u>phycol</u>. <u>J</u>. 20: 329-333.

Russell, G. 1963. A study in populations of <u>Pilayella</u> <u>littoralis</u>. <u>J</u>. <u>Mar</u>. <u>Biol</u>. <u>Assoc</u>. <u>U.K</u>. 43: 469-483.

Saito, Y. 1969. On morphological distinctions of some species of Pacific North American <u>Laurencia</u>. <u>Phycologia</u> 8: 85-90.

Santelices, B. 1978. The morphological variation of <u>Pterocladia</u> <u>coerulescens</u> (Gelidiales, Rhodophyta) in Hawaii. <u>Phycologia</u> 17: 53-59.

Schmitz, F. 1889. Systematische Uebersicht der bischer bekannten Gattungen der Florideen. <u>Flora</u> 72: 435-456, pl. 21.

----- & Hauptfleisch, P. 1897. Ceramiaceae. In: A. Engler
& K. Prantl, Die natuerlichen Pflanzenfamilien....1:
481-504, Figs. 267-272.

Schornstein, K.L. & Scott, J. 1981. Ultrastructure of cell
division in the unicellular red alga Porphyridium
purpureum. Can. J. Bot. 60: 85-97.

Scott, J. 1983. Mitosis in the freshwater red alga
Batrachospermum ectocarpum. Protoplasma 118: 56-70.

Scott, J.L. & Thomas, J.P. 1975. Electron microscope
observations of telophase II in the Florideophyceae.
J. Phycol. 11: 474-476.

----- Bosco, C., Schornstein, K. & Thomas, J. 1980.
Ultrastructure of cell division and reproductive
differentiation of male plants in the Florideophyceae
(Rhodophyta): Cell division in Polysiphonia. J.
Phycol. 16: 507-524.

----- Phillips, D. & Thomas, J. 1981. Polar rings are
persistent organelles in interphase vegetative cells
of Polysiphonia harveyi Bailey (Rhodophyta,
Ceramiales). Phycologia 20: 333-337.

Setchell, W.A. & Gardner, N.L. 1930. Marine algae of the
Revillagigedo Islands expedition of 1925. Proc.
Calif. Acad. Sci. 19: 109-215.

Sheath, R.G., Van Alstyne, K.L. & Cole, K.l. 1985. Distribution, seasonality and reproductive phenology on <u>Bangia</u> <u>atropurpurea</u> (Rhodophyta) in Rhode Island, U.S.A. <u>J</u>. <u>Phycol</u>. 21: 297-303.

----- Cole, K.M. & Hynes, B.J. 1987. Ultrastructure of polysporogenesis in <u>Pleonosporium</u> <u>vancouverianum</u> (Ceramiaceae, Rhodophyta). <u>Phycologia</u> 26: 1-8.

Sideman, E.J. & Mathieson, A.C. 1985. Morphological variation within and between natural populations of non-tide pool <u>Fucus</u> <u>distichus</u> (Phaeophyta) in New England. <u>J</u>. <u>Phycol</u>. 21: 250-257.

Siegel, S. & Castellan Jr., N.J. 1988. <u>Nonparametric</u> <u>Statistics</u> <u>for</u> <u>the</u> <u>Behavioral</u> <u>Sciences</u>. McGraw-Hill, New York, 399 pp.

Silva, P.C. 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. <u>Univ</u>. <u>Calif</u>. <u>Publ</u>. <u>Bot</u>. 25: 241-324.

Sokal, R.R. & Rohlf, F.J. 1969. <u>Biometry</u>. W.H. Freeman & Company, San Francisco, 776 pp.

Sommerfield, M.R. & Nichols, H.W. 1970. Comparative studies in the genus <u>Porphyridium</u> Naegeli. <u>J</u>. <u>Phycol</u>. 6: 67-78.

Stegenga, H. & Mulder, S. 1979. Remarks on the <u>Audouniella</u> <u>microscopica</u> (Naeg.) Woelkerling complex with a brief

survey of the genus _Chromastrum_ Papenfuss
(Rhodophyta, Nemaliales). _Acta_ _Bot_. _Neerl_. 28:
289-311.

----- & Van Erp, N.D. 1979. Morphological variation in the
genus _Acrochaetium_ (Rhodophyta, Nemaliales). _Acta_
Bot. _Neerl_. 28: 425-448.

Stewart, J.G. 1968. Morphological variation in _Pterocladia_
pyramidale. _J_. _Phycol_. 4: 76-84.

Steneck, R.S. & Adey, W.H. 1976. The role of environment
in control of morphology in _Lithophyllum_ _congestum_, a
Caribbean algal ridge builder. _Bot_. _Mar_. 19: 197-215.

Stosch von, H.A. 1965. The sporophyte of _Liagora_ _farinosa_
Lamour. _Br_. _phycol_. _Bull_. 2: 486-496.

Suh, Y. & Lee, I.K. 1984. Morphology and reproduction of
some species of _Ceramium_ (Rhodophyta) in culture.
Korean _J_. _Bot_. 27: 163-171.

Sundene, O. 1958. Interfertility between forms of
Laminaria _digitata_. _Nytt_ _Mag_. _Bot_. (_Oslo_) 6: 121-128.

----- 1962. Growth in the sea of _Laminaria_ _digitata_
sporophytes from culture. _Nytt_ _Mag_. _Bot_. (_Oslo_) 9:
5-24.

Svedelius, N. 1906. Reports on the marine algae from
Ceylon. Ecological and systematic studies of the

Ceylon species of _Caulerpa_. _Rep_. _Ceylon_ _Mar_. _Biol_.
Lab. 4: 81-144.

Taylor, W.R. 1960. _Marine_ _Algae_ _of_ _the_ _Eastern_ _tropical_
and _subtropical_ _coasts_ _of_ _the_ _Americas_. Univ.
Michigan Press, Ann Arbor. 870 pp.

Tomita, G. & Rabinowitch, E. 1982. Excitation energy
transfer between pigments in photosynthetic cells.
Biophys. _J_. 2: 483-499.

Tozun, B. 1974. Nuclear division in the red alga _Chondria_
nidifica and _Chondria_ _tenuissima_. _Br_. _phycol_. _J_. 9:
363-370.

Van der Meer, J.P. & Todd, E.R. 1977. Genetics of
Gracilaria sp. (Rhodophyceae, Gigartinales) IV.
Mitotic recombination and its relationship to mixed
phases in the life history. _Can_. _J_. _Bot_. 55:
2810-2817.

----- 1980. The life history of _Palmaria_ _palmata_ in
culture. A new type for the Rhodophyta. _Can_. _J_. _Bot_.
58: 1250-1256.

Waaland, J.R., Waaland, S.D. & Bates, G. 1974.
Chloroplast structure and pigment composition in the
red alga _Griffithsia_ _pacifica_: regulation by light
intensity. _J_. _Phycol_. 10: 193-199.

West, J.A. 1968. Morphology and reproduction of the red
    alga <u>Acrochaetium</u> <u>pectinatum</u> in culture. <u>J</u>. <u>Phycol</u>.
    4: 89-99.

----- 1969. Observations on four rare marine microalgae
    from Hawaii. <u>Phycologia</u> 8: 187-192.

----- 1970. The life history of <u>Rhodochorton</u> <u>concrescens</u>
    in culture. <u>Br</u>. <u>phycol</u>. <u>J</u>. 5: 179-186.

----- 1971. Environmental control of hair and sporangial
    formation in the marine red alga <u>Acrochaetium</u>
    <u>proskaueri</u> sp. nov. <u>Proc</u>. <u>Int</u>. <u>Seaweed</u> <u>Symp</u>. 7:
    377-384.

----- 1972. The life history of <u>Petrocelis</u> <u>franciscana</u>.
    <u>Br</u>. <u>phycol</u>. <u>J</u>. 7: 299-308.

----- & Hommersand, M.H. 1981. Rhodophyta life histories.
    <u>In</u>: C.S. Lobban & M.J. Wynne (eds.), <u>The</u> <u>Biology</u> <u>of</u>
    <u>Seaweeds</u>. Univ. Calif. Press, Berkeley, pp. 133-193.

----- & Norris, R.E. 1966. Unusual phenomena in the life
    histories of Floridae in culture. <u>J</u>. <u>Phycol</u>. 2:
    54-57.

----- Polanshek, A.R. & Shevlin, D.E. 1978. Field and
    culture studies on <u>Gigartina</u> <u>agardhii</u> (Rhodophyta).
    <u>J</u>. <u>Phycol</u>. 14: 416-426.

Wetherbee, R. 1979. "Transfer-connections": specialized pathways for nutrient translocation in red algae? _Science_ 204: 858-859.

----- & Kraft, G.T. 1981. Morphological and fine structural features of pit-connections in _Cryptonemia_ sp., a highly differentiated marine red alga from Australia. _Protoplasma_ 106: 167-172.

Whittick, A. 1978. The life history and phenology of _Callithamnion corymbosum_ (Rhodophyta, Ceramiaceae). in Newfoundland. _Can. J. Bot._ 56: 2497-2499.

Wollaston, E.M. 1968. Morphology and taxonomy of southern Australian genera of Crouanieae Schmitz (Ceramiaceae, Rhodophyta). _Aust. J. Bot._ 16: 217-417.

Wollman, F.A. 1979. Ultrastructural comparison of _Cyanidium caldarium_ wild type and III-C mutant lacking phycobilisomes. _Plant Physiol._ 63: 375-381.

Womersley, H.B.S. 1978. Southern Australian species of _Ceramium_ Roth (Rhodophyta). _Aust. J. Mar. Freshwater Res._ 29: 205-257.

----- & Cartledge, S.A. 1975. The southern Australian species of _Spyridia_ (Ceramiaceae: Rhodophyta). _Trans. Royal Soc. South Australia_ 99: 221-234.

CHAPTER II

TAXONOMY OF THE GENUS CERAMIUM IN HAWAII

Abstract

The scarcity of studies on the species of
Ceramium in the Hawaiian Islands, and the apparent
variability of some species in this genus has led to
research on the taxonomy and morphology of the local
species.

The definition and evaluation of morphological
characters in Ceramium taxa has resulted in the
recognition of 11 species of this genus present in Oahu.
Six of these species were previously described or
recorded in the tropical and subtropical North Pacific.
Five species are being reported from Hawaii for the first
time. This indicates floristic similarities with the
marine floras of southern North America and Central
America on one hand, southern Japan on the other in
addition to the Pacific Islands between the east and west
coasts of the North Pacific ocean. Two of the species
reported for Oahu in this study have not been previously

described and other three are of uncertain identification because of the scarcity and condition of the specimens collected.

Small size, a thallus of distinct cortical bands and two types of attachment structures characterize all known species of <u>Ceramium</u>. Most of the vegetative characters show variability within and between individuals, the degree of this variability depending on the particular character and on the species examined. The evaluation of the morphological variation of each species using a large number of specimens also proved to be extremely useful for comparison with counterparts from other parts of the world. The arrangement of cortical cells combined with the nature of the pericentral cells at the nodes are the most reliable and diagnostically valuable of all characters. Results from this study show that most characters should be used in combination and not by themselves for the recognition of species.

Introduction

Approximately 55 species of <u>Ceramium</u> Roth, 1797, p. 146 <u>nom.cons</u>. (Ceramiaceae, Ceramiales) have been

reported for the tropical and subtropical North Pacific
Ocean. This number represents about one half of the
described species. Detailed descriptions as well as brief
mention in accounts of marine floras of this region
include representatives mainly from the Pacific coast of
North and Central America (Dawson, 1944; 1945a; 1945b;
1949; 1953; 1954a; 1954b; 1954c; 1957; 1961; 1962;
Hollenberg, 1948; Setchell & Gardner, 1924; 1930; 1937;
Abbott & Hollenberg, 1976) and southern Japan (Yendo,
1917; Nakamura, 1950; 1965; Itono, 1972: 1977). The east
and west coasts of the North Pacific have about one-third
of the _Ceramium_ species in common which suggests that
these species are widespread throughout the North Pacific
Ocean. In addition the few studies of the marine flora of
North Pacific tropical and subtropical islands (Dawson,
1956; 1957; Tsuda, 1965; 1966; Hollenberg, 1968; Trono,
1969; Tsuda & Trono, 1968) indicate that almost the total
number of _Ceramium_ species recorded for these islands are
in common with those recorded for the coast of southern
California, the Gulf of California and Pacific Mexico, and
that 50% of these species are also reported from the
coasts of southern Japan.

Most _Ceramium_ species, of tropical and
subtropical distribution, show few affinities with the

North Atlantic Ocean or the Mediterranean Sea (Richards, 1901; Boergesen, 1930; Mazoyer, 1938; Feldmann-Mazoyer, 1940; Harvey, 1853; Funk, 1955; Athanasiadis, 1987), as well as with the flora in coldwater areas in the North Pacific Ocean. Yet, three of the species have a cosmopolitan distribution, _Ceramium_ _codii_ (Richards) G. Mazoyer, _C_. _rubrum_ (Hudson) C. Agardh, and _C_. _flaccidum_ (Kuetzing) Ardissone. Although a high level of endemism seems to be present for species from waters around southern North America and Japan, this may well be the result of the scarcity of studies rather than the rarity of specimens.

Further assessment of the genus which emphasizes recognition and interpretation of seasonal and environmental modifications of the thallus (Dixon, 1960; Womersley, 1978; Garbary et al., 1978; Suh & Lee, 1984) is an approach which contributed to a clarification of the taxonomic standing of species in _Ceramium_. As a result, some of the originally described species have been reduced to synonymy, which thereby modifies the interpretation of the species distribution. This genus is currently undergoing a series of changes in species delimitations derived from the critical examination of the diagnostic

features (Garbary et al, 1978; Suh & Lee, 1984; Boo & Lee, 1985).

In Hawaii, collections of Ceramium species are on record from about 1866 (Abbott, 1980) although only a few records of the genus have been published (MacCaughey, 1918; Hollenberg, 1968; Doty et al, 1974; Abbott, 1974; 1980). Ceramium is ubiquitous around the island of Oahu, appearing in almost any collection made, mainly as an epiphyte on macroalgae. In spite of its abundance, the species are not well-characterized for the flora in the island nor have their variabilities in the field or the characteristics of their reproductive features been clarified.

The present account of the species of Ceramium is based on a study of specimens collected around the island of Oahu as well as from collections made by others on other Hawaiian Islands. The aim of the present study has been to characterize the species based on large numbers of specimens, with the intention of compiling information on the intrapopulational variation of the diagnostic features, and to thoroughly describe reproductive material. The present status of the species is also discussed. In addition, the geographic distribution of

the genus is analyzed for the North Pacific in view of the results obtained from this study of Hawaiian species.

Materials and methods

Collections were made at selected sites around the island of Oahu (Fig. 2.1). Localities were chosen based on their habitat diversity and their accessibility. First, each site was haphazardly sampled and the algal collections were later sorted and examined in the laboratory under a dissecting microscope. Notes were made on the specific locations where Ceramium species were found, and if epiphytic, host species were noted. Subsequent collections were made at relatively accessible intertidal and subtidal sites in which plants were most abundant.

Several characteristics of Ceramium species affect the sampling regime. One aspect is thallus size, small species are up to 2.6 mm while tall species are up to 35 mm. A second constraint is that these algae are usually either strongly attached or entangled with other algae or sediment. This often results in the collection of specimens with basal portions and/or attachment structures incomplete. Therefore, internodal and nodal

information is based on two sets of measurements: 1) those made on the most basal of the plant, when this was collected undamaged and 2) those made from the first or second basalmost dichotomies. In addition, the entanglement of the branches does not allow the clear delimitation of one individual plant from another. As a way of handling this difficulty, a turf of axes, defined as all branches in 1 cm^2 area, was collected from the macroalgal host or cluster of algae. This unit was defined as one individual.

These collections were preserved in 2-5% buffered Formalin/seawater, dried as herbarium specimens, or fixed and preserved as whole mounts in permanent microscope slides. Observations and measurements were made using a Zeiss light microscope.

Thalli were liquid preserved with 10% Formalin/seawater. This fixation procedure of specimens minimized axial cells shrinkage.

Tissues were stained with 1% Aniline Blue in 95% ethanol slightly acidified with hydrochloric acid on Formalin preserved specimens (Tsuda & Abbott, 1985). This procedure differentially stained axial cells from cortical cells in Ceramium, and allowed observations of node structure. Primary pit-connections become visable

with this stain procedure. Although a staining procedure
with 1% Methylene blue in distilled water was used at the
beginning of this study, it was discontinued because of
its tendency to overstain.

After staining procedures were carried out, the
material was mounted in 25% solution of clear Karo corn
syrup (Trade Mark) in distilled water with phenol added as
a preservative.

Node and internode measurements, cell sizes,
number of cortical cell rows, number of cells per spine,
etc., are given in ranges in which the numbers between
parenthesis indicate the extreme values of the entire
range and the numbers outside the parenthesis are the
extremes that include 75% of the individuals recorded.

Results

The following are the results obtained from the
collection of _Ceramium_ specimens around the island of
Oahu during this research project, and includes the
observation of previously collected material on other
islands. A brief generic description is provided followed
by a key to the species included in this study. All

measurements included in this key are based on features
located above the first or second basalmost dichotomies.

Description of the genus.

Thallus of uniaxial construction, wholly erect or
prostrate and erect, rarely only prostrate, 0.1-30.0 cm
in length; axes terete, 0.1-1.5 mm in diameter,
pseudodichotomously or irregularly branched,
differentiated into axial cells and cortex; axial cells,
ovoid or cylindrical, faintly pigmented; cortex formed by
the condensation of filaments of limited growth, arranged
in bands which entirely or only partially cover the axial
cells.

Tetrasporangia borne laterally on filaments of
limited growth, either on their basal cells (pericentral
cells) or on other cells of the filament (cortical cells);
partially or completely embedded, tetrahedral or cruciate,
naked or with an involucrum.

Sexual thalli commonly dioecious, rarely
monoecious; spermatangia hyaline, developing superficially
but densely from the ultimate cells of the filaments of
limited growth; carpogonial branches and auxiliary cells
developing from the basal cells of the filaments of

limited growth near to the apex; carposporophyte
protruding, naked, sessile, subtended by a number of
adventitious branches; Carposporangia arranged in several
gonimolobes, usually maturing sequentially.

Key to the Hawaiian species of Ceramium.

1. Thallus consisting of only upright axes, in some cases
    with their basal portion parallel to the substrate
    becoming erect only in their upper portion, reaching
    up to 35 mm in height...................................2

1. Thallus clearly differentiated into a prostrate axis
    from which upright branches are adventitiously
    originated, upright branches 0.1 to 2.5 mm in height
    (occasionally up to 6 mm high)........................3

  2. Branching pattern dichotomous in the upper portion of
      the axes becoming alternate towards the base of the
      thallus, basipetal cortical cells initially
      horizontally elongated distinct from acropetal
      roundish cells....................................4

2. Branching pattern clearly dichotomous throughout the thallus, nodes with no initial formation of basipetal horizontally elongated cortical cells, but cortical cells more or less uniform in shape throughout the node...5

4. Nodes non-tumid to slightly tumid, long internodes (30) 80-300 (315) um, ocassionally gland cells present in acropetal position in nodes, very seldom clavate elongate sac-like hairs, tetrasporangia involucrate, protruding.................<u>C</u>. <u>flaccidum</u>

4. Nodes strongly tumid, short internodes (2) 8-20 (26) um,·gland cells absent, clavate elongate sac-like hairs abaxial to whorled in nodes, tetrasporangia involucrate, embedded in the cortex...............
.................................<u>C</u>. <u>fimbriatum</u>

5. Pericentral cells partially visible in well-developed nodes...................................6

5. Pericentral cells not or rarely visible in well-developed nodes.....................................7

6. Pericentral cells slightly flattened horizontally, internodes as long as broad, small adventitious branches extremely abundant (> 10 per plant)......

.................................._Ceramium_ sp.3

6. Pericentral cells usually rounded or slightly irregular in shape with rounded margins, not horizontally flattened, internodes not as long as broad except when underdeveloped, adventitious branches seldom present or abundant but as thick as main true branches and sometimes as long as these.......................8

8. Plants 2-15 mm in height, full-developed internodes always shorter than broad, tetrasporangia naked or involucrate, in whorls or scattered throughout the node...................9

8. Plants ranging from 9 to 35 mm tall, full-developed internodes, 1-5 times their diameter in length, tetrasporangia naked in whorls protruding from upper half of nodes............_Ceramium_ sp.1

9. Plants 2-9 mm tall, adventitious branches common
axial cells ovoid and horizontally flattened,
3-4 cortical cell rows (ocassionally up to 6-7
rows), gland cells absent, tetrasporangia
involucrate, arranged in whorls on upper half of
nodes........................... C. clarionensis

9. Plants 4-15 mm tall, adventitious branches very
ocassional, internodes barely visible, 3-6
cortical cell rows, gland cells common,
scattered throughout the node, tetrasporangia
naked, adaxial or around node (and along its
entire length)........................C. aduncum

7. Non-deciduous spines present, 3-6 cells long,
arranged in whorls at the upper part of the
nodes; cortical cells irregularly shaped,
mostly cuboidal....................C. hamatispinum

7. Spines absent, narrow cortical cells arranged
compactly in nodes, vertically elongated, inner
and outer edges of apical portion dentate......
....10

10. Internodes long and narrow, frequently 100 - 120
    um in diameter and 170 - 325 um in length........
    ...._Ceramium_ sp.4

10. Internodes broad and short, frequently 160 - 220
    um in diameter and 50 - 140 um in length........
    ...._Ceramium_ sp.5

3. Upright branches 1-2.5 mm tall, commonly no more than
    3 cortical cell rows, acropetal cortical cells
    bearing one-celled blunt projections, nodes tumid,
    ovate to obovate tetrasporangia, protruding in
    whorls, involucrate......................_Ceramium_ sp.2

3. Upright branches 0.1-6 mm tall, 1 - 2 cortical cell
    rows, no projections present in nodes, nodes
    non-tumid, tetrasporangia with a spur-like lower
    portion, 1 to 3 or in whorls, naked..................
    ...._C_.affine

Description of each of the species recorded in Hawaii.

The following are the descriptions of each of the species of Ceramium recorded in Hawaii, including their synonyms and records, an evaluation of their morphological variability, an evaluation of their status as species in comparison to other similar species of the genus, the specimens examined and their geographic distribution.

Ceramium hamatispinum Dawson

Pl.I, Figs. 1-4

Dawson,1950: 122, pl.3, figs. 20-22; 1962: 57, pl. 22, figs. 2-4; Hollenberg, 1968: 75, fig. 2.

Plants range from 3.0 mm to slightly over 10 mm in height; the branching pattern is regularly dichotomous, with adventitious branches occasionally formed. Axes have forcipate apices (Pl. I, Fig.1). Plants are attached to the substratum by means of long, non-branched rhizoids with blunt apices and by short,

one-celled rhizoids with basal digitate projections, both types arise adventitiously from the lowermost basal nodes.

Plants are epiphytic or saxicolous, forming entangled mats with other filamentous algae making difficult their detachment from the substrate because of the intricacy of attachment to other algae, other marine organisms, or debris.

Internodes are (60)108-132(180) um diameter and (48)84-180(420) um long in basalmost portions of the thallus, whereas they range (48)84-132(168) um in diameter and (12)60-132(396) um in length between the first and the second dichotomies from the base.

Nodes are composed of 3-10 cortical cell rows, 6-7 rows being most frequently seen; non-tumid or slightly tumid in most specimens (except close to the apices or in tetrasporangial plants where tetraspores disrupt the normal organization of the node). Nodes are (72)108-132(180) um diameter and (12)60-84(108) um long in the most basal portion of the plants, while they are (60)84-144(168)um in diameter and (12)48-84(96) um in length between the first and second dichotomies. Cortical cells are small, 10-11(12) um diameter, irregularly shaped, but mostly cuboidal and uniform in size throughout the node except in the last basipetal row and the highest

acropetal row where cells are smaller in size and somewhat vertically elongated (Pl. I, Fig.3).

Conspicuous, non-deciduous, robust spines are present in whorls (Pl. I, Fig.2) located in the upper middle portion of the nodes. Each spine consists of 3 to 6 cells, most frequently 5-celled, and oriented upwards, although sometimes this orientation changes because tetrasporangia are present. Spines are (43)50-80(92) um long, often occurring fully developed in nodal regions close to the apex where the nodal structure is masked (Pl. I, Fig. 2).

Tetrasporangial plants are common in the field, with tetrasporangia spherical to obovate, (31)34-53(62) um in diameter, involucrate, arising abaxially (Pl. I, Fig.4), later forming whorls around the nodes. Occasionally, one to several tetrasporangia are borne on the basal node of a dichotomy.

No female or cystocarpic plants were found.

Two spermatangial plants were collected. Spermatangia cover the entire nodes throughout the thallus except for those nearest the apices. One of these specimens (IAA 12544) shows fewer cell rows per node than those of sterile and tetrasporangial plants.

Evaluation of variability:

A few specimens were found growing on ropes at Malaekahana, northern Oahu Island (21º39'N; 157º56'E). These plants, although showing the general features of Ceramium hamatispinum (Dawson, 1950; 1962; Hollenberg, 1968) as well as those of other specimen collected during this study, were up to 10 cm tall, ten times larger than the tallest plants collected elsewhere. This size increase may be related to the type of substratum, e.g. ropes versus other algae.

The overall appearance of the plants is variable depending upon the length and diameter of nodes and internodes. Among the specimens collected, two morphological groups were detected, slender plants with long internodes alternating with poorly developed nodes (3 to 4 cortical cell rows), and coarse-habit plants with short internodes and wide and long nodes.

Most plants collected during this study showed the coarse habit (e.g. IM 750B, Makaha Beach Park, on eroded reef bench) and fit well in the ranges described above for nodal and internodal features. The large ranges of length and diameter for basal internodes as well as for internodes from the first and second dichotomies from the

base, indicate that axial cell magnitudes are features too
variable to characterize this species. Three specimens
(MSD 29396, IM 742c, IM 743b) are at the extreme ends of
the internodal ranges for the basal parts of the species;
one shows longer internodes, 276-420 um, than the majority
of the plants, and had broader internodes, 156-180 um,
than average. Less variable than internodes, nodal sizes
are fairly uniform among individuals except for a few
specimens. Dawson (1950) describes a sterile specimen
(EYD 3706) whose diameter in the old portion of the
thallus was 90-130 um. This diameter roughly approximates
the diameter of both nodes and internodes from the basal
portion of the Hawaiian plants. However, Hawaiian
material has nodes up to two times longer than the 40-60
um of the type specimen. The illustration of the type
specimen (Dawson, 1950, figs. 20-22) as well as shown by
an examination of other topotype material (EYD 10874 and
additional preserved material), indicates that c.
hamastipinum is a plant with slender filaments with long
internodes and few rows of nodal cells. This morphology,
although not that typical of most of the Hawaiian
specimens, was observed in some other Hawaiian specimens
(IAA 17173, IAA 18856, MSD 29396).

The most noticeable characteristic of the species is the presence of the whorled, robust, non-deciduous spines. The majority of the Hawaiian specimens exhibit 5 or 6-celled spines with only a very few with no spines, or any indication that these were either shed, or only developed partially (IAA 14870). A few Hawaiian plants show the 3-celled spines characteristic of the type and topotype material. The hooked tips of the spines described for the Mexican material (Dawson, 1950; 1962) were not observed in the Hawaiian plants. Hollenberg's (1968) specimen (GJH.65-119) collected at Hanauma Bay, Oahu shows only a slight indication of spine curvature, and his description of a single tetrasporangial collection agrees well with the specimens collected during this study, although they show longer nodes (116 um vs. (12)60-84(108) um) and longer spines (100-116 um vs. (43)50-80(92) um).

Evaluation of the species:

Only two species of _Ceramium_ that show nodal bands bearing conspicuous non-deciduous spines arranged in whorls have been recorded for the North Pacific (Hollenberg, 1968, Itono, 1972). They are _C_. _hamatispinum_

Dawson and C. ciliatum (Ellis) Ducluzeau. Ceramium ciliatum exhibits the same dimorphism of specimens with 3-celled spines, characteristic of the Atlantic Ocean specimens (var. ciliatum) and 5 or 8-celled spines in plants from the Mediterranean Sea (var. robustum), that respectively characterize Mexican and Hawaiian representatives of C. hamatispinum. Descriptions of C. ciliatum (Ellis) Ducluz. var. robustum G. Mazoyer from Japan (Itono, 1972) fit well with the Hawaiian material of C. hamatispinum. Unfortunately Itono did not include ranges of nodal and internodal features. Itono (1972) separated the two species on the basis of presence/absence of hooked spines which in view of morphological variation in the genus, does not offer a stable basis for species distinction. On the other hand, C. ciliatum var. robustum from the Mediterranean (Mazoyer, 1938; Feldmann-Mazoyer, 1940) was described as commonly 5-6(15) cm tall and fairly thick (175-400 um) compared to C. hamatispinum. In both species the spines are formed from a basal cell originating from a pericentral cell resulting in a modified determinate lateral (Dixon, 1960). The overall similarities in the morphotypes of both species suggest a relationship which can only be clarified with the comparison of both type materials.

List of specimens studied:

Topotype material: Mexico, Nayarit, Mira Mar, drift along beach, leg. E.Y.Dawson, June 4, 1952, US 083952, preserved material in slides # 445 & 446 and vial # 1344 (EYD 10874).

Hawaiian Islands, Oahu: Kaloko Point, low intertidal on turf, leg. I.A.Abbott, August 26, 1976, IAA 14821; Halona Point, low intertidal on coral, leg. I.A.Abbott & R.Norris, November 2, 1961, IAA 14870; Waikiki, west side of the Natatorium, subtidal on reef flat, 1.5-2 m depth, epiphyte on Gracilaria coronopifolia, leg. I.Meneses, June, 1986, IM 524, 525; Makaha, subtidal on eroded limestone, 7-12 m depth, epiphytic on Dictyota sp., leg. L.M.Hodgson, August 5, 1988, IA 18856; Makaha caverns, 20-40' depth, leg. L.M.Hodgson, August 5, 1988, IAA 18869; Keeau Beach Park, on eroded reef bench partially covered with sand, exposed intertidal, leg. I.Meneses, March, 1988, IM 742A, 742B, 742C, 743A, 743B, 743C, 744A, 744B, 745, 746A, 746B, 747, 748A, 748B, 750A, 750B, 751, 752.

Maui: Launiupoko, in drift, leg. I.A.Abbott, August 31, 1976, IAA 12544; Ahihi Bay, lava rock tide pools and

channels receiving brunt of waves, with _Laurencia_ and
Jania, in small turf, leg. I.A.Abbott, November 1, 1977,
IAA 13061; Kauiki Head, 4-8 ft. depth, on _Amansia_ blades
and on _Laurencia majuscula_ epiphytic on _Amansia_, mixed
with other epiphytes, leg. I.A.Abbott, August 26, 1976,
IAA 18004a; Hana Bay, intertidal and edges of pools
exposed to surge, leg. I.A.Abbott, August 26, 1976, IAA
14821; Kainalimu Bay, attached to articulated coralline
algae growing on exposed limestone, leg. K. McDermid,
March 29, 1984, IAA 17173.

Geographic distribution:

Pacific coast of Mexico, Nayarit, Mira Mar -type locality
-(Dawson, 1950; 1962); Hawaiian Islands, Oahu and Maui
Islands (Hollenberg, 1968 and this study).

<div align="center">

Ceramium aduncum Nakamura

Pl. II, figs. 1-4

</div>

Nakamura, 1950: 155, figs. 2b,3; 1965: 119-180, pl. II,
figs. 1-2; Itono, 1972: 81, fig. 11a.
= _C. circinatum_ Yendo (non Agardh), Yendo, 1917: 92-93.

= *Ceramium* sp. nov.? Setchell & Gardner, Setchell &

Gardner, 1930:

   173, pl.7, fig. 25.

= *C*. *clarionensis* Dawson (non Setchell & Gardner), Dawson,

1950:

   134, pl.4, fig. 29; 1954b: 448, fig. 55K; 1956: 54;

1961: 440; 1962:

   53, pl.18, figs. 5-6.

   Plants 4-15 mm in height, basal portions

creeping on the substrate, erect portions ending in

strongly forcipate apices with their outer edge dentate;

basal portion attached by means of multicellular rhizoids,

usually up to three cells long, (9.6)16 to 22(30) um

thick, ending in a blunt apex or in a discoid base with

small digitations. Branching is dichotomous, mature

plants not exceeding more than 6 dichotomies along the

entire thallus. Adventitious branches are not frequent,

if present up to 4 per plant. Nodes are far apart in the

basal portions of the plant; whereas they are become

closer because internodes are shorter towards the upper

part of the axes (Pl. II, Fig.1) and barely visible at the

apex. Internodes are nearly up to 1.5 times as long as

wide, in upright portions they are as long as wide. The

internodal diameter ranges (128)160-243(278) um and the
internodal length is (22.4)94-176(291) um in the lower
creeping portion of the plant. In the upper portions
internodes are slightly smaller, ranging (120)144-240(252)
um in diameter and 12-108(240) um in length. Nodes are
slightly protruding, their diameter not exceeding 1.9
times the diameter of the internodes, consisting of a
median row of large cells with 3 to 6 layers of outer
smaller cells which are irregularly arranged. Nodes are
(32)170-278(300) um diameter and (38)64-163(176) um long
in basal portions of the plant; (132)144-240(276) um
diameter and 48-144(156) um long in upright portions.
Cortical cells are roundish to somewhat angular in shape
except for those located in the lowest nodal row, where
they are vertically elongated; ranging (12.5)15-19(25) um
for the long axis and (5)6-9 um for the short axis. Gland
cells (Pl. II, Figs. 2 & 3) are abundantly scattered
throughout the nodes, especially in the younger parts of
the plant, but sometimes are scarce, measuring (15)19-31 x
(11)12.5-19(20) um.

Only tetrasporangial and sterile plants were
found. Tetrasporangia are scattered in the nodes, and are
borne adaxially on cortical cells first, and later around
the entire node (Pl. II, Fig.4). They are rounded, with a

thick wall, (38.4)42-48(51.2) x 35.2-48(54.4) um and lack an involucrum.

Plants are epiphytic on species of <u>Galaxaura</u>, <u>Acanthophora</u> and <u>Gracilaria</u> or entangled with other algae that form small turfs on protected shallow subtidal reef flats.

Evaluation of variability:

Plants are consistently epiphytic and attached to their hosts by means of two types of rhizoids. The most common type is a long, 2 to 3-celled type with blunt apices. The less frwquent is a short, one-celled type with basal digitate projections. Rhizoids arise two or more per node in the creeping part of the thallus and do not occur on erect portions. The number of nodes producing rhizoids varies with the extent to which the thallus is prostrate. These plants never acquire a true morphological differentiation between prostrate and upright portions, as some other species of <u>Ceramium</u> do, except for the presence of rhizoids. The circinate (or forcipate) apices, which has been used as a distinguishing feature by Dawson (1954) are conspicuous when present.

The gradual development of axial cells from the bottom to the upper parts of the thallus results in longer and conspicuous internodes in the basal portion of the filament but are reduced and almost absent in the apical region. Variability of internodal measurements is similar for the basal portion and the portion between the first and second dichotomies from the base, but some individuals fall to one side or the other of the recorded ranges of diameter and length. Nodal cell size is less variable than size ranges for internodal cells, with a tendency to increase proportionally in both basal and upper parts of the plant.

The most distinctive characteristics of this species are the presence of gland cells, although scarce in some specimens, and the scattered, mostly adaxial, arrangement of non-involucrate tetrasporangia produced by cortical cells. The overall appearance of the thallus, with forcipate apices, adaxial position of tetrasporangia and presence of gland cells is shared by the Hawaiian plants and the plants described from Goza, Sima Province, Japan (Nakamura, 1950; 1965) as _Ceramium aduncum_. The size of the tetrasporangia given by Nakamura (1950), 40-50 um in diameter, falls in the range of tetrasporangial size for Hawaiian material. Internodes in Nakamura's

description are 1 to 1.5 times longer than the diameter and the same is true for the specimens collected during this study. Nevertheless, the figures published in 1950 (Figs. 3a & 3f) show that the cortical bands in tetrasporangial plants are somewhat reduced when compared to the Hawaiian plants, whereas the broader nodes depicted for a cystocarpic plant seem more in agreement with the material collected on Oahu.

Evaluation of the species:

Ceramium aduncum was described by Nakamura (1950) and reported as widely distributed from Taiwan to Hokkaido. Nakamura mentions the similarity of his material with a possible new species of Ceramium reported by Setchell and Gardner (1930). This sterile specimen, from Guadalupe Island, was described by Setchell and Gardner in detail with respect to its vegetative structure. An illustration (Pl. 7, Fig. 25) was included, but the species was not given a name because of the scanty material available and its lack of reproductive organs. Examination of this material (UC 1462250/Mason 169) shows that it consists of one dichotomous branch with the typical well-developed Ceramium aduncum nodes and abundant

gland cells characteristic of this species. There is no doubt that the Ceramium sp. nov. of Setchell and Gardner (1930) corresponds to Ceramium aduncum Nakamura.

In the same publication, Setchell and Gardner (1930) described Ceramium clarionensis from Clarion Island as a species with distinctive protruding tetrasporangia, 65-75 um diameter, borne on the abaxial side of the filaments and bearing an involucrum. Dawson (1950) later reported Ceramium clarionensis for the Gulf of California and along the Pacific Coast of Southern and Baja California. However, Dawson's description and figures agree with descriptions of C. aduncum Nakamura and to the Ceramium sp. nov. of Setchell and Gardner (1930) and not to C. clarionensis of Setchell & ardner. Examination of material identified by Dawson as C.clarionensis (EYD 10964, 10909, 10890, 8600, 10944, 8377, 10767; US 006826, 006822, 006821, 006819, 006823, 006818, 006825) as well as the type material of Ceramium clarionensis clearly indicates that these are two different species, Dawson's material corresponding to C. aduncum of Nakamura, with its typical tetrasporangial arrangement and nodal characteristics.

Ceramium aduncum shows certain resemblances to Ceramium ornatum Setchell & Gardner (1930), a species

described from Isla Guadalupe as well. In spite of the similarities in the nodal structure, and in the occurrence of naked tetrasporangia in both species, C. ornatum lacks the typical gland cells of C. aduncum. In addition C. ornatum has tetrasporangia located in whorls, protruding from the upper half of the nodes. This differs from C. aduncum where tetrasporangia are adaxially scattered throughout the nodal length.

List of specimens studied:

as Ceramium clarionensis: Viet Nam, Cau Da, leg. E.Y.Dawson, January 29, 1953, US 03461 (EYD 11129)- in part C.aduncum and other Ceramium spp.

as Ceramium 'clarionense': Mexico. Isla Guadalupe: outer reef and pools at the extreme South end of the island, leg. E.Y.Dawson, December 18,1949, US 006818 (EYD 8377); 21/2 miles North of South Bluff, shore station on a -1.7 m tide, leg. E.Y.Dawson, December 20-21, 1949, US 006819 (EYD 8609); Baja California: Isla Asunción, leg. M.Neushul, August 25, 1957, US 006815 (EYD 20373); Bahía Santa María, Isla Magdalena, leg. E.Y.Dawson, May 6, 1955, US 006820 (EYD 13382) - in part 'C. clarionense' and C. sinicola var. sinicola (Dawson's annotation); Sinaloa,

Topolobampo, intertidal rocks near inner wharf, leg.
E.Y.Dawson, June 10, 1952, US 006821 (EYD 10890), US
006822 (EYD 10909); Punta Prieta, intertidal rocks, leg.
E.Y.Dawson, June 10, 1952, US 006823 (EYD 10944), US
006824 (EYD 10963)- only C. fimbriatum observed in the
slide-, US 006826 (EYD 10964); Oaxaca, Salina Cruz,
intertidal rocks, leg E.Y.Dawson, May 12, 1952, US 006825
(EYD 10767); vicinity of Punta Peñasco, leg. A.E.Dennis,
June 30, 1965, US 40834 (EYD 27517).

as Ceramium sp. nov.?: Mexico; Isla Guadalupe, intermixed
with Crouania attenuata, cast up at South Anchorage, leg.
H.L.Mason, 1925, CAS in UC 1462250 (Mason 169).

Hawaiian Islands. Oahu: Kaalawai, on Acanthophora, shallow
subtidal protected from wave exposure, leg. I.Meneses, May
3, 1988, IM 812, 813, 814, 815, 816, 817, 818, 819, 820,
821, 822, 823, 824, 825, 826, 827, 828, 829, 830, 831,
832, 833, 834, 835, 836.
Hawaiian Islands. Maui: Maalaea Bay, between 70-130 m out
from wall on profile, leg. D.P.Abbott, August 30, 1978,
IAA 14499.

Geographic distribution:

Pacific coast of Southern California: Corona del Mar,
Balboa Harbor, La Jolla (Dawson, 1950; 1961); Pacific
Mexico, Baja California: Isla Guadalupe, Isla Cedros,
Miller's Landing, Rocas Alijos (Dawson, 1950; 1961);
Pacific Mexico, Nayarit: Miramar; Oaxaca, Salina Cruz
(Dawson, 1950; 1962); Gulf of California, Sonora: Isla
Jorge, Isla Patos, Pto. Libertad, Ensenada de San
Francisco; Sinaloa: Bahía de Topolobampo (Dawson, 1961;
1962); Central Pacific: Hawaiian Islands, Oahu (this
study); Marshall Islands, Eniwetak Atoll, Majuro Atoll
(Dawson, 1956; 1957); Japan: Hizen, Osumi, Sima, Izu,
Iwaki provinces (Nakamura, 1950; 1965), Mage Island
(Itono, 1972); Taiwan (Formosa): Garambi (Nakamura, 1950;
1965); Viet Nam: Nha Trang (Dawson, 1954).

Ceramium clarionensis Setchell & Gardner
Pl. III, Figs. 1-6

Setchell & Gardner, 1930: 170, pl.7, figs. 26-27.
non C. clarionensis of Dawson. Dawson, 1950: 134, pl.4,
fig. 29.

non C. 'clarionense'of Dawson. Dawson, 1954b: 448,
fig.55K; 1956: 54; 1961: 440; 1962: 53, pl.18, figs. 5-6.

Plants are from 2.0 to 9.0 mm in height, basal
portions are horizontally attached to the substratum with
the upper portions of the plant remaining free and
upright. The branching pattern is dichotomous (Pl. III,
Fig.1) with usually 3 to 4 dichotomies throughout the
thallus, exceptionally up to 6 dichotomies present.
Numerous secondary branches are adventitiously formed
(originating from the pericentral cells and not from the
axial cells), up to 12-13 per plant. Thallus apices are
strongly forcipate or, if there are no dichotomies present
close to the apex, only the very tip of this is incurved.
Horizontal portion of the thallus attached to the
substrate by adventitious, multicellular, filamentous
rhizoids which either have a blunt apex or end in a base
with small digitations. Plants are always epiphytic on a
variety of red algae occurring subtidally, in areas
subjected to medium wave exposure.

Nodes and internodes are clearly
distinguishable throughout the thallus. Axial cells are
ovoid (Pl. III, Fig.2), flattened, shorter than wide,
except in most basal portions of the plants where they are

vertically elongated and slightly longer than wide. A
cytoplasmic strand running from cell to cell in the center
of the filament is present in living material as well as
fixed material (Pl. III, Fig.2). Internodes range
(96)144-198.4(224) um in diameter and (25.6)35.2
-112(137.6) um in length in the most basal portions of the
plant. In the upright portions of the thallus the
internodes are of similar diameter, (108)120-168 um and
shorter (becoming even shorter near the apices),
12-96(108) um long, than in the basal parts of the
thallus. Nodes are commonly non-tumid, i.e. they do not
have a swollen appearance, having a ratio of 1:1 in
node:internode diameter, although they can be slightly
thicker than adjacent internodes in a few plants. Nodal
diameter is (134.4)150.4-198.4(224) um in the creeping
part of the thallus, and (108)132-180 um in the upper part
of the thallus. Nodal length is (51.2)54.4-96(108.8) um
in the creeping portions and 60-84(96) um in the upper
parts of the plant. Cortical cell rows are 3 or 4 up to 6
or 7 in the most developed basal portions of the thallus;
initially a central row of large cells, corresponding to
the pericentral cells, is visible surrounded by 1-2 rows
of smaller, irregularly-shaped, either angular or rounded
cortical cells. The central row of large cells becomes

invisible in the basalmost portion of the thallus because it is covered entirely by smaller cortical cells (Plate III, fig.3). Cortical cells are (6.4)9.6-19.2(25.6) x (6.4)9.6-16(19.2) um.

Tetrasporangial plants are dichotomous and increase their diameter towards the upper portions of the plant. Nodes bearing tetrasporangia are located in the upper half of primary and adventitious branches. Tetrasporangia are obovate, (35.2)41.6-54.4(64) X 32-48(51.2) um located in whorl, lower half partially embedded in the cortical band, the protruding upper half surrounded by an involucrum (Pl. III, Fig.4). Involucres originate from the cortical cells and each usually consists of 3 to 4 cells.

Cystocarpic plants are more irregularly branched than the tetrasporangial plants and upper portion of the branches are slightly swollen. Cystocarps are subterminal, with up to 6 subtending branches (Pl. III, Fig.5), which are frequently incurved but without forcipate apices. Two equally developed gonimolobes are usually present. Cystocarps may appear terminal in some plants until the main axis reassumes its growth and becomes distinguishable from the rest of the subtending branches. Cystocarps are 21-53 x 20-41 um.

Spermatangial plants are primarily dichotomous with secondary formation of adventitious branches formation, the upper portions of branches are slightly swollen (Pl. III, Fig.6). Spermatangia cover the cortical cells in the nodes located in the upper half of the plant.

Evaluation of variability:

This species is especially distinctive in its tetrasporangial characteristics. Tetrasporangia have their lower half embedded in the cortical bands and their upper half protruding and subtended by a distinct involucrum. Tetrasporangia are in groups of two to three abaxially located in each node, or in groups of more than 3 located in a whorl in the upper part of each node. The thallus is not entirely corticated, internodes being almost always visible except close to the apices and in some tetrasporangial plants. Depending on the degree of nodal development, pericentral cells can be observed easily as a central row of large cells surrounded by 1 or 2 layers of smaller cortical cells, or become completely indistinguishable from the cortical cells. The formation of new layers of even smaller cortical cells considerably changes the appearance of the cortical band, but the

nodal diameter and length remain fairly uniform throughout
the thallus of an individual plant and between different
plants. In contrast, internodes show some variation,
being slightly longer and thinner in the basal creeping
portion of a plant as compared to the upright portion of a
plant.

Examination of the type specimen of Ceramium
clarionensis indicates that the Hawaiian plants described
above belong to this species. Both the type material and
the Hawaiian plants, have similar nodal structures.
Nevertheless, some of the Hawaiian material shows a
greater variability in nodal characteristics, including
nodes with more cortical rows and smaller cortical cells
than the type specimen. The type material of
C.clarionensis shows tetrasporangia initially abaxially
located and ultimately whorled with involucres, equal to
the tetrasporangia of the Hawaiian plants in every detail,
except for being slightly larger (65-75 um diameter).

Setchell and Gardner (1930) described stiff
trichoblasts, 30-35 um long, originating from the upper
cells of the cortical bands. These trichoblasts were not
observed in the type material nor were they detected in
the Hawaiian plants. Setchell and Gardner (1930) probably
referred to structures that did not withstand the methods

employed to preserve the type material. Because the presence of hairs has been known to vary with nutrient concentration (De Boer & Whoriskey, 1983) their occurrence is probably dependent on the growing conditions of the plant. Their usefulness for species concept is not clear.

Evaluation of the species:

Ceramium clarionensis Setchell & Gardner has been confused with Ceramium aduncum Nakamura (Dawson, 1950; 1962; see also discussion in Nakamura, 1965). Although the two species are clearly distinguishable on the basis of their tetrasporangial characteristics, features of the vegetative structure can overlap. Both species in Hawaii grow in the same habitats, both are plants with a creeping and an upright portion and both reach similar sizes in the field. The basal portions of some plants of C. clarionensis exhibit highly developed nodes similar to those of C. aduncum. Additionally, some plants of C. aduncum can exhibit gland cells, accentuating the similarity between the two species. Examination of apical regions in sterile plants however, have proved to be useful in separating specimens of the two species based on the following features: (1) Flattened, ovoid axial

cells are always visible in the upper portions of the branches of C. clarionensis, whereas in C. aduncum axial cells are progressively covered by cortical bands; (2) the presence/absence of gland cells in the nodes in most sterile plants; and (3) on the basis of their tetrasporangial features. C. clarionensis has slightly arger tetrasporangia which are involucrate and located in whorls in the upper half of the nodes while C. aduncum has mainly adaxially located tetrasporangia without involucres and distributed throughout the entire length of the nodes.

Whorled, involucrate tetrasporangia are also shown by Ceramium mazatlanense Dawson (1950). This species is apparently sympatric with C. clarionensis in certain areas (Dawson, 1962). Ceramium mazatlanense differs from C. clarionensis in having short cortical bands (25-30 um long) and in having tetrasporangia that reach a size of 35 um in diameter exceeding the nodal length.

List of specimens studied:

Type material: Mexico, Clarión Island, growing on Codium simulans, leg. H.L.Mason, June, 1925, CAS in UC 173620 (Mason 75).

Hawaiian Islands, Oahu: Kaloko Point, growing epiphytic on
Laurencia spp. turfs, leg. I. Meneses, July 17, 1986, IM
546. Hanauma Bay, epiphytic on _Galaxaura_ sp., leg. Jane
Lewis, August 9, 1985, IM 12, 13, 14, 32. Sans Souci
Beach, epiphytic on _Galaxaura_ sp., leg. Jane Lewis, August
8, 1985, IM 9, 10, 11; epiphytic on _Galaxaura_ sp., leg.
Jane Lewis, September 21, 1985, IM 25, 26, 26 b,c & d
(same slide), 27c, 28, 30, 31; on south face of Natatorium
wall, leg. I. Meneses, September 29, 1987, IM 703, 704,
705, 706, 707; leg. Jane Lewis, October 4, 1987, IAA
18520; on southeast wall of Natatorium, leg. I. Meneses,
November 11, 1987, IM 723 (3 slides). Makaha Caverns,
0.5-1 m depth, leg. L. M. Hodgson, August 5, 1988, IAA
18858. Kahanahaiki, leg. W. H. Magruder, November 23,
1984, IAA 17051.

Hawaiian Islands, Hawaii: Kona, Keahole Point, on buoy
(OTEC) 1.14 m depth anchored in 6.35 m water, 500 m due
West of lighthouse, leg. E. C. Haderlie, July 22, 1977,
IAA 12720a.

Geographic distribution:

Mexico, Revilla Gigedo Islands, Isla Clarión (Setchell & Gardner, 1930); Hawaiian Islands, Oahu: Kaloko Point, Hanauma Bay, Sans Souci Beach and Makaha (this study); Hawaii: Kona, Keahole Point (this study).

Ceramium sp.1

Pl. IV, Figs. 1-5

Plants erect, 9-35 mm in height; branching is dichotomous with all branches growing to a similar height giving the plant a corymbose appearance. Adventitious branches are occasional. Cortication is present only at the nodes, these and the internodes clearly distinct throughout the thallus (Pl. IV, Figs. 1-5), including the very apical portions of the plant. Apices forcipate, frequently inner and outer edges dentate. Plants saxicolous, attached to the substrate by multicellular, unbranched, filamentous rhizoids with blunt apices. Rhizoids arise adventitiously in clusters at the nodes all along the thallus, except near the apices, and are especially abundant in the basal portions of the plant.

Internodal length equivalent to 1-5 times the cell diameter, becoming progressively shorter towards the apex. Internodal and nodal measurements were made at the basalmost portions of the thallus, where axial cells seemed to be ultimately developed. Internodes are cylindrical, (96)120-192(240) um diameter and (192)204-372(528) um long. Nodes are non-tumid or scarcely tumid (Pl. IV, Fig.2), their diameter is 2 to 3 times their length and they consist of (4)5 to 8(9) cell rows. In partially developed nodes, close to the apices, the cell rows comprise irregularly arranged cells of variable shape and size. In nodes that are entirely developed, located in the lower portions of the thallus, pericentral cells are partially visible (Pl. IV, Fig. 3) as a central row of larger cells, surrounded and partially overlapped by cortical cells. The larger of these cortical cells are the cells which are first cut off from the pericentral cells. Their vertical axis ranges (6.4)9.6-26(32) um and the horizontal axis ranges (3.2)6.4-22.2(29) um. Cortical cell shape is extremely variable, from cuboidal to elongated and narrow, with either rounded and smooth or angular and sharp edges. Nodal diameter is (108)144-204(228) um, while nodal length is (48)60-96(108) um.

Tetrasporangial plants are dichotomously branched. Tetrasporangia are spherical, (32)35.2-48 um, protruding from the upper half of the nodes, naked (Pl. IV, Fig. 4), with a thick, transluscent sporangial wall. They are initially adaxial becoming later whorled around the nodes.

Cystocarps are subterminal, located abaxially in upper portions of the fronds. They usually have 1 to 3 gonimolobes at different stages of maturity, subtended by 3 to 4 adventitious branches (Pl. IV, Fig. 5), originating from the node immediately below the one bearing the gonimoblast. The subtending branches are normally unbranched and with straight apices, occasionally with one dichotomy and forcipate apices.

Spermatangial plants are dichotomously branched with nodes consisting of 4 to 5 cell rows. Fertile nodes comprise even the most basal nodes. Spermatangia are in clusters originated from cortical cells, never entirely covering the nodes in which the pericentral cells remain visible.

Evaluation of variability:

Ceramium sp.1 is apparently restricted to
shallow and highly protected reef areas, because no
similar material has been collected in other areas but in
inner areas of Kaneohe Bay. The plants are typically
saxicolous, growing on rock or coral, although
occasionally, some specimens were observed on other algae
such as species of (Acanthophora, Dictyosphaeria).
Possibly, the apparent habitat restriction accounts for
the uniformity of the species in appearance.
Nevertheless, the species has a large range of internodal
lengths and diameters with a few plants (e.g. IM 801, IM
789) which exceed the average internodal length, as well
as a few (e.g. IM 807, IM 811) exceeding the average
internodal diameter. These outliers show all 3 types of
reproductive features, which indicates that this
variability is not correlated to any particular phase of
their life history. The diameter and length of the nodes
are more uniform than those of the internodes, and are
proportionately correlated. The increase in nodal length
is accompanied by a proportional increase in diameter.
None of the reproductive structures, tetrasporangia,
cystocarps or spermatangia, alters the nodal structure or

the dichotomous branching pattern characteristic of the species.

Evaluation of the species:

Plants have a main erect axis with dichotomous branching and conspicuous nodes and internodes throughout the thallus. The arrangement of cells in the non-tumid or slightly tumid nodes, is a distinguishing characteristic of the species. This character, together with the occurrence of naked, spherical tetrasporangia placed in whorls, is different from other described taxa.

Ceramium sp.1 shows certain similarity with Ceramium subtile J.Ag. in its nodal structure. Both species exhibit a central row of large cells, the pericentral cells, which are surrounded by smaller, irregularly shaped cortical cells. A close examination of C. subtile description and figures (Agardh, 1851; Taylor, 1960) however, shows that the row of pericentral cells is limited above and below by cortical cells, which are not cut off between pericentral cells thus, only the upper and lower cell walls of the pericentrals overlap. Ceramium sp.1 differs from C.subtile in having cortical cells developed not only above and below the pericentrals (in

the vertical axis of the node) but also in between
adjacent pericentral cells. In addition, C.subtile
description indicates that the species displays an
alternate branching pattern in the upper parts of the
plants. For Ceramium sp.1, the branching pattern is
invariably dichotomous. C.subtile has also been reported
to reach a height of 150 mm, whereas Ceramium sp.1 has
never been observed attaining more than 40 mm in height.

Examination of the figures included in the
original description of Ceramium uruguayense Taylor showed
that this species exhibits nodes with a noticeable
similarity to those of Ceramium sp.1. Both species have
naked, whorled tetrasporangia, although in C. uruguayense,
tetrasporangia are larger than those for Ceramium sp.1 and
completely covered by cortical cells from their lower
half, while they are protruding in Ceramium sp.1. In
spite of the apparent disjunctive distribution of both
species, (C. uruguayense Taylor is reported from the
Atlantic coasts of South America) the slight morphological
differences between them may be attributable to
differences in growing conditions. Examination of the
type of C.uruguayense is required at this point in order
to establish the taxonomic affinities between these two
species.

List of specimens studied:

Hawaiian Islands, Oahu: Kaneohe Bay, on shallow reef flat
around Moku o Loe, growing on loose pieces of coral, 1m
depth, leg. I. Meneses, April 6, 1988; IM 775; 776; 777;
778; 779; 780; 781; 782; 783; 784; 785; 786; 787; 788;
789; 797; 798; 799; 800; 801; 802; 803; 804; 805; 806;
807; 808; 809; 810; 811. On shallow reef flat, on loose
pieces of coral, 50 cm depth, leg. I. Meneses, February 8,
1989; IM R-925; R-926; R-927 (culture collection).

Geographic distribution:

Hawaiian Islands, Oahu, Kaneohe Bay.

Ceramium sp.2

Pl. V, Figs. 1-4

Plants of this species are minute, creeping
filaments that range from 1 to 2.5 mm in height in their
upright branches. The thallus consists of a prostrate
portion with a horizontal axis which adventitiously
produces unilateral upright branches on the upright side

and rhizoids on the basal side (Pl. V, Fig.1). Both prostrate and upright axes are clearly distinct. Upright axes as well as prostrate axes rarely branch, but if they do, branching is dichotomous. Apices are straight or slightly curved at the very tip (Pl. V, Fig.2). Plants are attached to the substrate by means of short, 1-celled, rhizoids with digitate bases and by long, 2-3-celled, rhizoids with blunt apices. They are epiphytic on other red algae (e.g. _Laurencia nidifica_, _Amansia glomerata_).

Internodes are slender and long while nodes are short and tumid (Pl. V, Fig.3). Internodes are cuboidal, (24)36-48(64) um diameter and (24)36-48(156) um long in the prostrate axes. In the erect axes internodes are slightly narrower and shorter, (27)29-38(61) um diameter and (19)48-64(90) um long, than in prostrate parts of the plant. Nodes usually consist of no more than 3 cell rows, occasionally up to 6 cell rows. Pericentral cells are pyramidal when observed in surface (Pl. V, Fig.3), with the base of the pyramid oriented basipetally. The 2 first rows of cortical cells are formed acropetally, each of the cells cuts off a one-celled projection directed outwards in such a way that these projections are placed in whorls around the nodes (Pl. V, Fig.2). The third cortical cell row is formed basipetally after the projections have been

originated. Nodes are (34)48-50(96) um in diameter and (16)24-36(72) um in length in the prostrate filaments, smaller than in the upright branches where nodes are (35)42-55(74) um diameter and (16)19-27(32) um long. Cortical cells from the two upper rows are cylindrical with their long axis being horizontal. The cortical cells from the lower row are irregularly shaped, generally with angular margins and slightly elongated vertically. One-celled projections are 6-16 um long, most frequently 10 um.

Tetrasporangial plants are frequently swollen in the upper portion of the upright branches. Ovate to obovate tetrasporangia, (26)32-38(42) X (22)26-29(38) um, protruding from cortical band, upper half involucrate, located in whorls around the nodes (Pl. V, Fig.4). Tetrasporangia-bearing nodes placed at middle height of the upright branches, never at the base or apex of the branch.

No sexual plants were found.

Evaluation of variability:

The species habit is characterized by having clearly distinguishable prostrate and erect axes. The

axes differ not only in their position, but in their origin (true vs. adventitious branches formation) and dimensions. Internodal and nodal measurements of the prostrate axes are fairly consistent within the ranges given, except for one specimen with unusually long nodes (120-156 um long). The upright branches have slightly smaller internodes than the prostrate axes. Only one plant with extremely short and thick internodes exceeded the diameter and length ranges typical for the material recorded. The same plant had also thicker nodes than average, this being an uncommon condition except in nodes bearing tetrasporangia. In both prostrate and upright portions of the thallus, nodal length increases proportionally with nodal diameter within the specified ranges for the plants collected. The habit of the plant as well as the occurrence of one-celled projections located in two whorls around the nodes are two reliable vegetative characteristics for species recognition.

Evaluation of the species:

Among minute, epiphytic _Ceramium_, there are 3 species which share the prostrate and adventitious-upright habit characteristic of the this Hawaiian species.

Ceramium camouii, C. codii and C. serpens which have been recorded in the North Pacific, with C.codii also recorded for distribution also includes the Caribbean, the Mediterranean and the Baltic Sea. None of these species however, has the one-celled projections characteristic of the Hawaiian species. This unique vegetative feature stands alone in separating the Hawaiian material from all other species.

Further comparisons show that Hawaiian material is distinguishable from C.camouii in that the latter has tetrasporangia entirely embedded in the cortical bands, resulting in pronounced tumid nodes in reproductively mature asexual plants (Dawson, 1944). C.codii and C.serpens are very similar morphologically, both species have a single tetrasporangium per node (20-45 um diameter), with a clearly defined involucrum that covers it partially. The Hawaiian species has several tetrasporangia per node located in whorls therefore, differing from C.codii and C.serpens.

In summary, the thallus structure consisting of a prostrate axis with adventitiously borne upright axes which are scarcely branched, and the occurrence of one-celled projections located acropetally in the nodes,

are main characters that allow consideration of this as a separate species of <u>Ceramium</u>.

List of specimens studied:

Hawaiian Islands, <u>Oahu</u>: Kaloko Point, exposed rocky intertidal pools, on turfs with <u>Jania</u> sp. and <u>Polysiphonia</u> sp., leg. I. Meneses, April 4, 1986; IM 500; 502. Kaloko Point, exposed rocky intertidal, epiphytic on <u>Jania</u> sp. together with <u>Ceramium</u> sp. and <u>C.flaccidum</u>, leg. I. Meneses, February 5, 1988; IM 724a; 724b; 724c; 735; 735b; 735c; 735d; 736. Makaha Caverns, at 0.5-1 m depth, epiphytic on <u>Chondria</u>, leg. L. M. Hogdson, August 5, 1988; IAA 18860.

Hawaiian Islands, <u>Maui</u>: Kauiki Head, Hana, 1.2-1.8 m depth, epiphytic on blades of <u>Amansia glomerata</u>, leg. D.P. Abbott, August 26, 1976; IAA 18026-1; 18026-2. Kauiki Head, Hana, 1.2-2.4 m depth, growing on <u>Amansia</u> blades but also on <u>Laurencia majuscula</u> epiphytic on <u>Amansia</u>, mixed with other epiphytes, leg. D.P. Abbott, August 26, 1976; IAA 18004 slides 1-8.

Geographic distribution:

Hawaiian Islands, Oahu: Kaloko Point, Makaha Caverns.

Maui: Kauiki Head, Hana.

Ceramium affine Setchell & Gardner

Pl. VI, Figs. 1-6

Setchell & Gardner, 1930: 172; Dawson, 1944: 317, pl. 51,
fig. 4; 1950: 132, pl.2, figs. 16-17; Abbott & Hollenberg,
1976: 592, fig. 531.

C.affine Setchell & Gardner var. affine Dawson. Dawson,
1962: 50-51, pl. 17, fig. 6; Trono, 1969: 77, pl.10, figs.
16-17; Itono, 1972: 78, fig. 5.

C.affine Setchell & Gardner var. peninsularis Dawson.
Dawson, 1950: 132, pl. 2, figs. 16-17; 1962: 51, pl. 17,
figs. 9-10.

Minute, creeping thalli often ranging from 0.1
to 1.1 mm in height in their upright axes and from 0.4 to
6 mm in a few specimens. Plants consist of a prostrate
axis which runs parallel to the subtrate and cuts off
upright branches (Pl. VI, Fig.4) adventitiously from the

pericentral cells. Upright branches rarely rebranch, but some of the field-collected material showed dichotomous branching (Pl. VI, Ffig.1) in their unusually long prostrate portions (see under evaluation of variability). Plants are attached to the substrate by short rhizoids with digitate bases arising unilaterally from the prostrate axis. Apices are straight and seldom slightly incurved. Internodes are long, 2-3 times their diameter (Pl. VI, Fig.2) in both prostrate and erect portions of the plant. Nodes are slightly to fully tumid, and range from having 1-2 cortical cell rows to up to 5 cell rows. Commonly epiphytic on Codium arabicum.

In the prostrate portions of the plant, internodes are slightly longer and thicker than in the upright branches (Pl. VI, Fig. 3). Prostrate axes are 16-51.2(60.8) um in diameter and 19.2(28.8)-160(163.2) um in length. Upright axes are 16-38.4(64) um in diameter and 16(19.2)-108.8(112) um long. Nodes are from one to two times long as broad. Prostrate and erect axes show a slight difference in nodal diameter and length in the majority (88%) of the plants recorded. In prostrate portions nodes are 22.4-64.3(67.2)um in diameter and (9.6)12.8-32.7(35.2) um long. In upright portions nodes are 22.4-35.2(73.6) um diameter and 9.6-22.4(38.4) um in

length. Cortical cells are arranged in 2 to 3 rows of small cells.

The pericentral cells are visible in the lower part of the node having a somewhat pyramidal shape (Pl. VI, Fig.3) with the base of the pyramid directed basipetally. The first row of cortical cells is cut off acropetally and formed by roundish cells, the second is formed basipetally, partially overlapping the pericentrals. The cortical cells located in the lower nodal rows are slightly elongated in their vertical axis and outwardly directed in their lower half. Their size ranges (3.2)6.4-12.8 um in their horizontal axis and (6.4)9.6-12.8 um in their vertical axis. The cortical cells of acropetal rows are rounded and smaller than the lower ones.

Occasionally, some plants show adventitious branches with thicker than normal upright axes associated with highly developed nodes which have 4 to 5 cortical cell rows. These branches are either sterile or spermatangial (Pl. VI, Fig.5). Internodal diameter in these branches is 48-57.6 um and internodal length is 54.4-73.6 um. Nodes are 54.4-73.6 in diameter and 32-38.4 um in length.

Tetrasporangia are located in the upright axes. They are 1-3 per node but occasionally have 3 or more, placed in whorls around the fertile nodes. Tetrasporangial shape is subspherical, frequently with an elongated, spur-like, lower portion attached to the node (Pl. VI, Fig.4). There are no involucra present. Sporangia are prominent and strongly protruding. Frequently they exceed nodal length, 28.8-35.2 um and 19.2-28.8(32.2) um diameter in vertical and horizontal axes respectively.

Male plants have fertile nodes located in the middle part of such swollen upright branches (Pl. VI, Fig.5). Spermatangia are arranged in clusters of elongated cells borne in the cortex and bear a single spermatium at each parent cell.

Cystocarps are subterminal in upright branches. They consist of one or two gonimolobes at different stages of maturity. The gonimolobes are surrounded by subtending branches cut off from the node beneath the one bearing the cytocarp (Pl. VI, Fig.6).

Evaluation of variability:

This species is characterized by a combination of characters among which the prostrate habit with upright adventitious branches, naked protruding tetrasporangia and nodal structure are the most important. Some plants can show a certain degree of variability in the occasional formation of thicker branches with longer than usual nodes and internodes. These branches form whether or not there are reproductive structures, while other parts of the same plant can remain unchanged.

The specimens examined are divided into two groups according to secondary morphological characters. One group includes those plants which fit well into the preceding description of small(0.1-1.1 mm height) creeping plants, rarely branched, with 2 to 4 nodal cell rows. The second group consistently deviated from these characteristics by showing a dichotomously branched, partially prostrate main axis. This produces unilateral rhizoids and adventitious branches only on its prostrate portion. The adventitious upright branches are up to 4 mm height in this group and their nodes are reduced to 2 nodal cell rows. In some cases only the pericentral cells are present. These characteristics are variable and the

same specimen occasionally shows features of these two
artificially divided groups. In contrast, all specimens
share the same nodal structure and cortical cell shape.

Evaluation of the species:

Ceramium affine from Hawaii includes creeping
plants which do not exceed 1 mm in height in their upright
adventitious branches, and partially prostrate plants with
dichotomous branching with a few basal adventitious axes
reaching up to 4 mm in height. The first plants show
usually 2-3 nodal cell rows and no dichotomies whereas the
other plants do not have more than 1-2 nodal cell rows. A
similar variability is also found in C.affine var. affine
from the Caroline Islands (Trono, 1969). Hawaiian
material of C. affine as well as material from the
Caroline Islands (according to Trono's description) does
not fit well with Setchell and Gardner's description
(Setchell & Gardner, 1930). Setchell and Gardner
described a specimen with narrow nodes comprised of 2-3
rows of rounded cells, the larger cells below and the
upper smaller ones cut off from these. However, there is
no indication of the vertical elongation of the lower
cells, which is shown in Hawaiian material as well as in

Dawson's labeled collection as C. affine. This particular
character, although variable in some specimens, is clearly
distinctive of the species, and is shared by Dawson's
specimens of C. affine and C. affine var. peninsularis and
by the Hawaiian material (Table 3). Nodal and internodal
measurements as well as branching patterns are variable,
but overlapping among all the material observed (Table 3)
and the information available from Setchell and Gardner's
description. In addition, all of these plants show
tetrasporangia that are single or whorled, naked and
protruding. Based on these features, these entities
should be treated as variants of one single species until
further examination of C.affine Setchell & Gardner type
material can be made.

List of specimens studied:

Hawaiian Islands,Oahu: Waikiki, off beach lab, on Codium
arabicum, leg. Celia Smith, October 29, 1977; IAA 13143.
Mamala Bay, dredged with otter trawl 61 m, leg. Karen
Hunt, December 16, 1980, IAA 16089a, IAA 16089b, IAA
16089c. Barber's Point, epiphytic on Codium arabicum,
together with other epiphytes like Ceramium flaccidum,
Lyngbya, Crouania sp., leg. I. Meneses, February 28, 1987

IM 606, 607, 608a, 608b, 609, 611a, 611b, 611c.
Pacific coast of Mexico: Isla Santa Cruz, dredged from 18
- 55 m, leg. W. Baldwin & party, July 10, 1965, US 006797
(EYD 25823a), US 36566 (EYD 25823a). Isla Guadalupe, 2,5
miles north of South Bluff, shore station on a -1.7 m
tide, leg. E.Y. Dawson, December 20-21, 1949, US 006795
(EYD 8522). Sinaloa, Punta Prieta, outer Bahía
Topolobampo, intertidal rocks, leg. E.Y. Dawson, June 10,
1952, US 006796 (EYD 10962).

Geographic distribution:

Pacific coast of North America: California; Corona del Mar
(Dawson, 1950); Baja California; Guadalupe Island
(Setchell & Gardner, 1930), Isla Concha, Laguna de Salmon
and Punta
Frailes (Dawson, 1950; 1962); Gulf of California; Puerto
Refugio, Isla Angel de la Guarda (Dawson, 1944; 1962).
Caroline Islands: Palau Group, Koror Island (Trono, 1969).
Japan: Koniya, Amami Island (Itono, 1972).

Ceramium flaccidum (Kuetzing) Ardissone

Pl. VII, Figs. 1-6

Ardissone, 1971: 40; Womersley, 1978: 234, fig. 4,.

Hormoceras gracillimum Kuetzing, 1862: 21,pl. 69a-d.

Ceramium gracillimum Griffiths & Harvey ex Harvey, Harvey,
1848: pl. 206; J.Agardh, 1851: 118; 1876: 95; 1894: 43;
Harvey, 1855: 557; Nakamura, 1965: 136, pl.I, 5-6, fig. 6;
Athanasiadis, 1987: 76.

C. transversale Collins & Hervey. Collins & Hervey, 1917:
145, pl.
5, figs. 29-31.

C. gracillimum var. byssoideum (Harvey) Mazoyer. Mazoyer,
1938: 323; Feldmann-Mazoyer, 1940: 293, fig. 109; Dawson,
1944: 319; 1954: 448, fig. 55e,f; 1956: 53; 1957: 21;
1961: 440; 1962: 57, pl. 20, figs. 2-3, pl. 21, figs. 2-3.
Ceramium byssoideum Harvey. Harvey, 1853: 218; Stegenga &
Vroman, 1987: 405, figs. 15-18.

C. masonii Dawson. Dawson, 1950: 126, pl. 2, figs. 11-12.

C. taylorii Dawson, Dawson, 1950: 127, pl.2, fig. 13, pl.
4, figs. 31-33; 1954: 446, fig. 55b,c; 1957: 21; 1962:
65-66, pl. 26, fig. 1-3; Stegenga & Vroman, 1987: 405,
figs. 19-21.

Thallus is variable in height, 3 to 12 mm tall, slender, attached to the substrate by long, uniseriate rhizoids with blunt apices, arising in abundance from the most basal nodes and decreasing in frequency and number towards the upper portions of the plant. Branching is pseudodichotomous towards the apex (Pl. VII, Fig.1), becoming alternate in the middle and lower parts of the plant, because of the overtopping of one of the axes. Apices are straight, slightly incurved or forcipate. Nodes are non-tumid to slightly tumid in ultimately developed parts of the thallus; internodes are long, up to 16 times longer than broad in the same parts, short or barely visible in the apical parts, covered by tumid nodes. Adventitious branching is infrequent but when present, branchlets are thinner than parental axis.

Measurements of internodes and nodes were taken at the basal and upper portions of the plant. Differences in these parts of the same plant show that only internodal length varies. Internodal diameter of the lower and most developed parts of the thallus varies within the species for different populations. Plants may be thin, internodal diameters being 35.2-70.4(102.4) um or thicker showing, (76.8)115.2-268.8(614.4) um in diameter in their basal portion. The upper portions of the branches show no

significant differences in internodal diameter for plants
from different populations, (28.8)32-83.2(102.4) um.
Internodes vary in length between the upper parts of the
axis and the base, as well as between plants collected at
different sites. Basal internodal length range
(54.4)102.4-387.2(448) um for plants collected epiphytic
or range 192-1228.8(1920) um for saxicolous growing
plants. The internodal length in the upper portion of the
branches is (32)80-298(314) um and does not vary
significantly among epiphytic and epilithic plants.

Nodes on the basal portions of epiphytic plants
have a diameter of (51.2)64-109(128) um whereas in
saxicolous plants nodal diameter is larger,
(115.2)153.6-269(345.6) um.   When the nodes are measured
at the upper portion of the plants, this difference is
less pronounced for both epiphytic and saxicolous plants
can be included between (48)51.2 and 86.4(118.4) um. The
length of the nodes in the basal portions of the thallus
is (32)41.6-70.4(89.6) um for epiphytic plants and
115.2-230.4(268.8) um for epilithic plants. In apical
portions of branches the nodal length is less variable
ranging from (35.2)38.4-70.4(86.4) um including epiphytic
and epilithic specimens.

Numbers of pericentral cells are variable but
most frequently there are 5, each cutting off acropetally
2 small rounded cells which may divide further, and
basipetally a single cell which is horizontally
elongated. This last cell may divide off one or more
cells transversely, resulting in 2 or 3 rows of
longitudinally elongated cells characteristic of most
plants (Pl. VII, Fig.2), or at least at one stage of nodal
development in most plants. The basipetal horizontally
elongated cells can also cut off smaller cells by vertical
or oblique divisions, losing the typical arrangement
previously described. Cortical cells are arranged into 4
to 7 nodal rows, most frequently 5 cell rows. Gland cells
are occasionally present, scattered among cortical cells
in acropetal rows of the node.

Fertile plants are infrequent, and mostly
tetrasporangial. Tetrasporangial plants are
morphologically identical to sterile plants.
Tetrasporangia are involucrate, 1 or 2 per node in some
plants (Pl. VII, Fig.3), or 3 or more arranged in whorls
in others (Pl. VII, Fig.4). The fertile nodes are located
in the upper half of the thallus with spherical to oval
tetrasporangia, (22.4)35.2-44.8(51.2) X (22.4)41.6
-54.4(57.6) um in diameter.

Fertile female gametophytes are morphologically indistinguishable from sterile and tetrasporangial plants. Cystocarps are subterminal, consisting of 1 or 2 gonimolobes, 70-110 um across, surrounded by 3 to 4 subtending branches adventitiously originating from the node beneath the one bearing the cystocarp (Plate VII, fig.5). The axis bearing the cystocarp continues to elongate beyond the single gonimolobe.

Spermatangia cover the cortical cells of nodes located at the upper half of the thallus (Pl. VII, Fig.6). Each spermatangium bears 2 tear-drop-like spermatia.

Plants of this species are ubiquitous; they can be found in areas exposed to moderate wave action as well as areas with very low water movement. Commonly collected as an epiphyte on various algae, they can also be found growing saxicolous on rocks or pieces of dead coral.

Evaluation of variability:

Ceramium flaccidum (Kuetzing) Ardissone is a widespread species distributed in tropical and subtropical as well as temperate seas. The plants can be variable from one site to the next, and several taxa previously

thought to be different species have been grouped as different variants within the same species (Womersley, 1978). In Hawaii, C. flaccidum is found subtidally all around the island of Oahu either growing as an epiphyte or saxicolously. The collection of abundant material of C. flaccidum from three main study sites shows that plants can vary in their overall diameter, internode and node degrees of development, tetrasporangial size and arrangement, and branching pattern (Table 4).

At Kaalawai, C. flaccidum, collected epiphytic on Acanthophora spicifera, consists of plants that reach up to 8 mm in height, frequently with 11 dichotomies per plant. Their internodes range from 1 to 9 times as long as broad in the lower portions of the plant. The nodes, in those plants which are slightly swollen, clearly are divided into two portions, the upper 2/3 of the node consists of small round cortical cells and the lower third consists of 1-3 rows of horizontally elongated cells. The latter lose their initial appearance by undergoing longitudinal or oblique divisions. This last feature is characteristic of the species and was also recorded on plants from Kahala Beach Park and Kualoa reef area. In all instances, plants show a similar variation in the nodal structure which appears to depend on the position of

the node within one plant, and between plants. There is no apparent correlation to site, reproductive stage, etc. One or two tiers of horizontally elongated basipetal cells are formed and these eventually divide again in either longitudinal or oblique manner, cutting off several smaller angular cortical cells.

Plants from Kahala, only a few km to the southeast of Kaalawai, are saxicolous, growing on pieces of dead coral, and are up to 4mm taller than plants from Kaalawai. This population comprises plants that in general are more robust than those of Kaalawai, the internodes and nodes being considerably longer and broader. Plants from Kahala are not only longer but they also have fewer dichotomies, being slender in comparison with the bushy appearance of plants from Kaalawai. The specimens collected at Kualoa seem to be intermediate between the two other populations, but do not show significant differences from individuals from Kaalawai. Being also epiphytic, in this case on <u>Dictyosphaeria</u> <u>cavernosa</u> and <u>Laurencia</u> sp., the specimens from Kualoa are of the same size but less branched than those of Kaalawai and definitely smaller than those from Kahala. Internodes in Kualoa plants are almost as long and thin as those of Kahala, but their nodes are much more reduced.

Tetrasporangial plants were found in each population; in populations from Kaalawai and Kahala only a few of the collected individuals had tetrasporangia, while in the Kualoa population more than half of the plants collected were reproductive. Tetrasporangia thalli from the first two study sites have 1-2 tetrasporangia per node characteristically arranged abaxially, which are 35-51(58) X (38)42-54(58) um in diameter. In contrast, the plants from Kualoa exhibit tetrasporangia that are half the diameter of the other plants, 22-42 X 22-35(45) um and located in whorls in the nodes.

Measurements made in the upper portions of the plants show the reduction in length and diameter of the internodes which at this position in the plant are not entirely developed. The difference in diameter is particularly noticeable in plants from Kahala, whereinternodes are more robust in the older plants. Nodal diameter and length do not change considerably between the upper and lower portions of the thalli, except for plants growing at Kahala; again these plants seem to increase progressively in robustness (i.e. increase of node and internode sizes).

The variability of C. flaccidum in Hawaii reflects the overall variability of the genus recorded

throughout the world. Changes in the number of periaxial
cells, size of the plants, ultimate development of the
nodes, ratios of length/diameter of axial cells and nodes,
presence or absence of gland cells, tetrasporangial
characteristics, etc. have been detected within and
between most of the taxa now considered as synonyms of C.
flaccidum. Womersley (1978) revised representatives of
all the species which exhibit as a common character the
formation of 2 small round cortical cells acropetally and
a single cell horizontally elongated basipetally from each
periaxial cell. This author concluded that all of these
taxa are variants of a single cosmopolitan species. All
other characters are apparently too variable to have any
taxonomic value by themselves in recognition of species.

Hawaiian specimens of C. flaccidum fit well
with the qualitative and quantitative characters recorded
for this species as circumscribed by Womersley (1978). An
exception is the formation of elongate-clavate hairs.
These are a character of the "fimbriate forms" as defined
by Womersley (1978). Plants with this and other features
are here regarded as a separate species, Ceramium
fimbriatum Setchell & Gardner (1930), which was reduced to
synonymy of C. flaccidum by Womersley (1978) and will be
discussed in detail below.

Evaluation of the species:

Ceramium flaccidum as circumscribed by
Womersley (1978) includes the following taxa as C.
gracillimum Griffiths & Harvey, C. gracillimum var.
byssoideum (Harvey) Mazoyer, C. transversale Collins &
Hervey, C. taylorii Dawson, C. masonii Dawson and C.
fimbriatum Setchell & Gardner (Table 5), which were
previously regarded as separate species. Womersley (1978)
indicated that the species is variable in height and
robustness but that the development of the cortical cells
in the node is similar in all these variants. In
addition, all representatives of these names show the
habit, dimensions, and reproduction of C. flaccidum. The
main characteristics of Hawaiian material, material from
Dawson's collection identified as C. gracillimum and C.
taylorii as well as Dawson's description of the latter and
of C. masonii, and finally Nakamura's description of C.
gracillimum of Japan (1965) and C. flaccidum sensu
Womersley (1978) are summarized in Table 5. A comparison
of these characteristics indicates that all of these
entities share the same branching pattern, nodal
construction and most of the tetrasporangial features.
The variability in height and robustness mentioned by

Womersley (1978) can also be observed from this table, as well as the different degree in nodal development, and the variability in features such as adventitious branching and presence of gland cells.

Another species that seems to be a variant of C. flaccidum according to the nodal characteristics is C. dawsonii Joly (1957). The similarities of this species with C. byssoideum and C. taylorii was already noticed by Stegenga and Vroman (1987) who retain it as a separate species in view of the longitudinal divisions undergone by the initially horizontally elongated basipetal cells. Hoewever, C. flaccidum also exhibits nodes in which further division of these basipetal horizontally elongated cells has occurred (Womersley, 1978). A similar condition is recorded in Hawaiian material (IM 251, 255, 256, 257, 674, 676, 677). Consequently, further examination of C. dawsonii could result in the addition of this species to the extensive synonymy of C. flaccidum.

Womersley (1978) included C. fimbriatum Setchell & Gardner as a variant of C. flaccidum stating that the hairs, supposedly characteristic of this species, are of variable occurrence in specimens of the latter. Hawaiian material does not show the typical elongate-clavate hairs in C. flaccidum material. However,

these hairs are almost always present in plants identified as C. fimbriatum on other grounds. Plants exhibiting a combination of features from both species have not yet been recorded. Plants of these two species have been collected side by side at Kaalawai Beach, suggesting that these differences are not a result of environmentally controlled variation. Therefore, C. fimbriatum Setchell & Gardner is not included here as a synonym of C. flaccidum, but as a separate species pending the examination of Australian material reported to have a combination of characters from both taxa (Womersley, 1978).

List of specimens studied:

Hawaiian Islands. Leeward islands: Necker Bank, on antennae of spiny lobsters, leg. George Balazs, August 1977, MD 28452 A-D; on Laurencia majuscula, leg. George Balazs, August 1977, MD 28452 A,C (different slides). Oahu: Waikiki, epiphytic on Liagora, leg. I. Meneses, May 14, 1987, IM 674, 675; epiphytic on Cladophora, leg. I. Meneses, May 14, 1987, IM 676, 677; Kualoa Point, reef flat, epiphytic on Dictyosphaeria cavernosa, leg. I. Meneses, October 10, 1988, 970, 971, 972, 973, 974, 975, 976, 976, 977, 978, 979; epiphytic on Laurencia sp., leg.

I. Meneses, October 10, 1988, IM 980, 981, 982, 983, 984, 985, 986, 987, 988, 989, 991, 992, 993, 994; Kahala Beach Park, reef flat and sand, growing on pieces of dead coral, leg. I. Meneses, September 7, 1986; (Kahala transect collection numbers) IM K 856, 857, 862, 863, 865, 882, 883, 884, 885, 886, 887, 888, 890, 891, 912, 913, 914, 915, 916, 929, 930, 931, 932, 933, 934, 935, 936, 938, 939; September 10, 1986, IM 579, 580, 581, 582, 583, 584, 585, 586; Kaalawai Beach, subtidal reef and rocks, epiphytic on <u>Acanthophora</u> <u>spicifera</u> and <u>Laurencia</u> sp., leg. I. Meneses, February 3, 1986, IM 86, 89, 90; March 24, 1986, IM 108, 109, 119, 120, 129; June 27, 1986, IM 171, 172, 173, 175; August 3, 1986, IM 206, 207, 211; August 28, 1986, IM 228, 229, 234, 235, 237, 239-243; October 3, 1986, IM 244-259; November 13, 1986, IM 260-274; epiphytic on <u>Liagora</u>, leg. Celia Smith, September 25, 1977, IAA 13052. Maui: Lahaina district, Makiwa, offshore, 1.5-2 m depth, on eroded coral, leg. I.A. Abbott, August 22, 1978, IAA 14396, 14397; Hana, Kauiki Head, 1.2-1.8 m depth on old dead coral (<u>Porites</u>), leg. D.P. Abbott, August 26, 1976, IAA 12649.

As <u>C.gracillimum</u> var. <u>byssoideum</u>:

Mexico. Baja California: Punta Eugenia, 180 m transect, inside Point, depth 0 to 15 m, leg. M. Neushul, August 29,

1957, US 006846 (EYD 20848); between Cabo Pulmo and Punta
Frailes, from large quantities of beach drift cast up
after a strong wind, leg. E.Y. Dawson, May 11, 1946, US
006858 (EYD 3166). Sonora: Bahia San Carlos, sandy inner
lagoon bottom, leg E.Y. Dawson, June 11, 1952, US 006859
(EYD 11019). Isla Guadalupe: 2.5 miles north of South
Bluff shore station, on a 1.7 m tide, leg. E.Y. Dawson,
December 20-21, 1949, US 006860, US 006862, US 006863 (EYD
8525, 8511) ?. Guerrero: Acapulco, inner Bay in most
protected area, leg. E.Y. Dawson, February 3, 1947, US
006861 (EYD 3879). Costa Rica. Bahia Potrero Grande,
cobble and shell bottom in depth of 6 m, leg. E.Y. Dawson,
April 1, 1959, US 006849 (EYD 21471). Ecuador: Punta Santa
Elena, north side, intertidal, leg E.Y. Dawson, January
19, 1962, US 10975-other number 3969-(EYD 22704).

As C.taylorii:

Mexico. Sonora: Ensenada de San Francisco, leg. E.Y.
Dawson, May 18, 1946, US 006930, US 006931 (EYD 1957,
1961); drift along shore near Bahia San Carlos, leg. E.Y.
Dawson, June 10, 1952, US 006923 (EYD 11004); Sinaloa:
Mazatlan, intertidal rocky shore on north side of town,
leg. E.Y. Dawson, June 7, 1952, US 006921, US 006922, US
0066929 (EYD 10823, 10830, 10937); on a small reef 3 km
north of town, flora fairly good for the area but off

season and little developed, pronounced surf, few pools,
leg. E.Y. Dawson, December 8, 1946, US 006924 (EYD 3616);
off Mazatlan, Isthmus of Isla Venado, rocky shore, leg.
E.Y. Dawson, June 8, 1952, US 006925 (EYD 10926); Punta
San Eugenio, between light house and village, intertidal
rocky shore, abundant Macrocystis, leg. E.Y. Dawson,
November 1, 1951, US 006926 (EYD 10342). Ecuador. Punta
Santa Elena, north side intertidal, leg. E.Y. Dawson,
January 19, 1962, US 59736-other number 3847-(EYD 22721).

Geographic distribution:

As C.flaccidum: Aegean Sea (Athanasiadis, 1987).
   Southern Australia and Tasmanian coasts (Womersley,
   1978).

as C.gracillimum: Pacific coast of North America: Southern
   California:Laguna Beach (Hollenberg, 1948); Gulf of
   California: San Jose del Cabo (Dawson,1944). Southern
   Japan, Ryukyu Islands (Nakamura, 1965). Taiwan
   (Nakamura, 1965). Hawaiian Islands, French Frigate
   Shoals (Tsuda, 1966). Mediterranean (Feldman-Mazoyer,
   1940).

as C.gracillimum var. byssoideum: Pacific coast of North
   and Central America: Mexico, Gulf of California, Baja

California, Guerrero (Dawson, 1961; 1962); <u>Costa</u> <u>Rica</u>
(Dawson, 1961, 1962). Southern Japan, Amami Island
(Itono, 1972). Viet Nam, Nha Trang (Dawson, 1954).
Caroline Islands (Trono, 1969). <u>Marshall</u> <u>Islands</u>,
Kwajalein, Majuro, Jaluit and Arno Atolls (Dawson,
1956). Galapagos Islands (Dawson, 1961).
Mediterranean: Algeria and Tunisia (Mazoyer,
1938, 1940). Indic Ocean: Mauritius Island
(Boergesen, 1952).

as <u>C</u>.<u>taylorii</u>: Pacific coast of Mexico: Baja California
and Guerrero (Dawson, 1962); Gulf of California
(Dawson, 1950). Pacific coast of Costa Rica:
Puerto Parker, Puerto Culebra, outer Golfo
Dulce (Dawson, 1957). Viet Nam: Nha Trang
(Dawson, 1954). Caribbean: Curacao (Stegenga &
Vroman, 1987).

as <u>C</u>.<u>byssoideum</u>: Atlantic: Key West, Florida (Harvey,
1853). Caribbean: Curacao (Stegenga & Vroman, 1987),
Tortuga Island, Venezuela (Taylor, 1942).

as <u>C</u>.<u>transversale</u>: Atlantic: Bermuda (Collins & Hervey,
1917). Caribbean: Santo Domingo (Boergesen, 1924).

as <u>C</u>.<u>masonii</u>: Pacific coast of Mexico and California
(Dawson, 1950).

as _C. dawsonii_: Atlantic: Baia de Santos, Brasil (Joly,

1957). Caribbean: Curacao (Stegenga & Vroman, 1987).

Ceramium fimbriatum Setchell & Gardner
Pl. VII, Figs 1-5

Setchell & Gardner, 1924: 777, pl. 26, figs. 43-44; 1937: 88, pl. 7, fig. 18; Dawson, 1950: 123; 1954: 446, fig. 55a; 1956: 53; 1961: 440; 1962: 56, pl. 19, fig. 3, pl. 20, figs. 6-7; Nakamura, 1965: 143, fig.8; Trono, 1969: 76, pl.10. fig.9.

Plants are small, 3 to 8 mm of height, basal portion slightly prostrate, attached to the substrate by thin, long, filamentous rhizoids with blunt apices and thick, short rhizoids with a discoid, digitate bases. Branching pattern is dichotomous towards the upper half of the plant and alternate towards the lower half due to the overtopping of one of the axes (Pl. VII, Fig.1). Apices are almost invariably forcipate.

Internodes are short, frequently as broad as long throughout the thallus except the upper portions where they are barely visible (Pl. VIII, Figs. 2 & 3).

Nodes well developed, 4 to 6(7) cortical cell rows, most frequently 5 cell rows, strongly tumid all along the thallus. The reduced length of the thallus and the number of dichotomies, 5-9 dichotomies per plant, results in a somewhat bushy appearance, accentuated by the swollen nature of the nodes and the short length of the internodes.

Internodes are (84)100-160(200) um in diameter and (48)96-185(320) um in length in the basalmost portions of the plants, whereas they reach (22.4)28.8-50(51.2) um in diameter and (2)8-20(25.6) um in length in the most upper parts of the thallus where they are still visible. Nodes are (100)108-175(231) um in diameter, (48)60-100(216) um long in lower parts of the plants and (60)70-99.2(110) um in diameter, (20)30-48(54) um long in the upper parts. The nodal structure is characteristic in having 6-8 pericentral cells, each of them cutting off acropetally two rounded cells and basipetally a single elongated cell (Pl. VIII, Fig.2). The acropetal cells divide, increasing the number of nodal rows by cutting off smaller roundish cells. The basipetal cells undergo longitudinal and oblique divisions forming cuboidal or irregularly-shaped cells (Plate VIII, figs. 3 & 4). This basipetal portion remains distinguishable from the rest of

the node by a small annular space observable in fixed and sometimes in living material.

Clavate-elongate sac-like projections (Pl. VIII, Figs. 2-4), usually referred to as hairs, (20)32-50(56) um long and (12.4)14.4-32(34) um in diameter, originated from the upper outer cortical cells, are located either in whorls or occasionally singly at an abaxial position in the node or in pairs located bilaterally. The hairs are present throughout the thallus in some plants or restricted to the upper portions of the thallus in the majority of the specimens.

Tetrasporangial plants have fertile nodes in the upper portions of the thallus. Tetrasporangia are involucrate, entirely embedded in the cortex, spherical to oval, (24)32-40(42) um X (20)28.8-35.2(38.4) um, located in whorls (Pl. VIII, Fig.5).

Cystocarps are subterminal, with 1-2 gonimolobes, subtended by up to 5 branches, which can be occasionally branched and also exhibit clavate-elongate sac-like projections.

Spermatangia form clusters in the upper portion of the axes, partially covering the nodes. Only one male plant was recorded.

Evaluation of variability:

Plants of this species are readily recognizable
on the basis of their nodal structure, the arrangement of
the swollen nodes and short internodes, plus the
occurrence of clavate-elongate sac-like projections.
These characteristics are fairly constant in all the
specimens examined independent of the place where they
were collected. Cystocarpic and tetrasporangial plants
exhibit nodes slightly more tumid than sterile plants,
nevertheless, this feature does not substantially change
the typical appearance of the plants. Only one
tetrasporangial plant was observed to lack the typical
hairs located on the nodes, although it was still
recognizable by other vegetative features.

Ceramium fimbriatum from Hawaii resembles in
its vegetative structure the Dawson collected material
from Mexico and Ecuador (Table 6). Both materials exhibit
the same cortical cell arrangement having
the two upper thirds of the node clearly separated from
the lower third by a small space. The acropetal small
rounded cells as well as the basipetal horizontally
elongated cells are also characteristic in the Hawaiian
material and in Dawson's specimens. Plants from Mexico,

however, are apparently more robust than plants from
Hawaii, the former showing longer and thicker nodes and
internodes (Table 6). Tetrasporangia are also slightly
larger in Mexican plants, although in both sets of
specimens these are whorled, involucrate and partially or
totally embedded in the cortex.

The description and illlustrations of C.
fimbriatum (Setchell & Gardner, 1924) show a small plant
with a nodal structure similar to that of Dawson's and
Hawaiian material. As a main characteristic, Setchell &
Gardner (1924) mention the occurrence of thick, rounded,
deciduous hairs. This coincides with the typical sac-like
projections of the Hawaiian material. Unfortunately, the
original description does not include very much
information about the nodes and internodes size or
structure (Table 6), except the fact that the nodes are
70-90 um in diameter (smaller than in Hawaiian specimens)
and that the internodes are 2 or 3 times longer than the
nodes. These latter features, are important to show the
relation in the magnitudes of nodes and internodes, which
ultimately describe the shape of the plant.

Setchell & Gardner (1937) also recorded a
tetrasporangial specimen of C. fimbriatum from Baja
California. Their figure (Setchell & Gardner, 1937 pl.7,

fig.18) depicts a plant with whorled,
involucrate tetrasporangia embedded in the cortex, with
the same characteristics as the tetrasporangial plants of
C. fimbriatum from Hawaii and from Dawson's collection.

Evaluation of the species:

Ceramium fimbriatum Setchell & Gardner (1924)
is regarded by Womersley (1978) as a synonym of C.
flaccidum (Kuetzing) Ardissone on the basis of their
similarity of nodal development. This feature is
considered as the most reliable character in the genus
because developmental patterns seem to be constant in
Ceramium, whereas the diverse features so far used as
diagnostic characters show different degrees of
variation. Womersley (1978) indicated that some plants of
C. flaccidum produced few to many abaxial,
elongate-clavate hairs, these being of variable occurrence
and consequently not of diagnostic importance for
separating C. fimbriatum as a different species. In spite
of the similarity of both species, C. flaccidum and C.
fimbriatum, in their initial nodal formation they differ
in their final nodal structure. They also differ in the
ratios of node and internode measurements, in the number

of pericentral cells and in the occurrence of elongate-clavate hairs. This last feature has not yet been recorded in plants with the previous characteristics corresponding to C. flaccidum. However, Hawaiian plants with C. fimbriatum features have been commonly recorded with hairs with the exception of one tetrasporangial plant. Therefore, the presence of elongate-clavate sac-like projections is considered here as part of C. fimbriatum diagnosis, in combination with the nodal structure already described, the presence of 7-8 pericentral cells and the typical swollen nature of the nodes. Ceramium fimbriatum Setchell & Gardner is hereby considered a separate species from C. flaccidum (Kützing) Ardissone until examination of the type specimen and Australian material may prove otherwise.

List of specimens studied:

Hawaiian Islands, Oahu: Keahole Point, epiphytic on Champia, 11 m depth, leg. W.H. Magruder, April 19, 1988, IAA 18719; West beach, near Kahe Point, on reef bench at lagoon "A", epiphytic on Laurencia, leg. Shawn Carper, May 11, 1988, IAA 18684; Makaha, reef bench exposed, epiphytic on Laurencia, leg. I. Meneses, February 3, 1988, IM 753;

Halona Point, low intertidal, on coral, leg. I.A. Abbott &
R.E. Norris, September 2, 1961, IAA 14871a & b; Kaloko
Point, semi-exposed intertidal, epiphytic on <u>Griffithsia</u>,
leg I. Meneses, June 28, 1985, IM 1; epiphytic on
<u>Centroceras</u> <u>clavulatum</u>, leg. I. Meneses, June 28, 1985, IM
2, 3, 4, 458, 459; growing on turfs of <u>Boodlea</u>, leg. I.
Meneses, June 28, 1985, IM 5, IM 444; epiphytic on <u>Liagora</u>
sp. leg. I. Meneses, May 2, 1988, IM 733; on <u>Chnoospora</u>
<u>minima</u>, leg. Sandra Fotos, October 23,, 1977, IAA 13107;
epiphytic on <u>Gracilaria</u>, leg. I. Meneses, September 13,
1988, IM 963; epiphytic on <u>Centroceras</u> <u>clavulatum</u>, leg. I.
Meneses, September 13, 1988, IM 948, 968; Kaalawai Beach,
protected subtidal,, epiphytic on <u>Acanthophora</u> <u>spicifera</u>,
leg. I. Meneses, March 24, 1986, IM 126, 127, 128.

Hawaiian Islands, Maui: Ahihi Bay, lava rock tide pools
and sandy beach, collections made on tide pools and
channels receiving impact of waves, epiphytic on
<u>Laurencia</u>, leg. I.A. Abbott, November 1, 1977, IAA 13055b;
Hana Bay, intertidal and edges of pools exposed to surge,
leg. I.A. Abbott, August 26, 1976, IAA 14820a.

Mexico, Baja California: Campito, 1.2 miles east of Punta
San Eugenio on Bahía Vizcaíno, intertidal rocky shore,

leg. E.Y. Dawson, October 31, 1951, US 006482 (EYD 110502); opposite north end of Isla San José, on shore rock at 1.5 m, leg. John Bleck, July 11, 1965, US 36447 (EYD 25846a). Sonora: Ensenada de San Francisco, drift alog shore near Bahía San Carlos, leg. E.Y. Dawson, June 10, 1952, US 006844 (EYD 10987). Sinaloa: Punta Prieta, outer Bahía Topolobampo, intertidal rocks, leg. E.Y. Dawson, June 10, 1952, US 006843 (EYD 10936).

Ecuador: Punta Centinela, upper sublittoral rocks, leg. E.Y. Dawson & M. Gilmartin, January 21, 1962, US 44650, (EYD 22527); north side, near Santa Elena, intertidal drift, leg. E.Y. Dawson & M. Gilmartin, January 21, 1962, US 44693 (EYD 22582a); Punta Santa Elena, north side, growing on the base of _Polysiphonia_ sp., leg. E.Y. Dawson & M. Dawson, January 19, 1962, US 59457 (EYD 22731); Bahía Santa Elena, with _Jania capillacea_ Harv. and some _J.tenella_ Kütz., leg. E.Y.Dawson & M.Gilmartin, January 18, 1962, US 44658 (EYD 22553).

Geographic distribution:

Pacific coast of Mexico: _Baja California_; Agua Verde Bay, _Pond Island_, _Turner's Island_, Puerto Refugio (Dawson, 1944); Punta Banda (Dawson, 1961); Eureka, near La Paz,

San José del Cabo (Setchell & Gardner, 1924, 1937; Dawson, 1944, 1962); Sinaloa; Mazatlan (Dawson, 1950); Guerrero; Acapulco (Dawson, 1950); Gulf of California; Tiburón Island, Isla Espíritu Santo (Dawson, 1944); Isla Angel de la Guarda to Acapulco (Dawson, 1961).

Hawaiian Islands: Laysan (Tsuda, 1965), Oahu (this study), Maui (I.A.Abbott collection).

Caroline Islands: Palau group; Koror Island (Trono, 1969); Pulo Anna Island (Trono, 1969).

Marshall Islands: Jaluit and Kwajalein Atolls (Dawson, 1956).

Japan: Izu and Hyuga Provinces; Okinawa (Nakamura, 1965).

Viet Nam: Nha Trang (Dawson, 1954).

The following are the descriptions of three unidentified taxa of Ceramium which were occasionally collected and thus the number of specimens is not sufficient to provide an adequate identification. Most of this material is reduced to fragments of plants and plants poorly preserved. These taxa will be identified here with a number for the purpose of distinction among them according to their observable characteristics.

Ceramium sp.3.

Pl. IX, Figs. 1-3

Plants of this species reach 30 mm in height; they grow upright, their attachment to substrate being restricted to the most basal part of the thallus. They have a regularly dichotomous branching pattern showing abundant small adventitious branches, sometimes 20 or more. Short rhizoids with broad digitate basis arise from the nodes of the lower parts of the thallus, whereas in the upper parts of it, rhizoids are long, slender, uniaxial filaments ending in blunt apices.

Internodes are generally short, frequently as long as broad, (121.6)134-172.2(201.6) um in diameter and (32)61.6-111.1(160) in length. Nodes are not tumid (Pl. IX, Fig.1) except when tetrasporangial formation occurs, they reach up to 3 times their length in diameter, (124.8)140.5-182.8(208) um in diameter and (51.2)56.2-99.1(160) um long. Pericentral cells remain partially visible after the formation of cortical cells, slightly flattened horizontally. The first 2 rows of cortical cells formed consist of cuboidal cells with irregular margins, (9.6)12.8-16(19.2) um in diameter. These cut off acropetally and basipetally smaller roundish

cells which in turn continue to divide into cells of smaller size. Nodes comprise 4 to 7 cell rows, most frequently 6 cell rows, including the partially visible pericentrals.

Tetrasporangial plants showed abaxial to whorled tetrasporangia (Pl. IX, Fig. 2). Occasionally the nodes form short projections or bracts which subtend the naked, half-protruding tetrasporangia. Several obovate tetrasporangia are formed per node, becoming narrower to their basal point of attachment.

Cystocarps are borne subterminally (Pl. IX, Fig.3), consisting of 1-2 gonimolobes subtended by 4-5 short adventitious branches.

Plants of this species were collected at two nearby localities; Maili Beach Park and Keeau Beach Park, on exposed reef benches occasionally covered by sand. Most specimens collected at Maili Beach Park had lost the apices of their longer axes and most of the tetrasporangial plants show blue-green algae growing on the small nodal bracts in the position of the tetrasporangia. The plants collected in Keeau Beach Park have incurved apices. The major differences between plants from both sites are that Keeau plants are slightly thinner than the material from Maili Beach Park and that

Keeau plants occasionally show 1-2 celled small spine-like structures located abaxially in the apices of the branches.

The collection of this species is reduced to 15 fragmented plants or pieces of plants, most of them in decaying conditions making a positive species identification difficult unless more material in better condition becomes available.

List of specimens studied:

Hawaiian Islands, Oahu: Keeau Beach Park, on intertidal reef bench, growing epilithic, May 22, 1987, leg. I. Meneses, 695 A-D, 696, 697; Maili Beach Park, growing on reef bench surrounded by sandy beach, exposed to stong wave action, intertidal, epilithic, October 16, 1987, leg. I. Meneses, 708, 709, 710, 712, 713, 714, 715, 716, 717.

<u>Ceramium</u> sp. 4

Pl. X, Figs. 3,5

Six plants of distinctive characteristics were collected at Kaneohe Bay while gathering a collection of other <u>Ceramium</u> species. The specimens are uniformly 10 mm high, with regular dichotomous branching of a primarily

upright axis which decreases in diameter towards the apex. Short adventitious branches are frequently present all along the thalli. The apices are strongly forcipate (Pl. X, Fig.5) and dentate in the inner and outer edges. Nodes and internodes are clearly distinguishable throughout the axis.

Internodes are 96-120(144) um in diameter and (156)168-324(360) um in length. Nodes are short and tumid (Pl. X, Fig.3), (96)108-156 um in diameter and (36)48-60 um long. The pericentral cells are not visible after cortical cell formation and they are also difficult to visualize in early stages of nodal development. Four to five nodal cell rows are formed of narrow cortical cells elongated vertically, with angular or slightly rounded margins. Cortical cells are produced in several overlapping layers in such way that it is difficult to individualize each of the rows.

All six specimens collected were tetrasporangial. Tetrasporangia are spherical to obovate, 48-60(72) X 36-48(60) um in diameters, produced abaxially, involucrate (Pl. X, Fig.3), somewhat protruding in their upper half.

List of specimens studied:

Hawaiian Islands, Oahu: Kaneohe Bay, Moku o Loe, on subtidal sandy reef, 1 m depth, epilithic on pieces of dead coral, August 29, 1986, leg. I. Meneses, IM 578 A-E; October 25, 1988, leg. I. Meneses, IM 995.

Ceramium sp.5
Pl. X, Figs. 1,2,4

Plants are 5-9 mm high, dichotomously branched, 4-8 dichotomies per plant, with few and often small adventitious branches. The thallus is slightly curved in habit, showing a basal portion parallel to the substrate which bents vertically ending in an erect axis. Apices are strongly forcipate (Pl. X, Fig.4) and have dentate inner and outer margins.

Internodes are broad and short, (144)156-216(240) um in diameter and (36)48-132(180) um long. Nodes are extensively developed, slightly tumid in some cases (Pl. X, Fig.1), (156)168-216(264) um in diameter and 60-96(120) um in length. The pericentral cells are not visible in developed nodes, covered by 6 to 7 rows of longitudinally elongated cortical cells (Pl. X,

Fig.2). The cortical cells often have pointed or sharp acropetal and basipetal margins. They are (3.2)4.8-12.8(16) um and 9.6-22.4 um in their horizontal and longitudinal axes respectively.

Only one plant with a single tetrasporangial branch was collected. Tetrasporangia are ovoid, involucrate and abaxially located.

A single female plant was collected showing subterminal cystocarps with 5 subtending branches.

Also, one single male specimen was recorded with clustered spermatangia located in nodes at the middle part of the thallus.

List of specimens studied:

Hawaiian Islands, Oahu: Makaha, epiphytic, intertidal reef bench, semiexposed to wave action, March 2, 1988, leg. I. Meneses, IM 754, 755, 756, 757, 758, 759, 760, 761, 762, 763, 764.

Evaluation of the species:

Ceramium spp. 3, 4 and 5 share the upright axis habit and the dichotomous branching pattern, they all show

in more or less degree the presence of adventitious branches. Although overlapping in diameter ranges, a trend in increasing thickness is detected from _Ceramium_ sp. 4 to _Ceramium_ sp. 5 with _Ceramium_ sp. 3 in intermediate position. The three species are comparatively robust for Hawaiian _Ceramium_ taxa, reaching 10 mm of height or more. _Ceramium_ sp. 4 has the longest internodes in addition to the shortest nodes of the three species. The main differences among these species as well as from other species of _Ceramium_ from Hawaii are based in the cell arrangement at the cortical bands or nodes, and in the tetrasporangial characteristics.

Ceramium sp. 3 shows a highly regular arrangement of cortical cells in nodes, the nodal diameter in this species does not differ from its internodal diameter giving the plant an evenly straight appearance. The presence naked whorled tetrasporangia is a characteristic in common with _C.aduncum_, _Ceramium_ sp.1 and _Ceramium_ _affine_ from which _Ceramium_ sp. 3 differes in size, habit, nodal structure and node/internode ratios as well.

Ceramium sp. 4 and 5 are strikingly alike. Both sets of collected specimens show a similar cortical cell arrangement in which the overlapping layers of

elongated cortical cells obscure the nodal structure
itself. They also share the abaxial arrangement of
involucrate tetrasporangia. In fact the main difference
between these two species is that whereas _Ceramium_ sp. 4
is thinner and has comparatively long nodes and
internodes, _Ceramium_ sp. 5 is thicker and has shorter
nodes and internodes. _Ceramium_ sp. 4 is found in the
protected area of Kaneohe Bay while _Ceramium_ sp. 5
inhabits reef benches exposed to wave action. These two
species may well be two forms of the same taxon, the
coarser form growing on exposed sites and the slender form
adapted to calm conditions.

Discussion

Eleven species of _Ceramium_ were collected
during this study. These were recorded growing in almost
all possible habitats around the island of Oahu, except on
basaltic rocky substrate and in the high intertidal
region. Seven of the species were always epiphytic, three
of them were saxicolous and one, _C. flaccidum_ (Kuetzing)
Ardissone, grew in organic as well as inorganic substrate.

Of the 55 species reported for the tropical and subtropical north Pacific, six are confirmed for the Hawaiian Islands: _Ceramium_ _hamatispinum_, _C_. _aduncum_, _C_. _clarionensis_, _C_. _affine_, _C_. _flaccidum_ and _C_._fimbriatum_. Additionally five species were added: two are apparently undescribed species and three were inadequately collected for certain identification.

A primary common feature shown by the 11 species is a comparatively small size, usually a few milimeters in height. The tallest of the species, _Ceramium_ sp.1 reaches a maximum of 3.5 cm. Some of these species have been reported of larger sizes in other locations, e.g., _C_. _flaccidum_ reaches up to 5 (even 10) cm in the coast of southern Australia (Womersley, 1978) whereas in Hawaii it does not exceed 1.2 cm. _Ceramium_ _affine_ plants reported by Setchell & Gardner (1930) from the Revillagigedo Islands are twice as long as Hawaiian specimens and _C_. _aduncum_ length ranges reported by Nakamura (1950) from Japan are slightly larger than those for Hawaiian plants.

The second common feature shared by all of the species from Oahu is the clear distinction of cortical bands thoughout the thallus except in the most apical portion of the axes. Species with extended cortication have also been reported for tropical and subtropical

regions (e.g., C. sinicola Setchell & Gardner, Dawson,
1944; C. huysmansii Weber van Bosse, 1923; Dawson, 1954;
1956; Trono, 1969; C. codiophila Setchell & Gardner, 1937;
C. pacificum (Collins) Kylin, Dawson, 1962) but none of
these species has been recorded for the Hawaiian Islands.
This fact grants special significance to the arrangement
of cells in the node or cortical band as a specific
diagnostic character.

The third feature which is common to almost all
of the 11 species found is the presence of two types of
organs of attachment. Short, one-cell long rhizoids
ending in a discoid digitate base are observed in two
parts of the plants. They are characteristic in the most
basal portions of the plants that grow upright as well as
in the prostrate axes of those plants which show a
differentiation into prostrate and erect axes. Long,
multi-celled, non-branched rhizoids, end in blunt apices.
These arise from the nodes throughout the thallus except
for the most apical portions of the alga. These were
observed to be formed as a result of contact with the
substrate (see chapter III).

The validity of several features in the genus
Ceramium as diagnostic characters has been assessed by
Dixon (1960), Garbary et al (1978) and Womersley (1978).

The material examined in this study shows that while some characters exhibit great variation between plants or even between branches of the same plant in some species, the same characters are constant in other species.

Sexual structures have not been considered helpful in distinguishing among species (Womersley, 1978) because of their uniformity. Reproductive material of _Ceramium_ in Oahu seems to be confined for most species to late spring and summer. In fertile male plants, spermatangia are organized in compact clusters originating from the cortical cells; they either cover the nodes partially or entirely depending on their degree of development. _Ceramium flaccidum_ is the only species which seems to have spermatangia that slightly project from the node. All female plants found show subterminal cystocarps, some species exhibiting more clearly than others the elongation of the axis bearing the cystocarp beyond the cystocarp itself (i.e _C. flaccidum_). The number of subtending branches is variable from 3 to 6, but this variation is present in all species without noticeable differences among them.

Vegetative characters, on which the distinction among species of _Ceramium_ is based (Feldmann-Mazoyer, 1940; Dawson, 1950; 1962; Womersley, 1978) proved to be

the most useful ones in combination with the arrangement
of tetrasporangia. All vegetative characters show a
certain degree of variability, the magnitude of which
depends on the species. Measurements of nodes and
internodes appear to be uniform for a few species but not
others. For example, the use of nodal diameter allows
separation of _Ceramium_ sp. 1 and _C_. _clarionensis_ from
Ceramium sp. 2 and _C_. _affine_, just as internodal diameter
can. However, these measurements qualify as a useful
trait only when they are taken at a defined position in
the thallus. Apical portions are in the process of active
development and therefore do not provide stable nodal and
internodal sizes. Basal portions are difficult to measure
and apparently some elongation of the internodes is
produced in these older parts at a later stage of
development of the individual. The thallus seems to
stabilize in its growth between the first and the third
dichotomy (starting from the base) in most plants. The
variability shown in this portion of the plant for nodal
and internodal sizes is attributed to individual
variability and not to degrees of development or
age-related processes.

Branching pattern, with the exclusion of
formation of adventitious branches, is apparently

consistent within each species. According to this character the species of _Ceramium_ found in the Hawaiian Islands can be divided into two groups. One of them shows mainly dichotomous branching and this coincides with a basically erect habit of growth, where a short basal portion of the axes is parallel to the substrate and bends to acquire an upright position. To this group belongs _C. hamatispimum_, _C. aduncum_, _C. clarionensis_, _Ceramium_ spp. 1, 3, 4, 5, _C. flaccidum_ and _C. fimbriatum_. These two last species deviate from a typical alternate branching pattern in the older portions of the thallus. The second category includes _C. affine_ and _Ceramium_ sp. 2 with a prostrate axis which produces the upright axes of the plant exclusively by adventitious branch formation.

The condition of straight or incurved apices is variable often within branches of the same plant but a general tendency prevails in each species. The presence of gland cells is a variable character in specimens of _C. flaccidum_ although it is constant and reliable in _C. aduncum_.

Cortical cell arrangement in the nodes is one of the most useful traits to differentiate among species. However, this is also subjected to certain degree of modification depending on the degree of development, i.e.,

a node located in the basal portion of the thallus versus one located in the apical region. This is clearly noticeable in C. flaccidum (Womersley, 1978) where the cell shape and arrangement in the nodes is highly variable depending on the age of the branch. In Ceramium sp.1 the pericentral cells are clearly distinguishable as a central row in the older nodes, whereas this central row is not perceivable in the younger nodes.

Special non-deciduous structures such as the spines in C. hamatispimum, the one-celled whorled projections of Ceramium sp.2 and the elongate, clavate, sac-like projections of C. fimbriatum are extremely valuable as diagnostic characters and reduce the taxonomic confusion except among those species sharing them. In such a case, the nodal structure can be used to recognize taxa.

All identified species reported in the current study have been recorded for the Pacific coast of southern North America and Central America. Four of them can also be found in the coasts of Japan and in some location around the Indo-Pacific which confirms the affinities of the flora in this region. Ceramium fimbriatum, C. clarionensis, C. affine and C. flaccidum are new records for Hawaii and have also been reported in other islands of

the North Pacific as the Marshall and the Caroline
Islands. _Ceramium_ _fimbriatum_ and _C_. _clarionensis_ show an
extended tropical and subtropical distribution that
reaches the Galapagos Islands towards the South (Dawson,
1963) and the coasts of Viet Nam towards the West (Dawson,
1954). _Ceramium_ _flaccidum_ is a widespread species in
tropical, subtropical and temperate waters. _Ceramium_
aduncum, also a new record for the Hawaiian Islands, is
probably distributed throughout the North Pacific. Two
new species are being described for Hawaii and will
probably be recorded eventually for other of the North
Pacific Islands in the course of further studies of the
marine flora of this region.

Table 3. Characteristics of _Ceramium_ _affine_ as observed from Hawaiian specimens, Dawson's collection specimens and original description.

	Dawson's specimens	Setchell & Gardner's description	Specimens from Hawaii[a]	Specimens from Hawaii[b]	Dawson's material (var. peninsularis)
Branching pattern	dichotomous few adventitious branches	dichotomous, no adventitious branches	non dichotomous only adventitious branches	dichotomous with proliferating branches	dichotomous
Internodes					
length	30-50 um[c]	120-190 um[d]	22.4-36 um[e]	48-163 um	108-140 um[c]
diameter	40-46 um	24-28 um	16-31.2 um	22.4-61 um	60-90 um
Nodes					
length	20-24 um	.	13-32 um	9.6-3.2 um	40-50 um
diameter	32-40 um	.	22.4-54.4 um	22.4-67.2 um	102-108 um
Cortical cells	1-2 cell rows pericentrals elongated vertically and acropetals small	2-3 cell rows acropetals smaller	2-4 cell rows acropetals smaller, basipetals slightly longer	1-2 cell rows acropetals smaller, basipetals slightly longer	1-2 cell rows elongated vertically
Sporangia	naked, in whorls protruding	naked, singly protruding 30-40 um diam.	naked, in whorls protruding 20-35 um diam.	.	naked, singly protruding 40 um diam.

[a] I.Meneses collection (IM 606, 607, 608a, 608b, 609, 611a, 611b, 611c)

[b] I.A.Abbott's collection (IAA 13143, 16089a, 16089b, 16089c)

[c] Values obtained from E.Y. Dawson's collection (US 006795, 36566, 006797, 006796)

[d] Actual values not given in the description but calculated multiplying the diameter of internodes by 5, since Setchell & Gardner (1930) indicated that internodes are 4-6 times as long as broad.

[e] Ranges include 85-95% of the measurements recorded, these considered the most frequent

Table 4

Characteristics of collected specimens of _Ceramium flaccidum_ from three sites on Oahu.

Feature	Kaalawai Beach	Kahala Beach	Kualoa Point
Average thallus length	5 mm	7.4 mm	6.6 mm
Length range	3.0-8.2 mm	3.1-11.5 mm	2.8-9.3 mm
Adventitious branches	Occasional	Absent	Occasional
No. of pericentrals	5-7	5-6	5-6(7)
Internodal diameter[a]	35.2-70.4(112)	(76.8)115.2-268.8(614.4)	32-96
Internodal length[a]	(54.4)102.4-387.2(419.2)	192-1228.8(1920)	(83.2)160-352(448)
Nodal diameter[a]	(51.2)64.0-96.0(128)	(115.2)153.6-268.8(345.6)	(51.2)64-108.8(121.6)
Nodal length[a]	(38.4)41.6-67.2(89.6)	115.2-230.4(268.8)	(32)41.6-70.4(80.2)
Internodal ratio (length/diameter)	1-9 times	1-15 times	2-13 times
Branching pattern	alternate	alternate	alternate
No. dichotomies/plant	(4)6-11(14)	(4)5-(10)11	5-10(11)
No. nodal cell rows	(3)4-7(8)	(4)5-7	(4)5-6(7)
Internodal diameter[b]	(35.2)41.6-70.4(102.4)	(28.8)32-70.4(76.8)	(35.2)44.8-83.2(96)
Internodal length[b]	(6.4)32-297.6(310.4)	(32)80-291.2(313.6)	(86.4)118.4-295(310)
Nodal diameter[b]	(51.2)60.8-89.6(118.4)	51.2-86.4(112)	(48)54.4-112
Nodal length[b]	(35.2)38.4-64(80)	(35.2)38.4-60.8(76.8)	38.4-70.4(86.4)
Tetrasporangial characteristics	Involucrate, 1-2 per node	Involucrate, 1-2 per node	Involucrate, whorled
Tetrasporangial size	35.2-51.2(57.6) X (38.4)45-54.4(57.6)	41.6-44.8 X 41.6-44.8	22.4-41.6 X 22.4-35.2(44.8)

[a] measurements taken at the basalmost portion of the thallus.
[b] measurements taken at the upper portions of the thallus.

Table 5

Comparison of C. flaccidum characteristics according to descriptions in the literature including species currently under synonomy.

Feature	a C.flaccidum	b as C.gracillimum	c as C.taylorii	d C.taylorii	e C.masonii	f C.flaccidum	g C.gracillimum	h C.dawsonii
Thallus length**	0.3-1.2	-	-	0.5-1.6	0.4-0.5(1)	0.5-5(10)	0.1-0.5	up to 1
Branching pattern	pseudodichotomous to alternate	pseudodichot. to alternate	pseudodichot. to alternate	alternate	alternate	alternate or occasionally dichotomous	sparse, pseudodichot.	sympodial
Adventitious branching	infrequent	often	infrequent	-	-	often	-	-
Nodal characteristics	lower half of node with horiz. elongated cells	lower half of horizontally elongated cells	lower half of horizontally elongated cells	lower third of horiz. long cells	lower third of horiz. long cells	basipetals horizontally elongated	lower half with horiz.elongated cells	basipetals horizontally elongated
No. of cortical cell rows	4-7	3-5	-	-	-	5-9(11)	3-65	up to 6
Internodal diameter *	35-70(112) or (77)115-269(614)	(32)40-72	(56)64-120(128)	up to 180	60-80	-	20-22	63-92(96)
Internodal length *	(54)102-387(448) or 192-1229(1920)	(112)128-200(296)	(120)176-240(520)	150-700(800)	-	-	50-90(130)	11-148(192)
Ratio internode (length/diam.)	1-16 times	5-6 times	3-4 times	-	-	4-6 times	1.5-8 times	-
Nodal diameter *	(51)64-109(128) or 115(154)-269(346)	40-96	64(80)-136	-	-	100-250	50-140	66-130
Nodal length *	(32)42-70(90)	32(40)-48	(48)56-80(112)	-	-	-	40-85	21-65
Ratio node (diam./length)	up to 2 times	up to 2 times	-	2-3 times	-	-	-	-

Table 5. (Continued)

Comparison of C. flaccidum characteristics according to descriptions in the literature including species currently under synonomy.

Tetrasporangial characteristics	1-2(3) per node whorled, involucrate	-	involucrate, embedded in cortex, whorled	2-6 per node involucrate whorled	whorled, embedded involucrate	(2)4-7per node involucrate whorled	1-2 per node involucrate whorled	1-2 per node protruding partially covered
Tetrasporangial size *	(22)35.2-44.8(51) X (22)42-54(58)	-	(23.5)25.5-33.3 X (18)22-29.4(33.3)	30 um diam.	-	35-50	30-50	55-65 X 72-84
Gland cells	Occasional, in upper nodal rows	-	-	-	absent	in some plants variable	present	sometimes

a - material from Hawaii (this study); b,c - from Dawson's collection; d,e - original description (Dawson, 1950; 1962); f - sensu Womersley (1978); g - description of material from Japan (Nakamura, 1965); h - data gathered from original description (Joly, 1957) and subsequent records (Rios de Moura, 1977, Stegenga & Vroman, 1987); * data measured in um; ** data measured in cm.

Table 6. Comparison of characteristics of Ceramium fimbriatum Setchell & Gardner from field
collected material and descriptions from the literature.

	Hawaiian material[a]	Dawson's collection[b]	Setchell & Gardner's[c] description
Features			
Branching pattern	Alternate to dichotomous	Alternate to dichotomous	Alternate to dichotomous
Node structure	Divided into two portions	Divided into two portions	Horizontally elongated basipetals
Internode diameter	(84)100-160(200)	155-275(375)	-
Internode length	(48)96-185(320)	(400)450-695(925)	2-3 times nodal length
Node diameter	(100)108-175(231)	(180)225-280(395)	70-90
Node length	(48)60-100(216)	125-225(275)	-
Occurrence of hairs	abaxial, whorled & bilateral	abaxial and whorled	whorled
Hair dimensions	(20)32-50(56) long (12.4)14.4-32(34) diam.	(34)40-52(60) long (18)20-28(36) diam.	55-65 long 28-32 diam.
Tetrasporangial characteristics	whorled, involucrate embedded in cortex	whorled, involucrate embedded in cortex	whorled, involucrate protruding
Tetrasporangial dimensions	(24)32-40(42) X (20)29-35.2(38.4)	38-50 X 36-44	55-65

[a] Specimens included from Oahu and Maui islands (IAA 18719, 18684, 14871a, 13055b,...).
[b] From Dawson's collection (at the NMNH, US 006482, 36447, 006844....).
[c] Based on Setchell & Gardner's species description (1924; 1937).
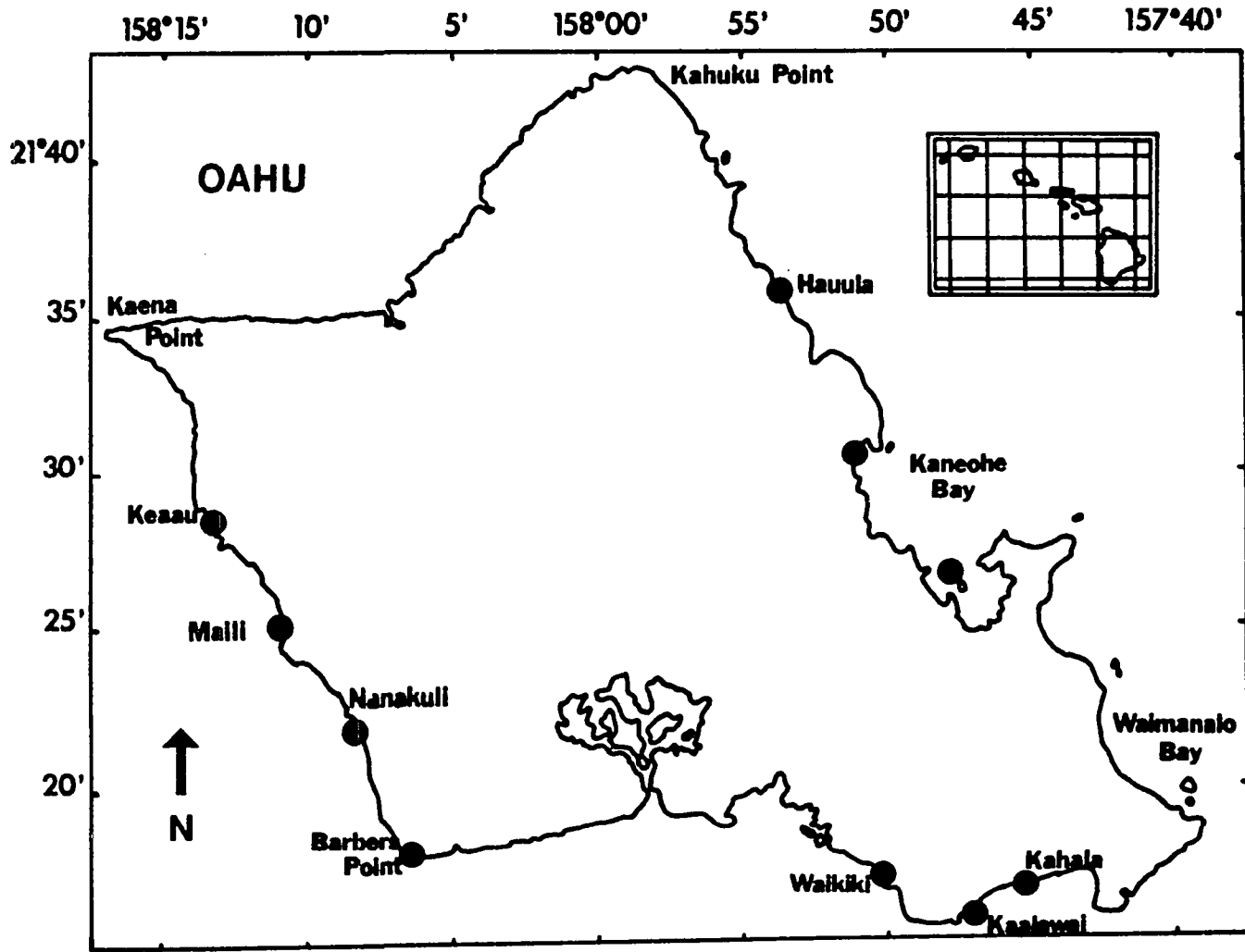
Fig.2.1   Map of the Island of Oahu showing the collecting sites.

Plate I.   <u>Ceramium</u> <u>hamatispinum</u> Dawson.

Fig. 1. Dichotomous branching pattern and forcipate
         apices. (Scale = 100 um).
Fig. 2. Spines arranged in whorls (IN=internode,
         NO=node, pc=pericentral cell, co=cortical cell,
         sp=spine). IM 742A from Keeau, Oahu (Scale = 20
         um).
Fig. 3. Nodal structure. IM 744A from Keeau, Oahu
         (Scale = 10 um).
Fig. 4. Tetrasporangial arrangement. IM 745 from
         Keeau, Oahu (Scale = 20 um).
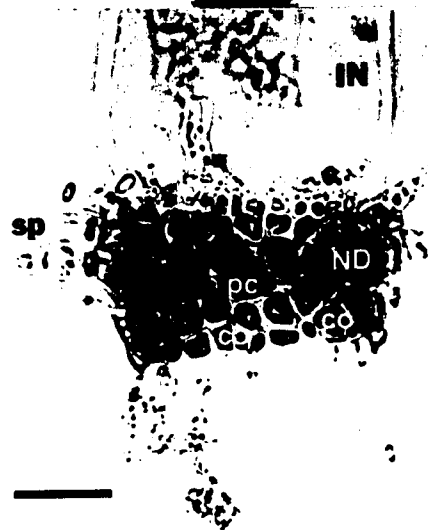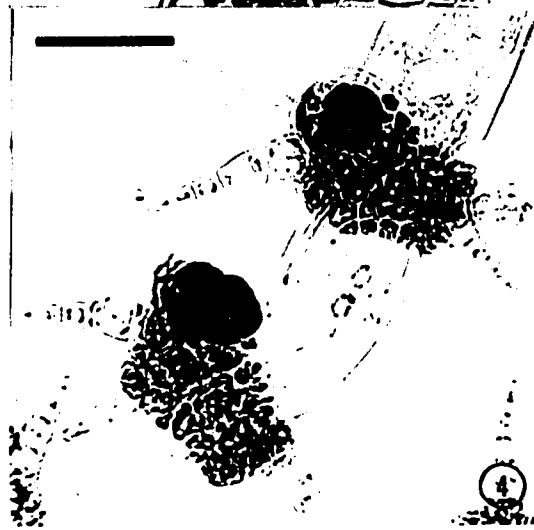
Plate II. **Ceramium** **aduncum** Nakamura.

Fig. 1. Upper portion of a plant with forcipate apices. IM 834 from Kaalawai, Oahu (Scale = 20 um).

Fig. 2. Enlargement of the upper portion of a plant with gland cells (arrow head). IM 834 from Kaalawai, Oahu (Scale = 20 um).

Fig. 3. Characteristic arrangement of internodes and nodes with gland cells (arrow head). IM 824 from Kaalawai, Oahu (Scale = 20 um).

Fig. 4. Scattered arrangement of tetrasporangia. IM 822 from Kaalawai, Oahu (Scale = 50 um).
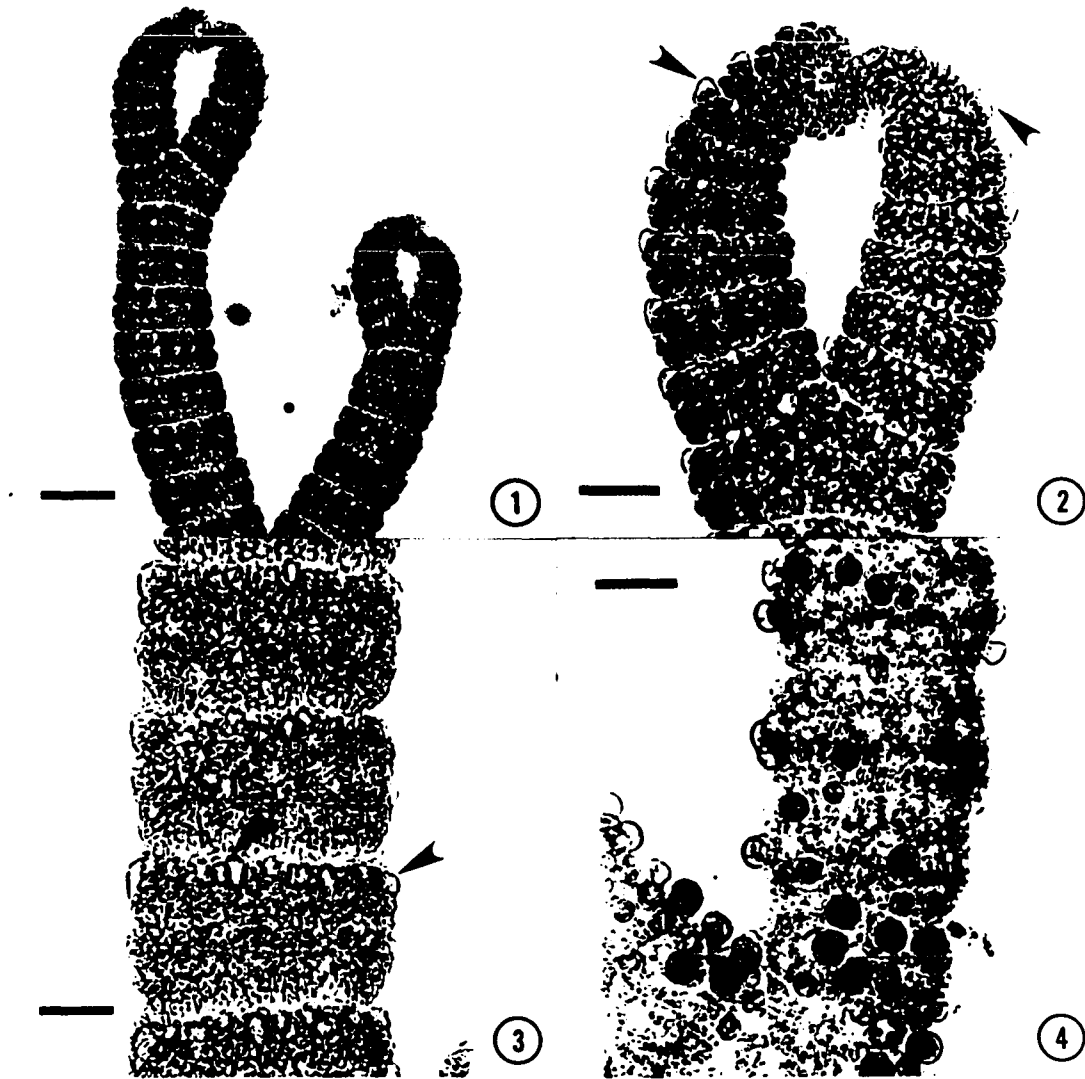
Plate III. Ceramium clarionensis Setchell & Gardner.

Fig. 1. General overview of branching pattern. IM 31
from Sans Souci beach, Oahu (Scale = 100 um).

Fig. 2. Upper portion of the thallus with flattened
ovoid axial cells and cytoplasmic strand. IM 30
from Sans Souci beach (Scale = 20 um).

Fig. 3. Lower portion of the thallus showing
comparatively more developed nodes and
internodes. IM 704 from Sans Souci beach
(Scale = 20 um).

Fig. 4. Tetrasporangial specimen. IM 20b from Sans
Souci beach (Scale = 100 um).

Fig. 5. Subterminal cystocarp and subtending branches
(Cy=cystocarp, sb=subtending branches). IM 32
from Hanauma Bay, Oahu (Scale = 100 um).

Fig. 6. Spermatangial specimen with swollen upper
branches. IM 28 from Sans Souci beach (Scale =
100 um).
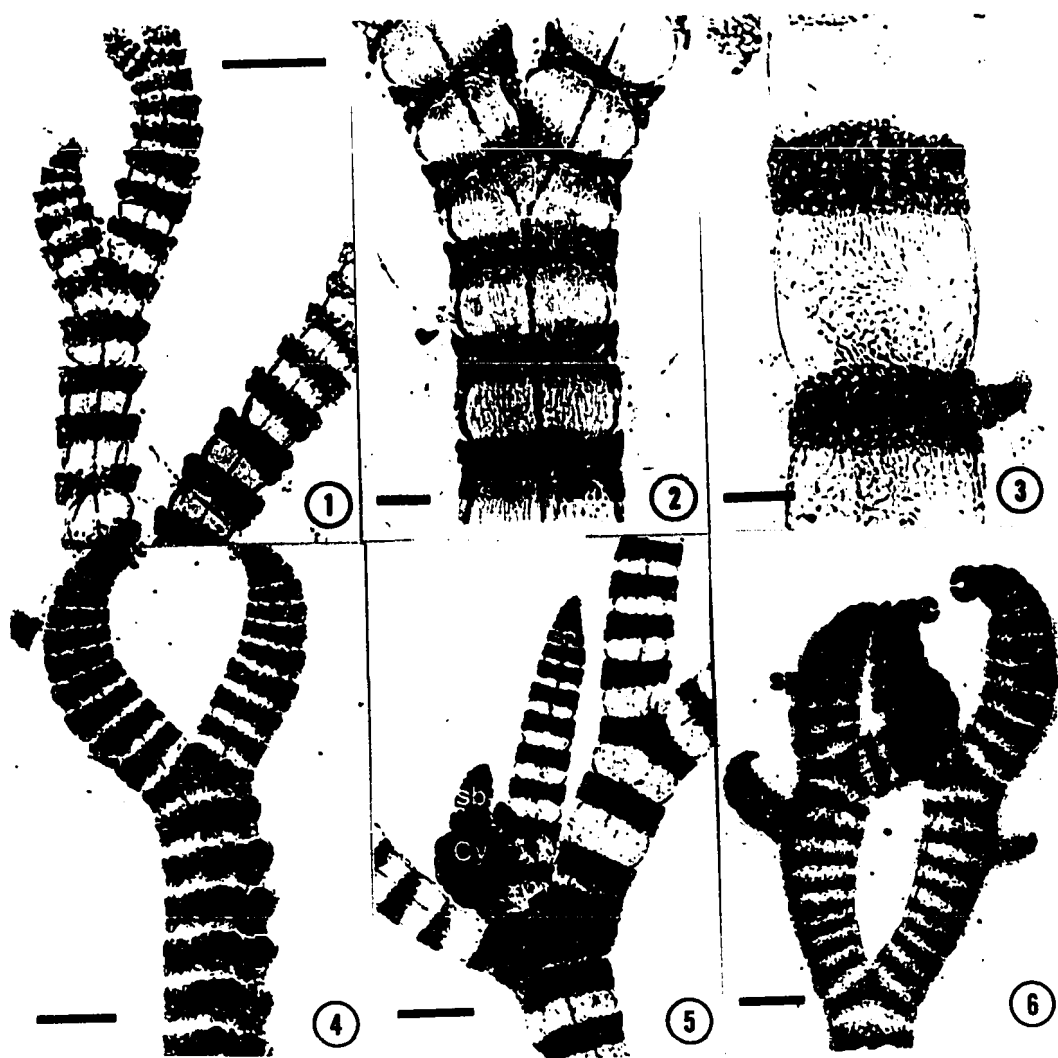
Plate IV. *Ceramium* sp.1

Fig. 1. Portion of the thallus with clearly
distinguishable nodes and internodes. IM 783
from Kaneohe Bay, Oahu (Scale = 100 um).

Fig. 2. Arrangement of non-tumid nodes and internodes.
IM 793 from Kaneohe Bay, Oahu (Scale = 20 um).

Fig. 3. Nodal enlargement showing central row of
pericentral cell (arrow head). IM 777 from
Kaneohe Bay (Scale = 20 um).

Fig. 4. Tetrasporangial specimen. IM 785 from Kaneohe
Bay (Scale = 100 um).

Fig. 5. Subtending branches surrounding a subterminal
cystocarp. IM 776 from Kaneohe Bay (Scale = 100
um).

Plate V.   _Ceramium_ sp.2

  Fig. 1.   Habit of a plant showing prostrate and erect
          portions. IAA 18004a from Hana, Maui (Scale =
          100 um).
  Fig. 2.   Curved apex of a plant with one celled
          projections (arrow heads) in nodal whorls.   IM
          735b from Kaloko Point, Oahu (Scale = 10 um).
  Fig. 3.   Nodal structure.   IAA 18026-2 from Hana, Maui
          (Scale = 5 um).
  Fig. 4.   Tetrasporangial branches.   IM 735c from Kaloko
          Point, Oahu (Scale = 50 um).
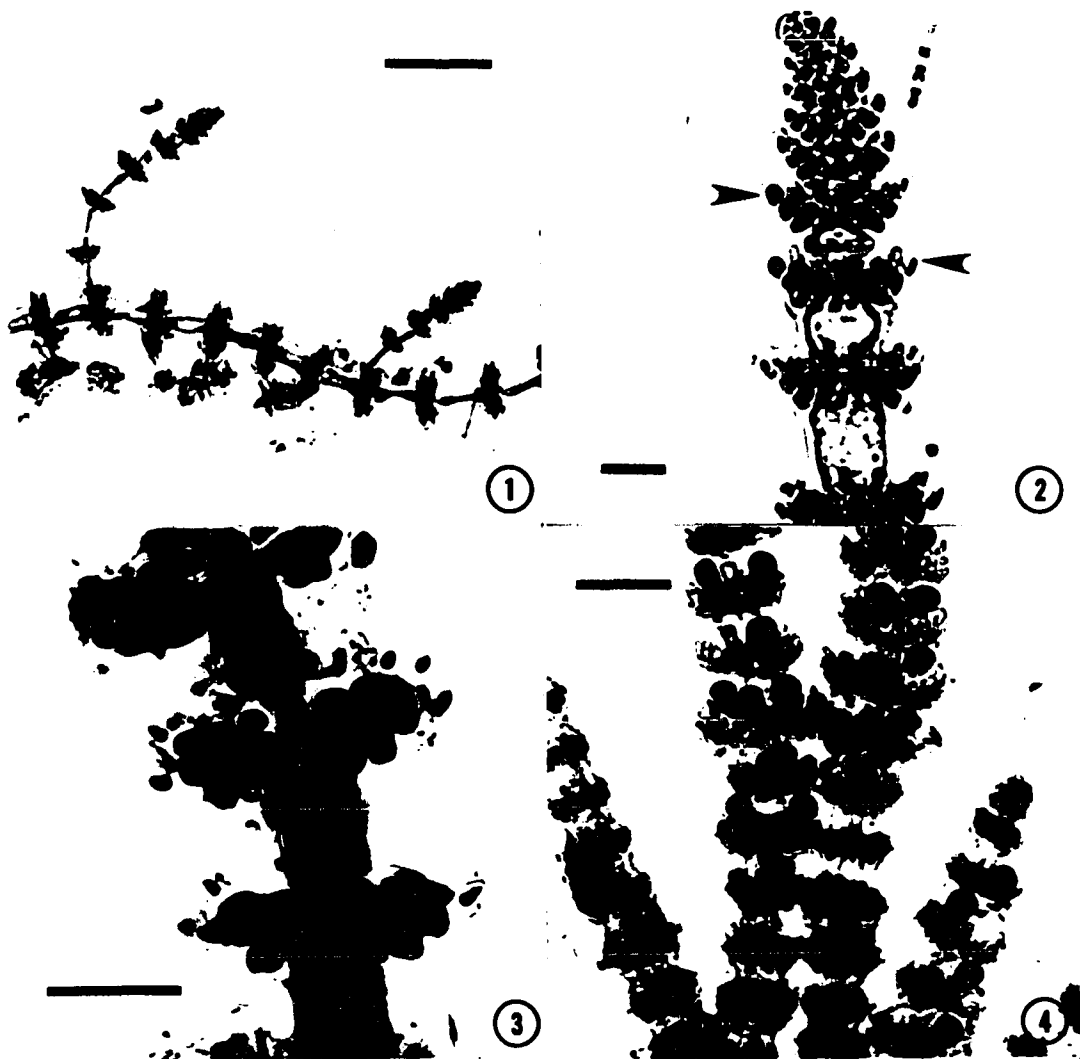
Plate VI.   <u>Ceramium</u> <u>affine</u> Setchell & Gardner.

Fig. 1.   Dichotomous branching.   IAA 16089A from Mamala
          Bay, Oahu (Scale = 50 um).
Fig. 2.   Upper portion of an upright branch.   IM 610
          from Barber's Point, Oahu (Scale = 2.5 um).
Fig. 3.   Pericentral cells (arrow heads) visible in
          nodes of prostrate branch.   IAA 16089 from
          Mamala Bay, Oahu (Scale = 2.5 um).
Fig. 4.   Characteristic habit of <u>C.affine</u>
          tetrasporangial plant. IM 611a from Barber's
          Point, Oahu (Scale = 50 um).
Fig. 5.   Spermatangial nodes in a swollen branch.   IM
          608a from Barber's Point, Oahu (Scale = 20 um).
Fig. 6.   Cystocarpic gonimolobes (Cy=cystocarp) with
          subtending branches.   IAA 16089 from Mamala
          Bay, Oahu (Scale = 20 um).
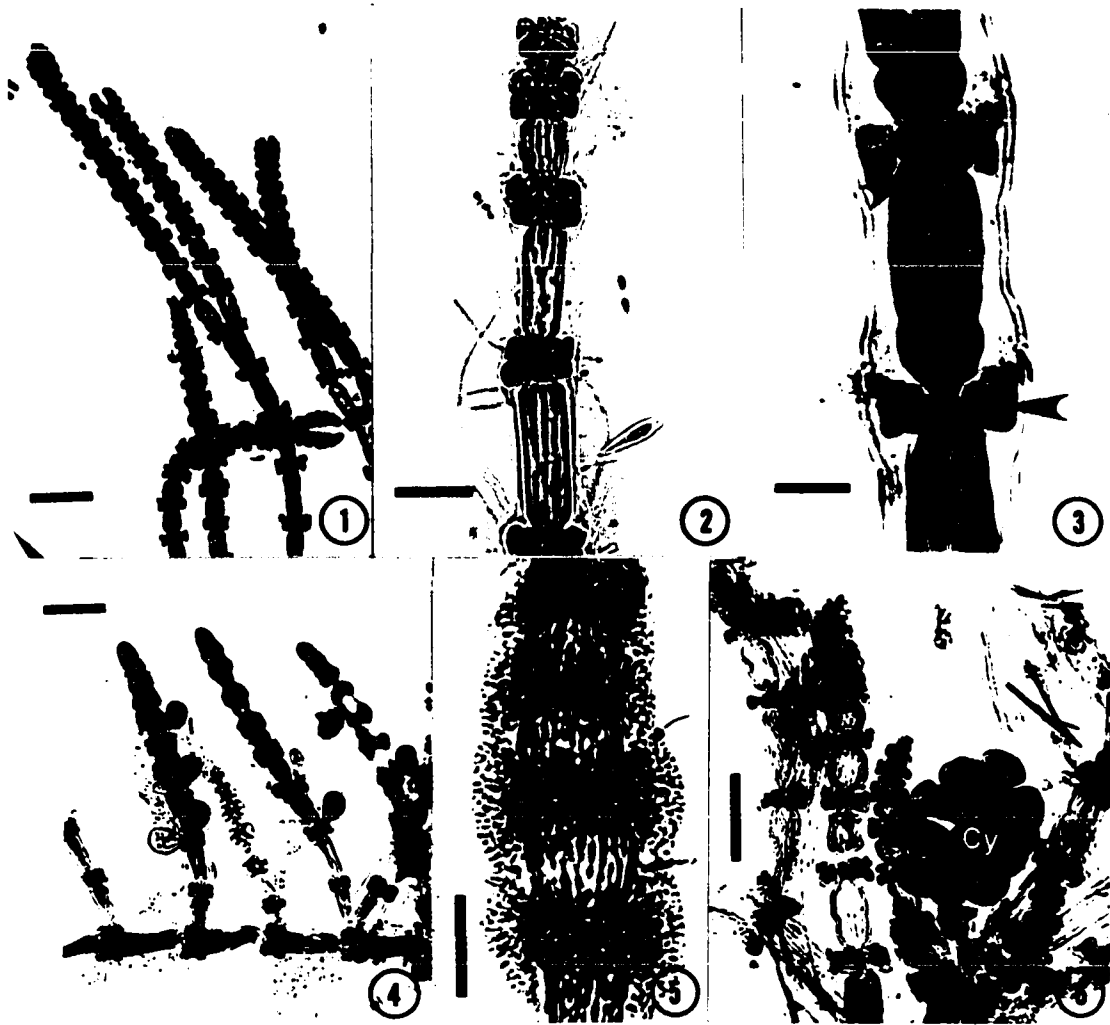
Plate VII. <u>Ceramium</u> <u>flaccidum</u> (Kuetzing) Ardissone.

  Fig. 1. Pseudodichotomous branching pattern typical of
            this species. IM 579 from Kahala,Oahu (Scale =
            500 um).

  Fig. 2. Nodal structure showing flattened lower
            cortical cells (arrow head). IM 582 from
            Kahala, Oahu (Scale = 20 um).

  Fig. 3. Tetrasporangial specimen with single sporangium
            per node. IM 580 from Kahala, Oahu (Scale = 100
            um).

  Fig. 4. Older tetrasporangial specimen with sporangia
            in whorls. IM 675 from Waikiki, Oahu (Scale =
            100 um).

  Fig. 5. Cystocarp and subtending branches. IM 674 from
            Waikiki, Oahu (Scale = 100 um).

  Fig. 6. Male plant with spermatangia around nodes
            (arrow head).
            IM 674 from Waikiki, Oahu (Scale = 20 um).
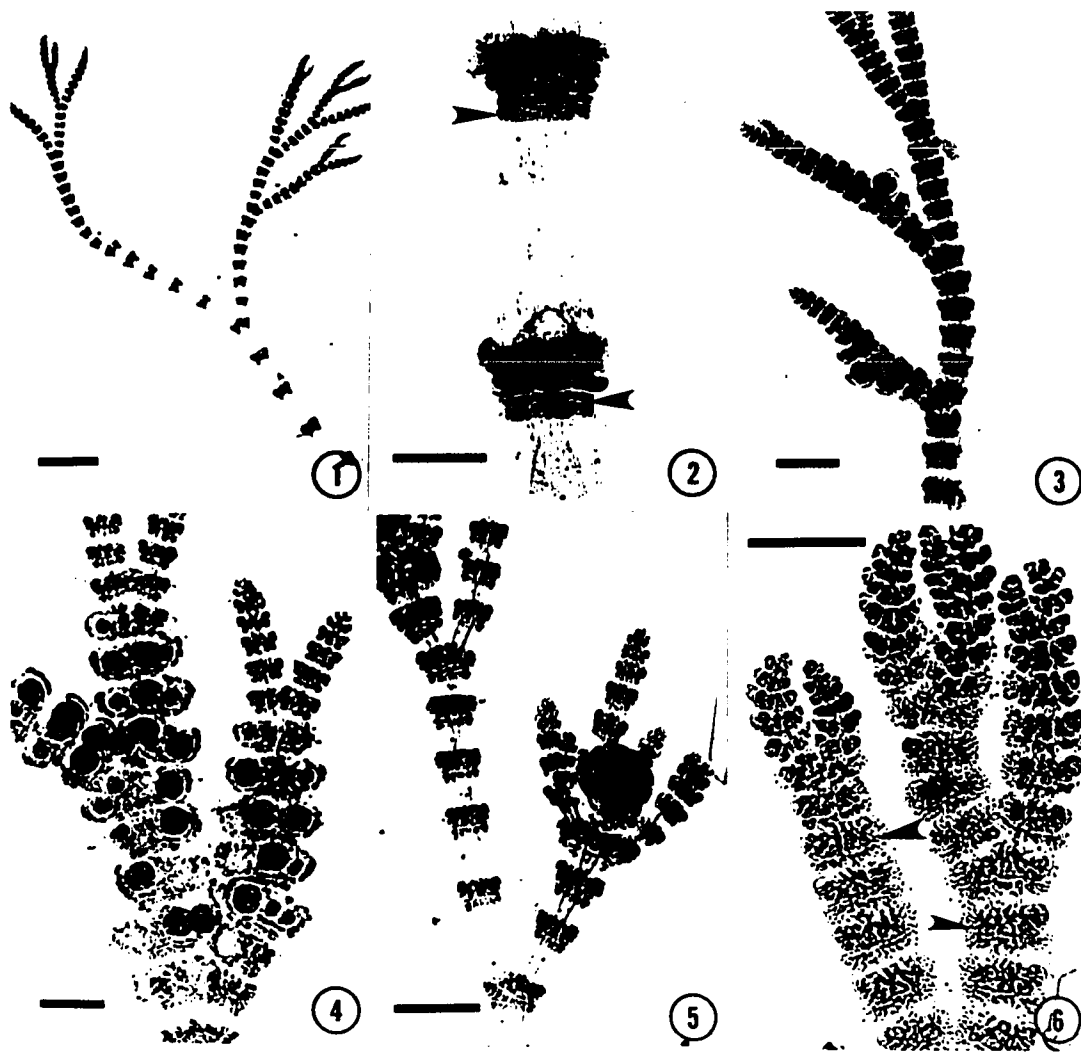
Plate VIII. <u>Ceramium</u> <u>fimbriatum</u> Setchell & Gardner.

Fig. 1. Upper portion of thallus with dichotomous-
         alternate branching. IM 951 from Kaloko Point,
         Oahu (Scale = 100 um).
Fig. 2. Apical portion of the thallus with horizontally
         elongated basipetal nodal cells (sch=sac-like
         hairs). IM 951 from Kaloko Point, Oahu (Scale =
         20 um).
Fig. 3. Apical portion of the thallus showing the
         effect of further divisions of basipetal nodal
         cells. IM 963 from Kaloko Point, Oahu (Scale =
         20 um).
Fig. 4. Basal portion of the thallus where further
         divisions in cortical cells have changed the
         original appearance of the node. IM 963 from
         Kaloko Point, Oahu (Scale = 20 um).
Fig. 5. Tetrasporangial specimen. IM 951 from Kaloko
         Point, Oahu (Scale = 50 um).
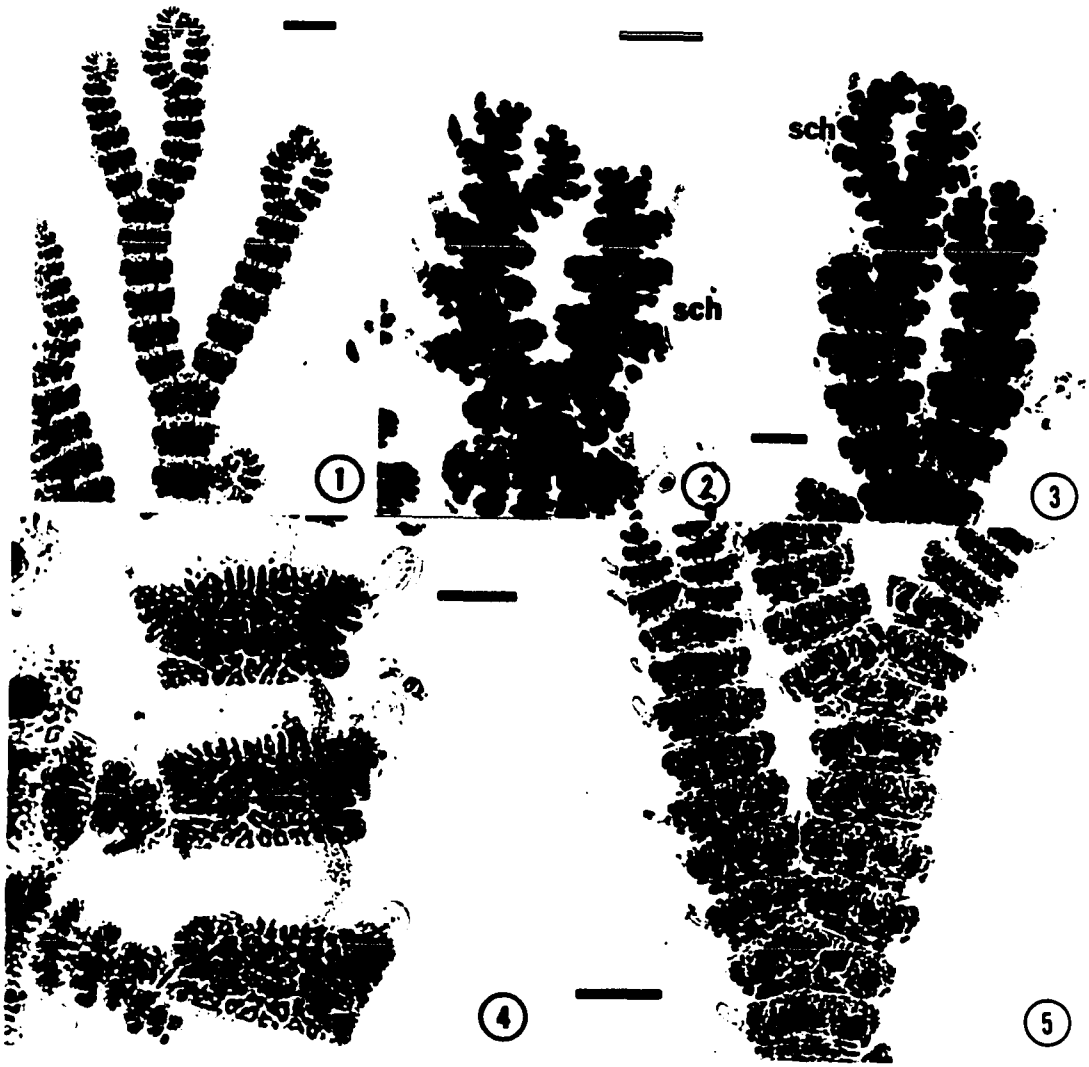
Plate IX.   <u>Ceramium</u> sp.3.

Fig. 1.   Apex of a plant showing short and non-tumid
          nodes. IM 710 from Maili Beach Park, Oahu
          (Scale = 100 um).
Fig. 2.   Tetrasporangial specimen.   IM 695b from Keeau
          Beach Park, Oahu (Scale = 150 um).
Fig. 3.   Subterminal cystocarp with subtending branches.
          IM 695d from Keeau Beach Park (Scale = 50 um).
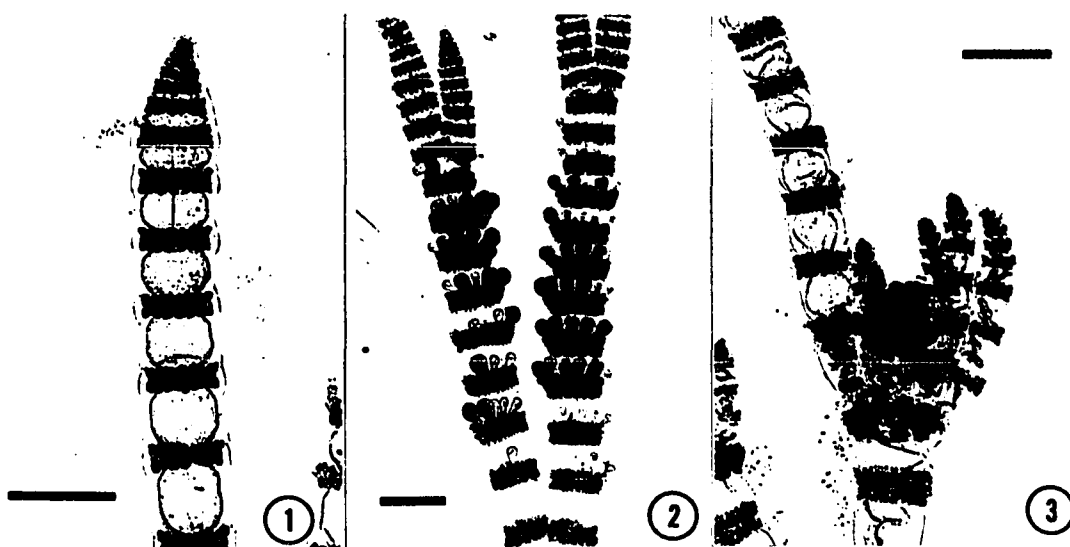
Plate X.   <u>Ceramium</u> sp.4 and <u>Ceramium</u> sp.5.

Fig. 1. Upper portion of the thallus of <u>Ceramium</u> sp.5.
         IM 757 from Makaha, Oahu (Scale = 10 um).
Fig. 2. Lower portion of the thallus of <u>Ceramium</u> sp.5.
         IM 764 from Makaha, Oahu (Scale = 20 um).
Fig. 3. Tetrasporangial branch of <u>Ceramium</u> sp.4 showing
         involucre subtending each tetrasporangium. IM
         578a from Kaneohe Bay, Oahu (Scale = 100 um).
Fig. 4. Forcipate and dentate apices of <u>Ceramium</u> sp. 5.
         IM 756 from Makaha, Oahu (Scale = 20 um).
Fig. 5. Forcipate apex of <u>Ceramium</u> sp.4. IM 995 from
         Kaneohe Bay, Oahu (Scale = 10 um).
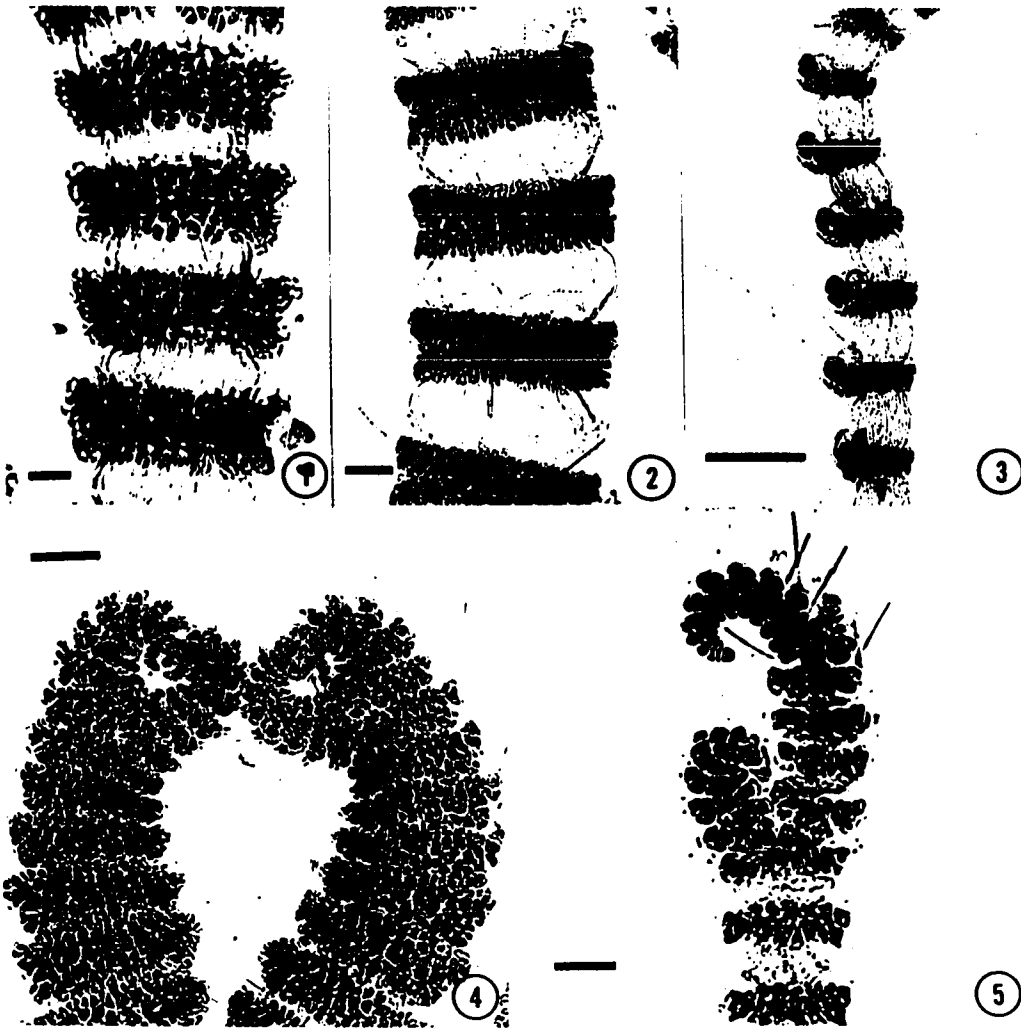
Literature cited

Abbott, I.A. 1974. Brackish-water algae from the Hawaiian
    Islands. Pac. Sci. 1: 193-214.

----- 1980. Early collections of Hawaiian marine algae.
    Pac. Sci. 34: 101-107.

----- & Hollenberg, G.J. 1976. Marine algae of California.
    827 pp. Stanford Univ. Press, California

Agardh, J.G. 1851. Species genera et ordines algarum
    ...vol. 2(1). p. (ii-iii), (i)-xii, (I)-351, Lund.

----- 1876. Species genera et ordines algarum...vol. 3(1).
    p. (ii-iii), (i)-vii, (I)-724, Lund.

----- 1894. Analecta algologica. Cont.II. Acta Univ. Lund
    30: 1-98.

Athanasiadis, A. 1987. A survey of the seaweeds of the
    Aegean Sea with taxonomic studies on species of the
    tribe Antithamnieae (Rhodophyta). vii + 174 pp, Dept.
    Marine Botany, Univ. Gothenburg, Gothenburg.

Boergesen, F. 1924. Marine algae. In: Ostenfeld,
    C.H.,Botanical results of the Dana-Expedition, 1.
    Plants from Beata Island, St. Domingo, collected by
    C.H. Ostenfeld. Dansk Bot. Arkiv. 4(7): 14-35.

----- 1930. Marine algae from the Canary Islands. III
Rhodophyceae. Kgl. Danske Vidensk. Selskab. Biol.
Medd. 9: 1-159.

----- 1952. Some marine algae from Mauritius, Additions V.
Kgl. Danske Vidensk. Selsk. Biol. Medd. 18: 1-72, 5
pl.

Collins, F.S. & Hervey, A.B. 1917. The algae of Bermuda.
Proc. Am. Acad. Arts Sci. 53: 3-195.

Dawson, E.Y. 1944. The marine algae of the Gulf of
California. A. Hancock Pacif. Exped. 3:189-454.

----- 1945a. Notes on Pacific coast marine algae, II.
Bull. So. Calif. Acad. Sci. 64: 22-27.

----- 1945b. Marine algae associated with upwelling along
the Northwestern coast of Baja California, Mexico.
Bull. So. Calif. Acad. Sci. 44: 57-71.

----- 1949. Contributions toward a marine flora of the
Southern California Channel Islands, I-III. A.
Hancock Found. Publ., Occas. Pap. 8:1-57.

----- 1950. A review of Ceramium along the Pacific coast
of North America with special reference to its
Mexican representatives. Farlowia 4: 113-138.

----- 1954a. The marine flora of Isla San Benedicto
following the volcanic eruption of 1952-1953. A.
Hancock Found. Publ., Occas. Pap. 16: 1-25.

------ 1954b. Marine plants in the vicinity of the Institute Oceanographique de Nha Trang, Viêt Nam. Pac. Sci. 8: 373-469.

----- 1954c. Notes on Pacific coast marine algae. VI. Wasmann. J. Biol. 11: 323-351.

----- 1956. Some marine algae of the southern Marshall Islands. Pac. Sci. 10: 25-66.

----- 1957a. An annotated list of marine algae from Eniwetok Atoll, Marshall Islands. Pac. Sci. 11: 92-132.

----- 1957b. Marine algae from the Costa Rican Gulfs. Contrib. Sci., L. A. Co. Mus. 15: 3-28.

----- 1961a. A guide to the literature and distributions of Pacific benthic algae from Alaska to the Galapagos Islands. Pac. Sci. 15: 370-461.

----- 1962. Marine red algae of Pacific Mexico. Part 7. Ceramiales: Ceramiaceae, Delesseriaceae. A. Hancock Pac. Exped. 26: 1-207.

----- 1963. New records of marine algae from the Galapagos Islands. Pac. Nat. 4:3-23.

De Boer, J.A. & Whoriskey, F.G. 1983. Production and role of hyaline hairs in *Ceramium rubrum*. Mar. Biol. 77: 229-234.

Dixon, P.S. 1960. Studies on marine algae of the British
    Isles: the genus Ceramium. J.Mar. Biol. Assoc. U.K.
    39: 331-374.

Doty, M.S., Gilbert, W.J. & Abbott, I.A. 1974. Hawaiian
    marine algae from seaward of the algal ridge.
    Phycologia 13: 345-357.

Feldmann-Mazoyer, G. 1940. Recherches sur les Ceramiacees
    de la Mediterranee occidentale. 510 pp. Imprimerie
    Minerva, Alger.

Funk, G. 1955. Beitraege zur kenntnis der Meeresalgen von
    Neapel. Publ. Staz. Zool. Napoli Suppl. 25: 178 pp.,
    30 pls.

Garbary, D., Grund, D.W. & McLachlan, J. 1978. The
    taxonomic status of Ceramium rubrum (Huds.) C. Ag.
    (Ceramiales, Rhodophyceae) based on culture
    experiments. Phycologia 17: 85-94.

Harvey, W.H. 1848. Phycologia Britannica. Reeve, London.
    Pp. * Pls. 145-216.

----- 1853. Nereis Boreali-Americana II, Rhodospermae.
    Smithsonian Contr. Knowledge 5: 1-258.

----- 1855. Some account of the marine botany of the
    colony of Western Australia. Trans. Roy. Ir. Acad.
    22: 525-566.

Hollenberg, G.J. 1948. Notes on Pacific marine algae.
Madrono 9: 155-162.

----- 1968. Phycological Notes III. New records of marine
algae from the central tropical Pacific ocean.
Brittonia 20: 74-82.

Itono, H. 1972. The genus Ceramium (Ceramiaceae,
Rhodophyta) in southern Japan. Bot. Mar. 15: 74-86.

----- 1977. Studies on the Ceramiaceous algae (Rhodophyta)
from southern parts of Japan. Nova Hedwigia Bibl.
Phycol. 35: 1-499.

Johansen, D.A. 1940. Plant Microtecnique. 523 pp. Mc
Graw-Hill Book Company, New York.

Joly, A.B. 1957. Contribuicao as conhecimento da flora
ficologica marinha da Baía de Santos e arredores.
Univ. Sao Paulo Fac. Filos., Cien. e letr. Bol. 217.
(Botanica 14) 195 pp.

Kuetzing, F.T. 1862. Tabulae Phycologicae. Vol 12.
Nordhausen.

Mazoyer, G. 1938. Les Ceramiees de l'Afrique du Nord.
Bull. Soc. Hist. Nat. Afrique du Nord 29: 317-331.

Nakamura, Y. 1950. New Ceramium and Campylaephoras from
Japan. Sci. Pap. Inst. Algol. Res. Hokkaido Univ. 3:
155-172.

----- 1965. Species of the genera Ceramium and
Campylaephora especially those of northern Japan.
Sci. Pap. Inst. Algol. Res. Hokkaido Univ. 14:
52-71.

Richards, H.M. 1901. Ceramothamnion codii, a new
Rhodophyceous alga. Bull. Torrey Bot. Club 28:
257-320, 2 pls.

Roth, A.W. 1797. Catalecta botanica..., pt. I. vii + 244+
2 pl. index + 8 name index,pls. 1-8. Bibliopolo
I.G. Mülleriano, Lipsiae.

Setchell, W.A. & Gardner, N.L. 1924. Marine algae of the
Gulf of California. Proc. Calif. Acad. Sci., 4th
Ser., 12: 695-949, pls. 12-88.

----- 1930. Marine algae of the Revillagigedo Islands
expedition of 1925. Proc. Calif. Acad. Sci. 19:
109-215.

----- 1937. The Templeton Crocker expedition of the
California Academy of Sciences, 1932. No. 31. A
preliminary report on the algae. Proc. Calif. Acad.
Sci., 4th Ser., 22: 65-98, pls. 3-25.

Stegenga H. & Vroman, M. 1987. Notes on some Ceramiaceae
(Rhodophyta) from Curacao, especially those from
exposed Northeast coast. Blumea 32: 397-426.

Suh, Y. & Lee, I.K. 1984. Morphology and reproduction of some species of Ceramium (Rhodophyta) in culture. Korean J. Bot. 27: 163-171.

Taylor, W.R. 1942. Caribbean marine algae of the Allan Hancock expedition, 1939. Rpt. A. Hancock Exped. 2: 1-193.

------ 1960. Marine Algae of the Eastern Tropical and Subtropical Coasts of America. 870 pp. Univ. Michigan Press, Ann Harbor.

Trono, G.Jr. 1969. The marine benthic algae of the Caroline Islands, II. Phaeophyta and Rhodophyta. Micronesica 5: 25-119.

Tsuda, R.T. 1965. Marine algae from Laysan Island with additional notes on the vascular flora. Atoll Res. Bull. 110: 1-37.

------ 1966. Marine benthic algae from the leeward Hawaiian group. Atoll Res. Bull. 115: 1-13.

------ & Abbott, I.A. 1985. Collection, handling, preservation and logistics. In: M.M. Littler & D.S. Littler (eds.), Handbook of Phycological Methods. Ecological Field Methods: Macroalgae. Cambridge Univ. Press, Cambridge. Pp. 68-85.

----- & Trono Jr., G. 1968. Marine benthic algae from

  Howland Island and Baker Island, Central Pacific.

  Pac. Sci. 22: 194-197.

Weber-van Bosse, A. 1923. Liste des algues du Siboga III.

  Rhodophyceae. Pt.II: Ceramiales. In: Weber, M. (ed.),

  Monogr. Siboga Exped. 59c: 311-392, pls. 9-10.

Womersley, H.B.S. 1978. Southern Australian species of

  Ceramium Roth (Rhodophyta). Aust. J. Mar. Freshwater

  Res. 29: 205-257.

Yendo, K. 1917. Notes on algae new to Japan, VI. Bot. Mag.

  Tokyo 31: 92-93.

CHAPTER III

MORPHOLOGICAL VARIATION OF SELECTED SPECIES OF CERAMIUM

Abstract

As in several other algal species, _Ceramium_ species can exhibit a wide range of morphological variability. This variability often affects the taxonomic identity of species and obscures the boundaries among taxa. In Hawaiian species of _Ceramium_, some features selected for taxonomic evaluation can vary and the character variation can be statistically significant ($P<0.01$) even among branches of the same plant. A survey of plants of _C. flaccidum_ (Kuetzing) Ardissone was made from individuals in i) different localities, ii) along a transect across the reef within one of the chosen localities and iii) throughout a 9-month period within the same natural population. In these instances variability was detected in most of the characters evaluated. Nevertheless, this did not affect the recognition of this particular species, since its nodal structure is a stable character which can stand alone for its identification.

Plants of C. flaccidum and the undescribed
species Ceramium sp.1 showed differences in morphological
characters between progenies from different parental
plants when cultured under the same laboratory
conditions. On the other hand, clones of both species
also showed statistically significant differences when
cultured under different conditions. These two results
suggest that this variation has genetic as well as
phenotypic components, and that environmental conditions
contribute to the overall magnitude of interpopulational
variation.

Variability in morphological characters of
Ceramium species was not only present within and among
individuals of the same generation but also between
individuals in different life-history stages. Growth of
tetrasporophytes of C. clarionensis Setchell & Gardner
significantly differed from gametophytes of the same
species under identical culture conditions. Differences
in vegetative morphology may also occur even between male
and female gametophytes of the same species when these are
grown under the same conditions.

Thus although most morphological characters in
Ceramium taxa are highly variable, the taxonomic

consequences of this variability depend on the particular species and its diagnostic characters.

Introduction

Taxonomic distinction among species of Ceramium Roth is obscured by morphological variation (Dixon ,1960). Species which display a variety of forms that overlap each other or with other species have been frequently treated as 'complexes' (Levring, 1937; Feldmann-Mazoyer, 1940). The lack of understanding for this degree of variation that represents character limits for each species, has led to observations of phenotypic variability of three major features: i) natural populations, ii) age or reproductive phases of plants, and iii) environmentally induced changes. As a result, descriptions of Ceramium species have become more precise by including a larger number of specimens and have taken into account the developmental aspects of diagnostic characters (Dixon, 1960; Womersley, 1978).

Later studies which focused on those characters which apparently were taxonomically reliable (Dawson, 1950; Nakamura, 1954; Dixon, 1960) demonstrated that several features could be modified in culture (Garbary et

al, 1978) to the extent of "making" one Ceramium species identical with another in morphology . Under light and temperature regimes, changes such as cell elongation, cortical band development, cell size and shape and other characteristics were produced so that the validity of approximately 12 species of Ceramium has been questioned (Garbary et al, 1978). Moreover, characters that were used to delimit the species such as C. paniculatum Okamura and C. aduncum Nakamura (Suh & Lee, 1984) were completely changed when plants were grown under artificial conditions.

Response to environmental factors is not expected to affect all species in the same way. This may explain why the taxonomic limits (Dixon, 1960) of some species are apparently well defined while the species limits of others undergo constant change. Similarly, not all characters are expected to be equally variable or constant within each species. The circumstances under which these characters are affected might also vary. Certain features such as branching pattern and thallus size are variable between gametophytic and tetrasporophytic generations (Garbary et al, 1980); cortical band development seems to be affected equally in both phases by light duration (Garbary et al, 1978).

Species such as <u>Ceramium</u> <u>paniculatum</u> and <u>C</u>.
<u>aduncum</u> (Suh & Lee, 1984), or <u>C</u>. <u>clarionensis</u> (Setchell &
Gardner, 1930; Dawson, 1950; Nakamura, 1950) and <u>C</u>.
<u>flaccidum</u> (Womersley, 1978) which are part of the Hawaiian
algal flora, are morphologically variable or taxonomically
difficult to delimit. Plants of <u>C</u>. <u>clarionensis</u>, <u>Ceramium</u>
sp. 1 and <u>C</u>. <u>flaccidum</u> were examined in the field and
under controlled laboratory conditions. Morphological
variability of these species was analyzed to dtermine the
basis of variation. Specifically, observations and
experiments were aimed at assessing the role of internal
factors (reproductive phase, genetic variability among
individuals) and responses to changes in environmental
conditions (photon flux density, photoperiod, nutrient
concentration) in producing overall variation of <u>Ceramium</u>
taxa.

This chapter evaluates and analizes experimental
data on morphological characteristics of cultured
specimens to test the validity of features used to delimit
taxa.

Materials and Methods

Three defined taxa of <u>Ceramium</u> were selected as material for morphological studies: <u>Ceramium clarionensis</u>, <u>Ceramium</u> sp. 1 and <u>C</u>. <u>flaccidum</u>. These species were the most accessible and abundant at collecting sites, and were the ones which grew well in culture conditions. The material utilized for laboratory experiments was collected at the same sites and handled similarly throughout this study.

<u>Ceramium clarionensis</u> was collected from the south wall of the Waikiki Natatorium at Sans Souci Beach (Fig. 2.1 in chapter II) where it was abundant during the Fall of 1987. <u>Ceramium</u> sp. 1 is present all year round on the reef flats around Coconut Island in Kaneohe Bay. <u>Ceramium flaccidum</u> was obtained from a shallow subtidal population at Kaalawai Beach.

Studies of temporal changes in morphology of <u>C</u>. <u>flaccidum</u>.

Monthly monitoring of a natural population of <u>C</u>. <u>flaccidum</u> was undertaken during 1986. The population

consisted of a well defined group of plants growing epiphytically on <u>Acanthophora</u> <u>spicifera</u>. Host plants grew attached to a prominent rock approximately 20 m from shore at Kaalawai Beach. <u>Ceramium</u> plants were always submerged, confirmed by observations over 3 years. Fifteen plants were collected each month by clipping the host branches to which they were attached. From each plant 5 to 6 branches were detached and mounted on permanent slides for observation. Node and internode measurements were made on cells of the most basal portion of the thallus, located below the second dichotomy. Cells at that level of the alga seem to have attained their final size and stopped further development.

Spatial variation in morphology of <u>C</u>. <u>flaccidum</u>.

Plants of this species were observed growing at Kahala Beach Park on pieces of dead coral. A 100 m transect was set perpendicular to shore and sampling stations were established at 5 m intervals along the transect. A 50 x 50 cm quadrat of flexible plastic was placed on the bottom at each side of the transect line at each 5m point, giving a 100 cm X 50 cm cm sampling area. All material of <u>Ceramium</u> enclosed in the quadrats was

collected in plastic bags, labeled and taken back to the laboratory. Subsamples of each plant were mounted as permanent slides for observation. Quantitative characters recorded included: length of the main axes, node diameter and length, internode diameter and length, number of dichotomies per plant, distance between consecutive dichotomies, number of cells between dichotomies, and number of adventitious branches. Node and internode dimensions and structure were chosen because they are the main characters on which the vegetative structure of Ceramium is based. The number and distance between dichotomies as well as the number of adventitious branches were selected because they are the main components of the branching pattern of the species, a feature whose significance as a diagnostic character is to be explored.

Morphological variability in different life-history stages of C. clarionensis in culture.

Ceramium clarionensis is an epiphyte on Galaxaura and Laurencia. Because it is too small to reliably detect in the field, macroalgal anchor species were hapazardly collected across the Waikiki Natatorium wall, placed in plastic bags and carried back to the

laboratory where they were examined under a Zeiss light microscope for epiphytic _Ceramium_ plants. Reproductive specimens of _C_. _clarionensis_ were separated and cleaned in sterilized seawater. Pieces of branches bearing reproductive structures were cut off and left overnight in disposable plastic Petri dishes containing sterilized seawater. Spores released from several individuals were collected the next morning with a micropipette and transferred to fresh Petri dishes with full strength von Stosch culture medium (McLachlan, 1979). Culture medium was changed every six days. Four to six Petri dishes with carpospores were placed in a Psycrotherm controlled environment incubator under photon flux densities of 35-62 uE m^{-2} s^{-1}, at 20-25°C and 16:8 h LD daylength regime. Illumination was provided by fluorescent cool-white tubes (Sylvania 32W). Four to six Petri dishes containing carpospores from the same pool of plants used for the previous experiment were kept on a counter next to a window facing South, allowing them to receive natural sunlight.

Tetraspores were obtained the same way as carpospores. Experiments were kept until plants achieved the average size (2.0-9.0 mm tall) of adult plants in the field or until they became reproductively mature, in

approximately 30 days. Specimens were mounted on
microscope slides to evaluate morphological characters. A
second set of tetraspores collected a month later was
treated in the same way as those set up in the culture
chamber. These experiments were also monitored in the
same way, and they are mentioned in the Results section as
the second set of gametophytes. Field plants were
collected at the same time the cultures were ended and
used for morphological comparison with
artificially-cultured material.

Morphological variability in different life-history stages
of _Ceramium_ sp. 1.

Plants of _Ceramium_ sp. 1 were collected in
Kaneohe Bay reefs and cultured in the same way as plants
of _C. clarionensis_. Three light intensity ranges were
obtained by changing the number of fluorescent tubes in
the culture chamber and by placing sheets of tracing paper
as a screen on top of the Petri dishes. Direct light was
equivalent to a photon flux density range between 36 and
61 uE m^{-2} s^{-1}; light I was obtained by placing two
sheets of tracing paper allowing a photon flux density of
22 to 35 uE m^{-2} s^{-1}; light II is equivalent to 17 to

25 uE m^{-2} s^{-1} and was obtained with four sheets of
tracing paper. Two sets of spores, one of carpospores
and the other of tetraspores were placed on a counter
allowing natural sunlight to illuminate them; these plants
were treated as a control for photon flux density and
daylength. Comparisons of all specimens grown under
artificial culture conditions was made with plants
reproductively mature collected from the field at the time
the experiments ended.

Morphological variability in branches of Ceramium sp. 1
and C. flaccidum under different daylength regimes.

A few selected specimens on the basis of their
branch abundance were collected and brought in plastic
bags with seawater to the laboratory. Ceramium plants
were separated from other algae, animals and substrate
particles in sterilized seawater. Upper portions of
branches were cut off, placed in a Petri dish with culture
medium and counted as one individual. Each branch
comprised 3 to 4 dichotomies and had their apices intact.
A minimum of 30 branches was placed per Petri dish and
replicates were made when the number of branches in the
parental plant were abundant enough. Occasionally, some

branches were injured during the handling process and divided into two fragments, with each fragment growing into a fully developed individual, or sometimes loosing their pigment and dying. A permanent microscope slide was made from each plant at the end of one week. Three daylength regimes, 16:8, 12:12 and 8:16 h LD were used for culturing Ceramium sp. 1. Each new algal collection received the same treatment, as did the C. flaccidum cultures. The scarcity of abundantly branched individuals of C. flaccidum did not allow a thorough analysis among progenies cultured under 12:12 and 8:16 h LD daylength regimes.

Morphological variability in Ceramium sp. 1 and C. flaccidum under different nutrient concentrations, water movement conditions and daylength regimes.

Cultures of following treatments were started from branches treated in the same way as in the previous experiments. Branches of the same plant were used each in set of six experimental conditions (summarized in Table 7). Combinations of 3 daylength regimes, 3 different concentrations of nitrate and phosphate and, 2 conditions of water movement were used. Three solutions of von

Stosch s medium were used: a full strength medium
solution; a solution with 90% of the original
concentration of nitrate and 97.5% of the original
concentration of phosphate; and a third solution with 80%
of the original concentration of nitrate and 95 % of the
phosphate concentration (Table 2). Although no
information is available about the nutrient requirements
of this genus, these concentrations have been used to
induce formation of reproductive structure (McLachlan,
1979) and thus, they are assumed to have a detectable
physiological effect on plants. It is expected that these
physiological changes have a counterpart in the morphology
of the plants. Water movement was provided by a Lab-Line
Juniot Orbit Shaker set at 2500 (rpm).

Characters analyzed are listed in Table 1.
Quantified characters were all tested for normality
(Shapiro-Wilks statistic for small samples and Kolmogorov
statistic for large samples) before any further analysis.
Since most quantitative characters tested were not
normally distributed, all comparisons were made using
non-parametric tests (Wilcoxon- Mann-Whitney test for two
sample comparisons; Kruskal-Wallis one-way analysis of
variance for k independent samples) (Siegel & Castellan,
1988). All analyses were made using the Statistical

Analysis System (SAS) program (SAS Institute Inc., 1987),
Release 6.03. All quantitative characters are reported in
ranges in which the numbers between the parenthesis are
the extreme values of the range which includes all
measurements done. The numbers outside the parenthesis
indicate the limits of the range that include 85% of all
measurements taken.

Results

Studies of temporal changes in morphology of _C. flaccidum_.

All plants of Ceramium flaccidum collected
throughout the 9 months of filed sampling from the
Kaalawai population were sterile. Thalli were always
easily recognizable due to their characteristic alternate
branching pattern and nodal structure. Qualitative
characters remained the same with no observable major
variations. Elongate-clavate sac-like hairs identical to
those of _C. fimbriatum_ were recorded only once in 2
plants. The four quantitative characters recorded showed
overall changes throughout the sampling period without any
apparent pattern. Significant variation ($P<X^2 = 0.001$,
Kruskal-Wallis test) can be present from one month to the

next or several months apart (Table 8). No correlation
is observable between the morphological variation of any
of the characters and the month sampled.

Spatial variation in morphology of C. flaccidum.

The abundance of plants of C. flaccidum
decreases abruptly (Fig. 3.1a) 30 m from the shore line.
Thirty to 50 plants are present per m^2 near shore,
while there are less than 3 per m^2 from 30 to 50 m from
the shore, and then none seaward after 50 m. Plants are
visible against the sandy bottom of the reef and often
they are the only algae present at certain areas,
although frequently combined with other filamentous
genera (e.g., Centroceras, Lyngbya, Polysiphonia, etc).
The absence of Ceramium flaccidum specimens after 50 m
coincides with an increase in water turbulence as well as
a change from a sandy bottom to rocky and coral heads
substrate. The few plants collected between 30 and 50 m
from the shore were commonly fragmented and several
morphological characters could not be determined.

The analysis of the plants collected between 5 to 25m along the transect shows that there are no significant differences in most of the characters measured among plants from different stations. The branching pattern does not change, being always alternate. Moreover, the distance between dichotomies and the number of cells between dichotomies remain constant for plants along the transect. Nodal and internodal lengths show no significant variation (for measurement ranges of these and other plants see Appendix). Nodal structure is easily recognizable as a stable characteristic of this species. Nodal and internodal diameters display some variation at 10 m station, otherwise no patterns are noticed (Fig. 3.1c & d).

Morphological variability in different life-history stages of C. clarionensis in culture.

Tetraspores were found in approximately 40% of the 60 plants collected in the field for culture experiments. Spores occurred commonly in adventitious lateral branches or in the upper part of the main axes. The release of spores occured on the second day after isolating the reproductive branches. After 5 days of

culture, all the Petri dishes showed abundant germlings developing. A few plants were sacrificed and mounted on slides in order to observe developmental processes. Sixteen- day-old germlings showed formation of two to three dichotomies in their main axes and proliferation of adventitious branches. Male gametangia were also detected in plants at this stage (1.25 to 2.6 mm in length). After 20 days of culture cystocarps were formed in those plants not showing gametangia, some of them mature enough to release carpospores. Plants kept under natural conditions of light produced reproductive structures at the same time as did plants kept under controlled conditions. Experiments were completed after 35 days. At this point, the carpospores released by the female plants reached the stage of 20 axial-celled-germlings and in a short time (approximately 5 days more) attained the size of the parental plants. Five plants were transferred to another Petri dish and kept for an additional month to observe any further development. These never increased in length, but produced a significant number of branches, becoming bushy in appearance.

Gametophytes grown under 16:8 h LD daylength developed into one of three 3 different morphotypees (Pl. XI) which also seemed to differ in their functional

aspects. The first type consists of small male plants with 4 to 6 dichotomies and clearly distinguishable cortical bands (Pl. XI, Figs. 2 & 6); the second type is represented by female plants with a similar number of dichotomies and size of the male plants, but with a distinct node-internode pattern (Pl. XI, Figs. 3 & 7); and the third type consists of sterile prostrate plants with 1 to 2 dichotomies and abnormally developed nodes (Pl. XI, Figs. 1 & 5). Quantitatively measured characters relating to node diameter, node length, internode length, internode diameter, number of cortical cells per node and total number of dichotomies were significantly different using a one-way Kruskal Wallis analysis of variance test (Fig. 3.2). The three morphological types of plants are easily recognizable from each other in these and other characteristics.

The second set of gametophytes grown under the same culture conditions a month later also showed distinct functional and morphological types, although not as clear as in the previous experiment. Female (cystocarpic) plants (Pl. XII, Figs. 3 & 6) and sterile plants looked similar in size and other features and male plants (Pl. XII, Figs. 2 & 5) were shorter and smaller than female and sterile plants (Pl. XII, Figs. 1 & 4). Multiple

comparisons among these three types of plants (Fig. 3.2) indicated that male plants differed from cystocarpic plants by being thinner, with fewer dichotomies per plant, and from both cystocarpic and sterile plants by having less developed nodes. On the other hand, among cystocarpic and sterile plants there were no significant differences.

When gametophytes originating from the same pool of tetraspores used in the previous experiment were grown under natural light conditions, they developed into reproductive female (Pl. XIII, Figs. 2 & 5) and male specimens (Pl. XIII, Figs. 3 & 6) as well as sterile plants (Pl. XIII, Figs. 1 & 4). These three groups of plants are morphologically indistinguishable except for the kind of reproductive structures they possess, or potentially possess.

Carpospores released by the first set of cystocarpic specimens grown under 16:8 h LD daylength germinated into plants that became reproductive after 34 days of culture. Tetrasporangia were involucrate, arranged in whorls in the upper portion of main or adventitious branches. The same structural arrangement is found in field collected tetrasporophytes.

Plants of C. clarionensis were collected from the field including all reproductive stages available at the time of the experiments. Comparisons within this material indicated no apparent differences among cystocarpic, tetrasporangial, spermatangial and sterile plants, except shorter internodes in male plants (P< 0.0001, Kruskal-Wallis test) and less developed nodes (P< 0.001, Kruskal-Wallis test) in tetrasporophytes.

When analyzed separately, the cystocarpic plants grown under 16:8 h LD daylength did not differ, from the cystocarpic plants or from the sterile plants grown a month later in any of their quantitative characters except for having slightly thinner internodes (Table 9, see also appendix tables A2, A4 & A9). In addition, they did not differ significantly in any characteristic from the plants collected directly from the field, except for a larger number of cortical cell rows. Therefore, it is assumed that the conditions the plants were growing in the field were similar to those in the laboratory at that particular time or, that phenotypically the female gametophytes are not susceptible to changes in the physical environment. However, the latter is not supported by the results of the comparison of plants grown under 16:8 h LD and natural daylength (Table 9, see also appendix tables A2, A6 & A8

for raw data and comparisons). Gametophytes grown under natural daylength were significantly more slender, with shorter nodes, consisting of fewer cortical cell rows, and longer internodes than gametophytes grown under 16:8 h LD daylength.

Tetrasporophytes also showed longer internodes and shorter nodes than gametophytes (Tables A2, A4, A7 & A9) this latter due to the less developed nature of their nodes with fewer cortical cell rows. The comparison of tetrasporophytes grown under culture conditions with tetrasporophytes collected in the field at that time (Tables 9 & A10) indicated that field plants were thicker than cultured plants. Cultured tetrasporophytes (Pl. XI, Figs. 4 & 8) were not only thinner but also had shorter nodes and longer internodes, resulting in more delicate appearance.

Moreover, the sterile prostrate plants cultured from the first set of gametophytes were different from all other reproductive plants cultured under the same or different conditions, and also differed from the field plants. These plants were clearly thicker (P<0.0001) than the rest of the observed material, with extensively

developed nodes which almost cover the entire internodal
space (Pl. XI, Figs. 1 & 5).

Morphological variability in different life-history stages
of _Ceramium_ sp. 1.

The following results were obtained utilizing
either carpospores or tetraspores originating from a
single individual, thus this condition was predicted to
reduce genotypic variation. Nevertheless, for
carpospore-based cultures, several cystocarps of the same
plant were used and although the female genotype was the
same, sexual recombination with different male genotypes
had probably occurred. In the case of tetraspore-based
cultures meiotic recombination is bound to produce a
number of possible different results, some of which are
suggested here.

Gametophytic growth from tetraspores was
characterized by the abundant formation of long, uniaxial
rhizoids all along the thallus (Pl. XIV, Figs. 1 & 2),
including the uppermost portion of the axes. In other
words, although the plants did not show a typical
prostrate habit (see examples in chapter II) they became
attached throughout their length to the bottom of the

Petri dish. The frequent formation of condensed nodes (Pl. XIV, Fig. 2) and barely developed internodes was observed in the middle part of the branch between dichotomies. The resulting plants were thin and many showed nodes reduced only to the pericentral cells. In specimens in which nodal formation was more pronounced, angular or rounded cortical cells grew in tightened rows in which pericentral cells are not as visible as they are characteristically seen in field-growing plants.

No significant differences were detected in any of the characters measured among gametophytes grown under different photon flux densities or the control, except for the internodal length obtained under 17-25 uE m^{-2} s^{-1} and the nodal length between the two lowest experimental photon flux densities (Fig. 3.4).

A comparison between the experimentally grown gametophytes and plants collected from the field (Fig. 3.4) shows that the field plants are more developed in all the characters measured in this material, except for the number of adventitious branches. Field plants display thicker nodes and internodes, more developed nodes, and a larger number of dichotomies, but fewer adventitious branches than gametophytes (see appendix table A13 for statistical comparisons). In addition, field plants have

the characteristic nodal structure of several cortical rows with a central row of larger cells which corresponds to the pericentral cells, a feature not shown by the cultured plants.

Morphological characters in tetrasporophytes are less stable under different laboratory-growing conditions than in gametophytes. Differences in internodal diameter and nodal length (Fig. 3.5) indicate that the lowest experimental photon flux density (17-25 uE m^{-2} s^{-1}) produces the least developed thalli (Table A14). The light control shows the longest internodes and the adventitious branches are more frequent in plants grown under the lowest photon flux densities tested (Fig. 3.5). Similarly to gametophytes, differences are significant between cultured and field plants (Fig. 3.5) and as in the previous case the development of cultured plants is significantly less.

Morphological variability in branches of <u>Ceramium</u> sp. 1 under different daylength regimes.

Comparison of several characters in specimens grown from different parental plants under the same experimental conditions indicates that the variation found

in these characters is a result of genotypic variability.
For plants grown under long photoperiods (16:8 h LD) three
replicates including branches from two original plants
were analyzed. The two sets of plants did not show
significant differences within replicates in any of the
morphological characters recorded, although two
characteristics differed between the two sets. The
characteristics of both sets of plants and which of these
characteristics are significantly different (Wilcoxon
test) are summarized in Table 10. In brief, both sets of
plants displayed a similar development in their internodes
and in their nodes. One of the progenies (parental plant
2) showed a greater abundance of adventitious branches and
the other (parental plant 1) showed a higher number of
cells between consecutive dichotomies than the previous
one. At first, this was not clear, since both
experimental sets have similar distances between
dichotomies. Nevertheless, this may be because those
plants that showed more cells between dichotomies, also
had slightly shorter nodes. The shorter nodes could
account for the space "available" for more cells within
the same distance.

While there was uniformity of characters in
specimens originating from different parental plants

showed grown under 16:8 h LD there was character
variability among progenies cultured under 12:12 h LD
(Table 11). Significant differences (Kruskal-Wallis test)
were detected in the distance between dichotomies among
progenies originating from three different parental
plants, but not between replicates within progenies.
These differences are due to a combination of the number
of internodes (axial cells) between consecutive
dichotomies and the length of these internodes, two
factors that were significantly different among progenies
(Table 11). In addition, one of the progenies (from
parental plant 1) had distinctively fewer adventitious
branches, as was also seen in the 16:8 h LD cultured
plants. Furthermore, the diameter of both nodes and
internodes showed significant variability among progenies
(Table 11).

For plants grown under short photoperiod (8:16 h
LD) several characters were significantly different
between specimens originating from two parental plants
(Table 12). In this case the set of plants 1 had more
dichotomies than the set of plants, although the distance
between these dichotomies was shorter than in the plants
with fewer dichotomies. The plants of set 1 showed a
shorter distance between dichotomies also had a

significantly lower number of shorter axial cells between
dichotomies than those plants with longer distances
between dichotomies. Plants of set 1 also had thicker
nodes, with the overall appearance of the plant being
coarser. A difference in the number of adventitious
branches present was also detected between those two sets
of specimens (Table 12).

The only stable characters detected in all the
specimens grown under the 3 different photoperiods, were
node length and the number of cortical cell rows present
in the nodes. None of the plants of _Ceramium_ sp. 1 grown
under artificial conditions achieved the degree of nodal
development of plants collected from natural populations
at the time. Field plants were always taller, thicker and
had significantly fewer adventitious branches
$(P>X^2=0.0001)$. It is obvious that Hawaiian plants in
the field would never experience the short day (8:16 h LD)
experimental condition.

Morphological variability in branches of _C_. _flaccidum_
under different daylength regimes.

Branches of _C_. _flaccidum_ grown from different
parental plants under the same conditions showed the same

significant variation in morphological characters of
Ceramium sp. 1. Progenies originating from three parental
plants cultured under long daylength (16:8 h LD) were
shown to be similar in most characters except for the
progeny originating from parental plant 1 (Table 13).
Progeny of parental plant 1 hade a significantly shorter
distance between consecutive dichotomies than plants from
the two other progenies. This difference in distance
between dichotomies is due to the occurrence of shorter
internodes (Table 13) that contributes to the bulk of the
thallus length in this species. These progeny also
possessed fewer dichotomies than the sets of plants two
and three.

Branches of C. flaccidum originating from 6
different parental plants and grown under 12:12 h LD
daylength, also showed variation (P<0.05, Kruskal-Wallis
test) in some of their characters. However, these
differences were always detected between two or three
progenies consisting of a small number of plants each
(n<10). A similar result was found among progenies
cultured under short day photoperiods (8:16 h LD).
Significant differences (P<0.05, Kruskal-Wallis test) in
the internodal diameter were detected in one progeny and

in internodal length of another progeny different from the
first one. A summary of these results are in Table 14.

Morphological variability in Ceramium sp. 1 under
different nutrient concentrations, water movement
conditions and daylength regimes.

Branches of Ceramium sp. 1 cultured under the
experimental combinations of nutrient concentrations, and
with and without water movement under 8:16 h LD
photoperiod grew considerably, attaining lengths of 7 to
17 mm after one week. Despite the fast growth rate, these
artificially grown plants were always less robust than
field plants. Often, one branch of a dichotomous division
would develop into the main axis whereas the other
remained short regardless of the culture conditions. All
plants showed strongly forcipate apices, occasionally with
outer dentate margins. Laboratory grown plants do not
resemble the species in the field, mainly because of their
delicate appearance due to thinner thalli and less
developed nodes (Pl. XIV, Figs. 3 & 4).
     In several instances the pericentral cells are
clearly visible due to the poorly developed cortex (up to
4 cortical cell rows, see Table 15), resulting in thalli

similar to _Ceramium_ _affine_ var. _peninsularis_ Dawson.

Nodal development in terms of node length, node diameter and, number of cortical cells was mostly uniform under all conditions at 8:16 LD photoperiod, except for a few experiments (Fig. 3.6). There was no clear pattern in the increase or decrease of node length or diameter related to the nutrient or water conditions.

The branching pattern among experimental plants was also uniform since most plants were within a similar range of 4 to 7 dichotomies. However, the number of adventitious branches formed in plants grown under full strength culture medium is significantly lower than for plants grown with less nitrates and phosphates independent of having water movement (Table 15a). In addition to the number of adventitious branches formed, the distance between consecutive dichotomies and the internodal length are the most variable of the characters under these conditions of culture (Fig. 3.6).

The variation in the distance between dichotomies seems to be directly related to the variation in internodal length since the number of cells between dichotomies remains uniform among plants cultured under different conditions (Table 15a).

Internodal length did not vary among plants cultured under different nutrient concentrations and without water movement, although the lengths differed considerably among plants grown under different nutrient concentrations with water movement. Similarly, plants grown under the same nutrient concentrations differed in their internodal length depending on their water movement conditions. Plants cultured without water movement always had longer internodes.

Cultures under 12:12 h LD photoperiod showed a completely different outcome than those in a shorter photoperiod. Regardless of the conditions tested, most algal specimens originally placed in the Petri dishes lost their pigments and apparently died and disintegrated after the first two days of culture. Nevertheless, adventitious branch formation was detected from the remaining fragments. In the course of a week each remaining fragment of a branch had developed 2 to 4 adventitious new branches, that were pigmented and apparently healthy, some of them displaying one dichotomy (Pl. XIV, Fig. 6). Because most of these new grown branchlets were not fully developed, measurements of internode length and diameter were not recorded in most cases (Table 15b). It was observed that the majority of the branchlets arose close

to the apices of the original algal material. Several of these branchlets were reproductively mature male specimens showing normally developed spermatangia. Gland cells, similar in shape and location to those found in $\underline{C}$. aduncum were also observed in some of the plants. The characters recorded for this set of plants were highly uniform, except for the internodal length being significantly shorter in specimens grown under lower concentrations of nutrients (Fig. 3.7).

Similarly to plants grown under 12:12 h LD photoperiod, the occurrence of gland cells was also common in plants grown under longer daylength (16:8 h LD). Nodes were also extremely reduced in this set of plants, never surpassing three cortical cell rows. Although most plants had long and thin internodes giving them a fragile appearance with few (<6) dichotomies, a few plants grew into short and thick internodes with a higher number of dichotomies (Pl. XIV, Fig. 5). No particular set of conditions seemed to control the occurrence of these coarser plants. Two or three specimens were observed with immature tetrasporangia.

Only three characters are affected differentially by the experimental conditions; (1) distance between consecutive dichotomies, (2) internodal length, and (3)

the number of cells between dichotomies. Within each
nutrient concentration tested, dichotomies of plants grown
with water movement were always significantly further
apart than those of plants grown without water movement
(Fig. 3.8). In only one case was this difference due to
the number of axial cells between dichotomies, while in
most groups of plants it is explained by their differences
in degree of internodal elongation.

A comparison of plants from each set of
conditions among the different daylengths shows that
larger internodes (in length as well as diameter) are
produced when the amount of light received is less,
regardless of nutrient and water conditions. This results
in more robust plants when light quantity is reduced. The
fact that some plants develop significantly longer
distances between dichotomies is in almost all instances
due to the increase in internodal length except in
experiment number 3 (90% N, 95% P, no water movement). In
this case a combination of internodal elongation and
number of axial cells is responsible for the variation in
the distance between dichotomies.

In the majority of the conditions tested, the
number of dichotomies present in a plant will increase
with decreasing the amount of light from 16:8 h LD to 8:16

h LD (Table 15). Plants grown under short daylength are
generally slightly longer than plants grown under long
daylength. Since the latter also showed a shorter
distance between dichotomies their appearance is short and
profusely branched in comparison with plants
experimentally grown under short photoperiod.

The adventitious branch formation seems to be
affected differentially by the amount of light received
under limiting nutrient conditions. When nitrate and
phosphate concentrations were reduced in the culture
medium, more adventitious branches were formed under short
compared to long photoperiods.

In view of the differences displayed by newly
grown branches of _Ceramium_ sp. 1 under 12:12 h LD
photoperiod, no statistical comparison is possible on
characters such as the number of dichotomies, the distance
between consecutive dichotomies, the number of axial cells
between dichotomies and the number of adventitious
branches produced. In the characters recorded (more than
10 plants measured), there are no observable differences
between these and plants grown under 16:8 h LD daylength.
Therefore, the node and internode development is much less
noticeable in 12:12 h LD - grown plants than in those
cultured under more restricted amounts of light.

Morphological variability in C. flaccidum under different
nutrient concentrations, water movement conditions and
daylength regimes.

Most plants originally placed in the Petri dishes
with full strength medium, without water movement and
under 8:16 h LD daylength, died after two days of setting
up the experiment, except for two or three plants that
survived the entire duration of the experiment. Plants
grown with water movement and with 90% of the full
concentration of N and 95% of that of P (experiment 6,
Table 7) developed poorly and the distance and number of
cells between dichotomies were not possible to record
(Table 16). All the other sets of plants underwent new
growth from the apices of the original axes. These showed
a short thallus portion with much closer nodes as if
internodal elongation had stopped before readapting to the
new conditions. All plants had an alternate branching
pattern and no adventitious formation of axes (Pl. XV,
Fig. 2). The number of dichotomies formed is
significantly lower in plants of experiment 6 (Table 7) in
comparison to other experiments. The only other
significant variation is in the nodal diameter between

plants grown with and without water movement at the same nutrient concentration (Fig. 3.9).

Similarly in cultures under short daylength, plants grown at 16:8 h LD, full strength medium and no water movement did not grow and eventually died. In addition, plants of experiment 6 (which developed poorly in the previous experiment) also did not develop (Table 16). The rest of the specimens grew normally, often displaying gland cells, and in several instances, nodes in which the horizontally elongated cortical cells were not formed.

These plants also showed an alternate branching pattern with a significantly higher number of dichotomies in those experiments with higher nutrient concentration. Adventitious branches were either absent or frequently up to 5 per plant under these conditions. Most characters showed significant differences between plants grown under different nutrient concentrations regardless of water movement conditions. The distance between consecutive dichotomies is considerably longer in plants grown under low nutrient concentrations, which are also the same that had longer internodes and highest number of cells between dichotomies. Nevertheless, the nodal development is significantly low in plants grown under low nutrient

concentrations. As a consequence, the appearance of these plants is more slender and delicate than that of the rest of experimental plants. The shortest nodal length, recorded in plants cultured under low nutrient concentrations is probably due to a smaller size of the individual cortical cells since the number of cortical cell rows is actually the same or larger in these plants than in specimens grown under higher nutrient concentrations (Table 16b).

Ceramium flaccidum was only cultured under 16:8 h LD and 8:16 h LD daylengths and in both cases, plants failed to grow in full strength medium with or without water movement, and in culture medium containing only 80% of the initial concentration of N and 95% of P. In contrast with the absolute absence of growth at these conditions under 16:8 h LD daylength, short daylength experiments resulted in survival and later growth (Pl. XV, Fig. 1) of a few plants under these conditions.

Most of the characters available for statistical analysis underwent some detectable variation under 16:8 h LD (Fig. 3.10). The number of dichotomies per plant does not differ between daylengths in plants grown with 90% of N and 97% of P, but they increase in number when water movement is present and decrease while lowering nutrient

concentrations. Node length and diameter are significantly larger under both nutrient concentrations at 8:16 h LD daylength, although this difference is not present when cultures have water movement. The number of cortical rows present per node increases significantly when reducing the amount of light received by the plants, independent of nutrient concentration or water conditions. The internodal length as well as the number of axial cells formed between consecutive dichotomies decreases at short daylength only when nutrients are highly limited, whereas internodes are thinner only when cultures are with water movement.

Discussion

The close examination of several morphological features, that characterize the vegetative structure of three selected Hawaiian species of <u>Ceramium</u> indicates that most of these features are highly variable within each species. None of these features remains stable under all the conditions tested in artificially-grown plants.

Internodal length, whic represents the visible portion of the axial cells, is a variable character in plants of <u>C</u>. <u>rubrum</u> (Garbary <u>et</u> <u>al</u>, 1978). The reported

variability in this species is a result of the changes in morphology induced by photoperiod regimes. This character is also variable between female and male gametophytes as well as between gametophytes and tetrasporophytes of Ceramium clarionensis grown under the same conditions in laboratory, although it remains constant under most of the same combination of conditions in Ceramium sp. 1. Internodal length seems to have a strong genetic component in C. flaccidum where it varies depending on the original parental plant from which the artificially-grown progeny plants originate. This genetic component is probably in part responsible for much of the overall variation of this species in the field in combination with the plastic responses of this character to the environment. In Ceramium sp. 1, on the other hand, variation in internodal length is largely induced by environmental conditions. In comparison, the same character, does not show the same degree of plasticity in C. flaccidum. In the latter species, axial cell elongation is constant under most of the conditions tested, except when decreasing at short photoperiods (8:16 h LD) when nutrients are highly limited. This indicates that this character is less sensitive to the experimental variations than Ceramium sp.1.

Internodal diameter shows the same general outcome in variability as internodal length. It differs among reproductive stages of the life history of C. clarionensis but remains uniform in Ceramium sp. 1. Genotypic variation is detected, but not in C. flaccidum. Both species display a high phenotypic variability in this character.

The degree of node development is shown by nodal length and the number of cortical cell rows per node. If node length varies while the number of cortical cell rows remains constant, it can be attributed to changes in the size of cortical cells. The degree of nodal development has been reported as a character which varies depending on the culture conditions (Garbary et al, 1978; Suh & Lee, 1984), but is not as dependent on the life-history phase of the individual. Nodal length is variable among gametophytes of C. clarionensis, although this variation depends on the environmental conditions under which the plants are growing. This character does not differ between different stages of the life history of Ceramium sp. 1, although it is sensitive to changes in environmental conditions as demonstrated by comparisons of

artificially-grown plants and field-collected specimens.
Neither nodal length nor the number of cortical cell rows
seem to be variable among different progenies of C.
flaccidum and Ceramium sp. 1. In Ceramium sp. 1 these
two characters are highly stable independent of the
conditions under which the plants were grown, instead the
general trend is a reduction in node development in
artificial cultures in comparison to plants grown in the
field. In C. flaccidum the number of cortical cell rows
may remain stable whereas nodal length is variable,
indicating that the size of the cortical cells changes
depending on the prevailing environmental conditions.

The degree of "robustness" of a plant of Ceramium
can be directly related to the diameters of both nodes and
internodes, two highly variable features which affect the
overall appearance of the plants. These characters are
probably the most variable of those evaluated in this
study. In C. clarionensis they clearly have a genetic
component associated with the life-history stage, but this
genetic component can have distinct phenotypic expressions
depending on the environment in which these stages are
developing. In Ceramium sp. 1 the variation of the same
characters is not dependant on the life history phase but
on the surrounding environment. Both node and internode

diameters are phenotypically variable, its variability results from a combination of genetic and environmentally induced components. In $\underline{C}$. $\underline{flaccidum}$ as well as in $\underline{Ceramium}$ sp. 1 nodes and internodes tend to develop less under all the culture conditions tested than in nature. Thus, the artificially-grown plants of both species always look thinner and smaller than the field specimens. Among the features that contribute to the branching pattern of the plants are the number of dichotomies and the number of adventitious branches formed. In $\underline{C}$. $\underline{clarionensis}$, the number of dichotomies present in a plant depends on the reproductive stage of the life-history and also on the gene pool of the population sampled since the second set of gametophytes cultured showed fewer differences in this character. As with most of other characters in $\underline{Ceramium}$ sp. 1, the number of dichotomies is not modified in either gametophytes or tetrasporophytes grown in the laboratory, but it differs from the field plants. The number of dichotomies is variable depending on the genotype of the plant and the conditions under which this is growing. A similar result is evidenced in $\underline{C}$. $\underline{flaccidum}$ where this character shows some genotypic variation as well as variable responses to changes in the nutrient concentrations and conditions of water movement. The

presence of adventitious branches in _Ceramium_ sp. 1 and _C._ _flaccidum_ in laboratory-grown plants depends strictly on the prevailing nutrient conditions. Adventitious branches develop abundantly under low nutrient concentrations, however, they are not of such a common occurrence in _C._ _flaccidum_ as they are in _Ceramium_ sp. 1. In _C._ _clarionensis_ adventitious branching was not affected by the experimental variables of this study. Thus, it appears to be under more direct genetic control.

The distance between consecutive dichotomies is a genetically variable feature which in some cases depends on the number of axial cells between dichotomies and in others on the degree of elongation of these cells. Phenotypic variability in this character is expressed only under certain culture conditions in _Ceramium_ sp. 1 as well as in _C._ _flaccidum_. The occurrence of gland cells in _Ceramium_ sp. 1 was unexpected since they were never found in nature. In _Ceramium_ sp. 1 as well as in _C._ _flaccidum_ the presence of gland cells is induced by long daylength regimes.

Most of the characters evaluated in this study have different degrees of variability depending on the species examined. The effect that this variability has on the delimitation of taxa also varies from species to

species. Changes in the morphology of gametophytic and
tetrasporophytic plants of C. clarionensis are unique to
this species in that they are expressed as a result of the
reproductive stage of the plant. Except for size and
branching patterns (Garbary et al, 1978; 1980), no
characters have been carefully studied in Ceramium in
regard to their possible variation among life-history
stages. Differences between spermatangial and cystocarpic
individuals are not uncommon in red algae, e.g.,
observations in Polycavernosa (Abbott, 1988) and
Gracilaria (Abbott, 1985) among others. This type of
morphology associated with the life-history stage and
reproductive characteristics of the individual were not
detected in Ceramium sp. 1. However, this fact does not
exclude the possibility of differences at a physiological
level which may not affect the morphology of the
individuals. For example, indirect effect of this type of
differences has been observed in Iridaea laminarioides and
I. ciliata where the ecological distribution is not shared
by cystocarpic and tetrasporic plants of the same species
(Hannach & Santelices, 1985). Furthermore, tolerances to
dessication and grazing preferences are clearly distinct
between tetrasporophytes and carposporophytes of I.
laminarioides (Luxoro & Santelices, 1989). In C.

clarionensis the description requires the inclusion of an account of the distinct morphological variability for each of its life-history stages, whereas this is not necessary in Ceramium sp. 1.

Also, the stability of certain characters affecting the overall morphology of plants independent of their life-history phase is different between species. Internodal length, nodal development and occurrence of adventitious branches are stable characters in C. flaccidum while highly variable in Ceramium sp. 1. Moreover, if certain changes that may affect the overall morphology of C. flaccidum do not affect recognition of this species since its diagnostic characters of branching pattern and nodal structure, remain stable. In Ceramium sp. 1, none of the characters that comprise its vegetative structure remains stable to the extent of making the species unrecognizable. The reduction in node development (up to 4 cortical cell rows) in branches grown under all acombinations of nutrient concentrations, water movement conditions and daylength regimes, results in a resemblance of Ceramium sp. 1 to C. affine var. peninsularis (Dawson, 1950). The fragile appearance attained by most specimens under all culture conditions differs from the original species description of Ceramium sp. 1, but nevertheless

the features are not those of any _Ceramium_ species
described for the North Pacific.

In summary, the phenotypic variability of most
vegetative characters in the three species of _Ceramium_
evaluated indicates that detailed examination of these
characters for all species is a prerequisite to the
formulation of adequate species descriptions. The
knowledge of species variability in nature as well as
their potential variability under culture conditions will
facilitate a more realistic and useful taxonomy for the
genus _Ceramium_.

Table 7. Combination of culture media and water motion experiments of
Ceramium sp. 1 and C. flaccidum.

Experiment number	Phosphate concentration*	Nitrate concentration*	Water movement conditions **
1	100	100	−
2	100	100	+
3	97.5	90	−
4	97.5	90	+
5	95	80	−
6	95	80	+

* expressed as percentage from original full strength concentrations
  in Grund medium.
** − without water movement; + with water movement (2500 rpm)

Table 8. Temporal character variability of a natural population of
C. flaccidum. Results expressed as the P<X^2 of significant
differences in the characters between months (Kruskal-Wallis
one-way analysis of variance test).

Month interval	Internodal length	Internodal diameter	Nodal length	Nodal diameter
Feb.-April	>0.05	>0.05	0.0001	>0.05
April-May	>0.05	0.0001	0.0001	>0.05
May-June	0.0001	0.0001	0.0001	>0.05
June-July	0.0001	0.0001	0.0001	>0.05
July-Aug.	0.0001	>0.05	>0.05	0.0001
Aug.-Sept.	0.0001	0.0001	0.0001	>0.05
Sept.-Oct.	>0.05	>0.05	0.0001	0.0001
Oct.-Nov.	>0.05	>0.05	>0.05	0.0001

Table 9. Comparison of morphological characters among artificially-
grown gametophytes, tetrasporophytes and field plants of
C. clarionensis. ** indicate significant differences
(P<0.0001, Kruskal-Wallis test) between plant types.

Character	Plant groups	Character	Plant groups
Internodal length	C(1) — C+S(2)	Internodal diameter	C(1) — C+S(2) **
	C(1) — C+M+S(3) **		C(1) — C+M+S(3) **
	C(1) — T **		C(1) — T **
	C(1) — F		C(1) — F
	C+S(2) — C+M+S(3) **		C+S(2) — C+M+S(3) **
	C+S(2) — T **		C+S(2) — T **
	C+S(2) — F **		C+S(2) — F
	C+S+M(3) — T		C+M+S(3) — T **
	C+S+M(3) — F		C+M+S(3) — F **
	T — F **		T — F **
Nodal length	C(1) — C+S(2)	Nodal diameter	C(1) — C+S(2)
	C(1) — C+M+S(3) **		C(1) — C+M+S(3) **
	C(1) — T **		C(1) — T **
	C(1) — F		C(1) — F
	C+S(2) — C+M+S(3) **		C+S(2) — C+M+S(3) **
	C+S(2) — T **		C+S(2) — T **
	C+S(2) — F **		C+S(2) — F
	C+S+M(3) — T **		C+M+S(3) — T **
	C+S+M(3) — F **		C+M+S(3) — F **
	T — F **		T — F **
Number of cortical cell rows	C(1) — C+S(2)		
	C(1) — C+M+S(3) **		
	C(1) — T **		
	C(1) — F **		
	C+S(2) — C+M+S(3) **		
	C+S(2) — T **		
	C+S(2) — F		
	C+S+M(3) — T **		
	C+S+M(3) — F **		
	T — F **		

(1) 1st experiment, plants grown under 16:8 h LD daylength; (2) 2nd
experiment, plant grown a month later under 16:8 h LD daylength; (3)
plants grown under natural light conditions; M= male gametophytes; C=
female gametophytes; S= sterile gametophytes; T= tetrasporophytes;
F= field-collected plants.

Table 10. Summary of morphological characteristics of <u>Ceramium</u> sp. 1 plants grown under 16:8 h LD daylength.

	Parental Plants		
Character	1 (n=140)	2 (n=138)	P> z *
Node diameter	72-120(132)	(72)84-108(132)	>0.05
Node length	24-36(48)	(24)36-48(60)	>0.05
Internode diameter	(72)84-120(132)	(72)84-120(144)	>0.05
Internode length	(72)96-252(324)	(96)108-252(324)	>0.05
No.of cortical			
cell rows	2-4(5)	(2)3-4	>0.05
No.of dichotomies	(6)7-9	(6)7-9(10)	>0.05
No.of cell between			
dichotomies	(6)8-11(18)	8-11(12)	0.01
No.of adventitious			
branches	(0)2-17(26)	(1)2-17(36)	0.01
Distance between			
dichotomies	1200-3300	1150-3250	>0.05

* Wilcoxon 2-sample test

Table 11. Summary of morphological characteristics of <u>Ceramium</u> sp. 1 plants grown under 12:12 h LD daylength. Character measurements in micrometers. Last column indicates which characters are significantly different among progenies.

Parental plants

Character	1 (n=134)	2 (n=120)	3 (n=106)	$P>X^2$ *
Node diameter	(48)60-84(108)	(48)60-72(84)	(48)6072(84)	0.0001
Node length	12-36(48)	(12)24-36	(12)24-36	>0.05
Internode diameter	(48)60-120	(48)60-96(108)	60-84(96)	0.0005
Internode length	(60)84-192(300)	(132)144-276(288)	(96)108-204(240)	0.0001
No.of cortical cell rows	(1)2-3(4)	2-3	2-3(4)	>0.05
No.of dichotomies	(3)4-5(6)	(3)4-6(7)	(3)4-6(7)	>0.05
No.of cells between dichotomies	(8)-12(30)	(21)25-48(69)	(10)22-37(52)	0.0001
No.of adventitious branches	0-1(2)	0-16(18)	(0)4-11(16)	0.0001
Distance between dichotomies	600-2050	500-4700	500-4850	0.0001

* Kruskal-Wallis one-way analysis of variance test

Table 12. Summary of morphological characteristics of <u>Ceramium</u> sp. 1
plants grown under 8:16 h LD daylength. All measurements
in micrometers. Last column indicates which characters are
significantly different among progenies.

Parental plants

Character	1 (n=32)	2 (n=24)	P> z *
Node diameter	84-96(108)	72-96(120)	0.0015
Node length	(24)36-48	36-60	>0.05
Internode diameter	84-96(108)	(36)84-108(120)	>0.05
Internode length	132-252(276)	(144)168-324	0.0248
No.of cortical cell rows	3-4(5)	3-4	>0.05
No.of dichotomies	(5)6-7(8)	4-5	0.0001
No.of cells between dichotomies	9-18(21)	(13)15-19(22)	0.0001
No.of adventitious branches	0-3(5)	1-6(7)	0.0036
Distance between dichotomies	2100-4050	500-4550	0.0001

* Wilcoxon-Mann-Whitney test

Table 13. Summary of morphological characteristics of Ceramium flaccidum grown under long photoperiod (16:8 h LD) conditions. All measurements in micrometers.

Parental Plants

Character	1 (n=39)		2 (n=123)		3 (n=82)		$P > X^2$*
Node diameter	(48)60-72(84)		48-84		(48)60-84		>0.05
Node length	36-48(60)		(24)48-60		(24)36-48(60)		>0.05
Internode diameter	(36)48-60(72)	(a)	(24)36-60(72)	(a)	36-60	(a)	>0.05
Internode length	84-216(264)	(a)	(36)84-312(336)	(b)	(60)84-300(444)	(b)	0.01
No.of cortical cell rows	5-6(7)	(a)	(4)5-6(7)	(a)	(4)5-6(7)	(a)	>0.05
No.of dichotomies	(6)8-10(13)	(a)	(5)6-12(15)	(b)	7-13(15)	(c)	0.01
No.of adventitious branches	(0)2-5(8)	(a)	1-6(11)	(a)	1-7(23)	(a)	>0.05
Distance between dichotomies	400-1400	(a)	100-2400	(b)	450-2100	(b)	0.01
No.of cells between dichotomies	4-5	(a)	(3)4-5(6)	(a)	(3)4-5(8)	(a)	>0.05

Progenies sharing the same letter () indicate that there is no significant difference among them in that particular character
* Kruskal-Wallis one-way analysis of variance test

Table 14. Morphological characteristics of C.flaccidum grown under
12:12 h LD and 8:16 h LD daylengths. All measurements in
micrometers.

Daylength regimes

Character	12:12 LD (n=46)	8:16 LD (n=38)
Node diameter	48-60(72)	48-60(72)
Node length	24-48	24-36
Internode diameter	48-60(72)	(24)36-60
Internode length	48-300(360)	(24)48-108(348)
No.of cortical cell rows	(2)3-4(5)	(2)3-4
No.of dichotomies	(3)5-7(9)	(3)5-7
No.of adventitious branches	Only small proliferations	1-20(small)
Distance between dichotomies	650-4250	84-588
No.of cell between dichotomies	(4)6-9(14)	5-11(17)

Table 15. Summary of morphological characteristics of <u>Ceramium</u> sp.1 grown under different nutrient concentrations, water movement conditions and daylengths. All measurements are in micrometers.

Character	Exp.1 *	Exp. 2	Exp. 3	Exp.4	Exp.5	Exp.6
15a. 8:16 h LD daylength.						
Node diameter	(72)84-96(120)	(72)84-96(108)	(72)84-96(108)	(60)72-96	(72)84-108	(60)72-96(108)
Node length	(24)36-48(60)	24-36	36-48	24-36(48)	36-48	24-36(48)
Internode diameter	(60)84-96(108)	72-108	(60)84-108(120)	(72)84-96(108)	84-108(120)	(60)72-96(108)
Internode length	(132)192-276(348)	(72)96-156(216)	(84)120-348(456)	(84)96-324	(96)204-324(408)	108-240(300)
No.of cortical cell rows	3-4(5)	3-4	(2)3-4	2-4	2-4	(2)3-4
No.of dichotomies	4-7(8)	(4)5-7(9)	(4)5-7(8)	(3)4-7	4-8	5-7(8)
No.of cells between dichotomies	9-19(22)	9-22	9-22(31)	(11)12-25(31)	9-20(25)	(10)11-21(25)
Distance between dichotomies	500-4550	1050-2850	500-4900	500-4850	500-4900	2000-4750
No.of adventitious branches	0-6(7)	(0)1-4(5)	2-7(10)	(1)3-7(13)	(1)4-7(13)	1-6(9)
15b. 12:12 h LD daylength.						
Node diameter	(48)72-84	(48)60-84(96)	(48)60-72(84)	(48)60-84(96)	60-72	60-84(96)
Node length	24-36	24-48	24-36	(12)24-36	24-36	24-36(48)
Internode diameter	72-96	(60)72-96(120)	....	(72)84-96	....	60-84
Internode length	132-228	(96)108-264(288)	....	96-144	....	60-72(96)
No.of cortical cell rows	(2)3-4(5)	(2)3-4(5)	2-5	(2)3-5	3-4	3-4(6)
No.of dichotomies	0-2	1-3	0-2	0-2	1-2	1-2

344

Table 15. (Continued) Summary of morphological characteristics of <u>Ceramium</u> sp.1 grown under different nutrient concentrations, water movement conditions and daylengths. All measurements are in micrometers.

15c. 16:8 h LD daylength.

Node diameter	(48)60-84(120)	(48)60-72(84)	(48)60-72(96)	(48)60-84(120)	60-72(120)	(48)60-72(120)
Node length	(12)24-36(48)	12-36	12-36	(12)24-36(48)	24-36(48)	(12)24-36(48)
Internode diameter	(48)60-108	(60)72-84(96)	(48)60-72(96)	(48)60-84(132)	60-72(108)	60-84(120)
Internode length	(36)84-132(204)	(63)108-156(180)	(36)48-108(132)	(60)84-132(180)	(60)72-120(180)	(84)120-144(192)
No.of cortical cell rows	2-3(4)	2-3	2-3(5)	2-3(4)	2-3(4)	2-3(4)
No.of dichotomies	4-7(8)	(4)5-6(7)	3-5(7)	4-6(8)	4-6(8)	
No.of cells between dichotomies	(8)10-12(24)	(10)12-20(23)	8-10(22)	(8)10-15(21)	(8)12-15(20)	10-15(16)
Distance between dichotomies	550-2700	1450-3150	650-1850	900-2850	1000-2850	1500-3100
No.of adventitious branches	1-5(17)	1-13(17)	0-12	0-3(8)	1-7(20)	0-5(20)

* Experimental conditions in Table 7.

Fig. 3.1   Variation of morphological characters of
                  C. flaccidum along the reef flat. A.
                  abundance of plants of C. flaccidum in each
                  sampling station. B-E. Character variation
                  expressed as range of measurements
                  recorded. Thin bar indicates overall
                  range, wide bar indicates range including
                  85% of the plants measured, median is
                  indicated by ■ .

DISTANCE FROM THE SHORELINE (M)

Fig. 3.2   Comparison of characters among gametophytes
                of C. clarionensis grown under culture
                conditions (1st set of plants). Results of
                Kruskal-Wallis test one-way analysis of
                variance. Significant differences
                are indicated with **.

CYSTOCARPIC

SPERMATANGIAL

Node length **
Node diameter **
Internodal length **
Internodal diameter **
No. cortical cell
rows **
No. dichotomies

Node length **
Node diameter **
Internodal length **
Internodal diameter **
No. cortical cell rows **
No. dichotomies **

STERILE

Node length **
Node diameter **
Internodal length **
Internodal diameter **
No. cortical cell
rows **
No. dichotomies**

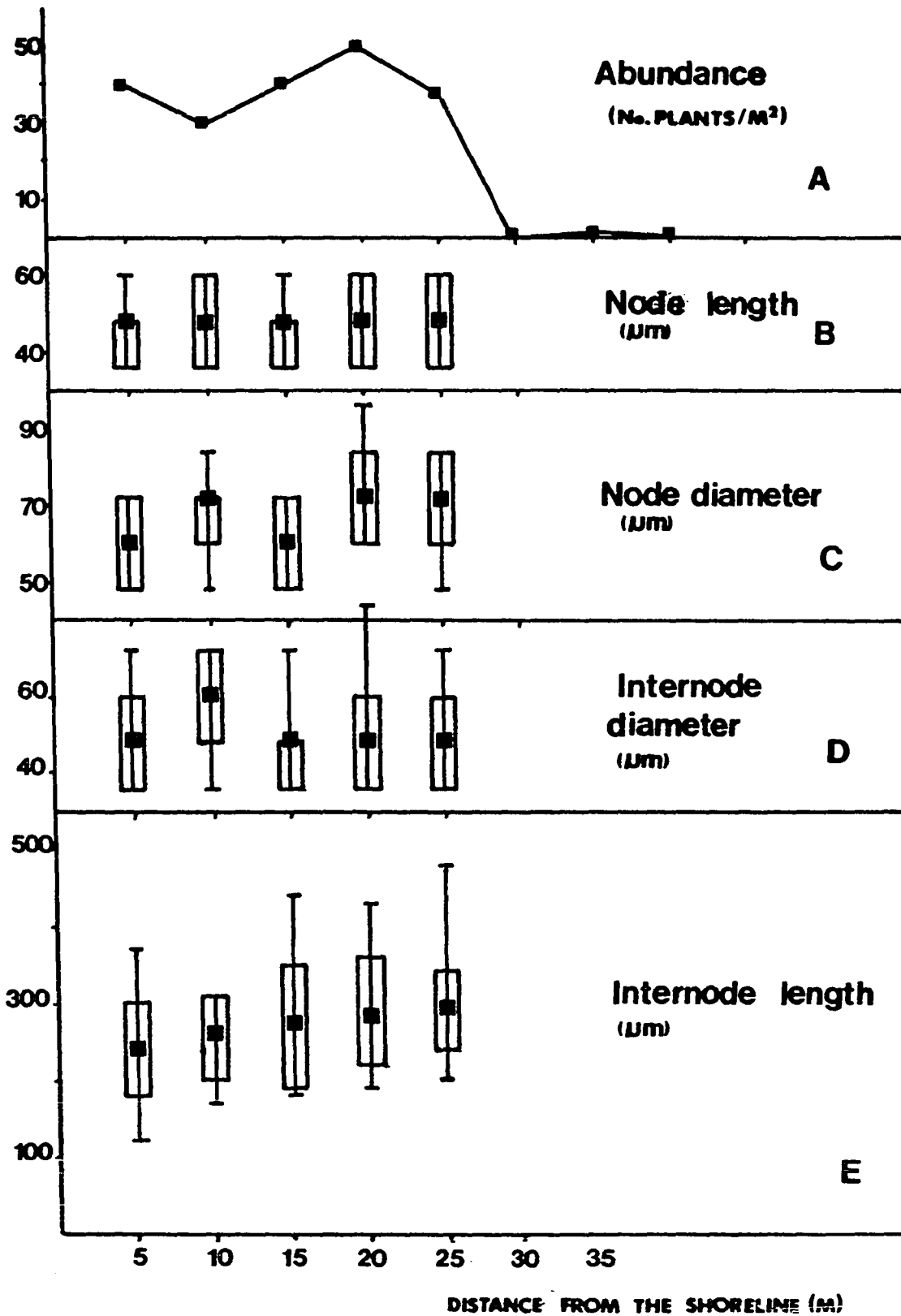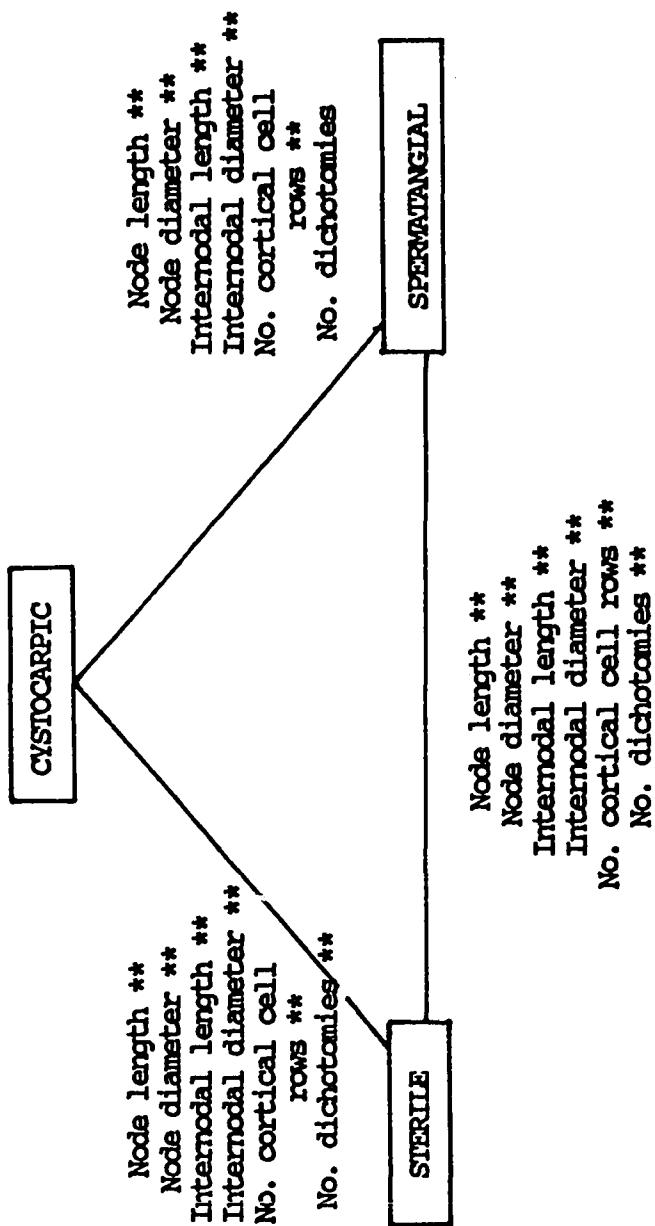Fig. 3.3   Comparison of characters among gametophytes
                  of <u>C</u>. <u>clarionensis</u> grown under culture
                  conditions (2nd set of plants). Results of
                  Kruskal-Wallis test one-way analysis of
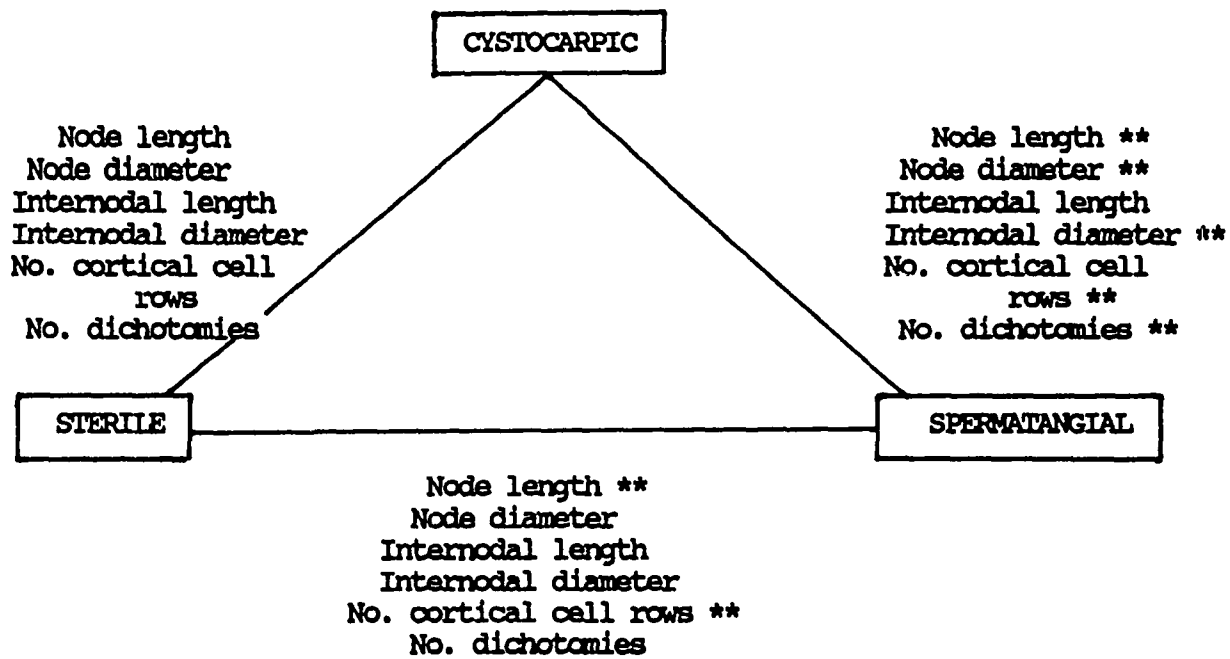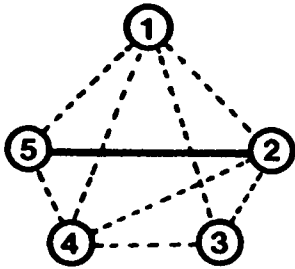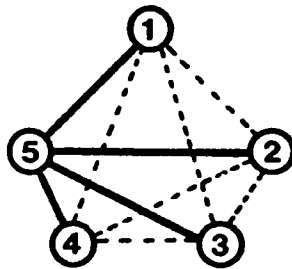   variance. Significant differences
                  are indicated with **.

```
                        ┌─────────────┐
                        │ CYSTOCARPIC │
                        └─────────────┘
                          ╱         ╲
Node length             ╱             ╲           Node length **
Node diameter         ╱                 ╲         Node diameter **
Internodal length    ╱                    ╲       Internodal length
Internodal diameter ╱                       ╲     Internodal diameter **
No. cortical cell  ╱                          ╲   No. cortical cell
        rows      ╱                             ╲         rows **
No. dichotomies ╱                                ╲ No. dichotomies **
       ┌─────────┐                          ┌──────────────┐
       │ STERILE │──────────────────────────│ SPERMATANGIAL│
       └─────────┘                          └──────────────┘

                    Node length **
                    Node diameter
                    Internodal length
                    Internodal diameter
                No. cortical cell rows **
                    No. dichotomies
```

Fig. 3.4   Comparison of morphological characters
              among artificially-grown gametophytes and
              field-collected plants of __Ceramium__ sp.l.
              Solid lines indicate significant
              differences (P< 0.0001, Kruskal-Wallis
              test, one-way analysis of variance) between
              plants, broken lines indicate that no
              significant differences were detected,
              circled numbers represent the growth
              conditions: (1) 36-61 uE m^{-2} s^{-1}
              (direct light), (2) 22-35 uE m^{-2} s^{-1}
              (light I), (3) 17-25 uE m^{-2} s^{-1} (light
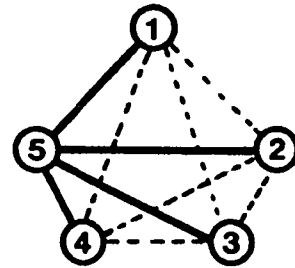   II); (4) natural daylight; and (5) field
              plants.
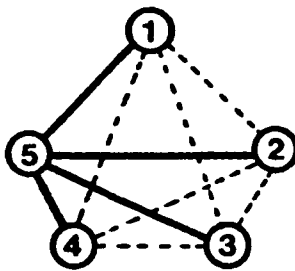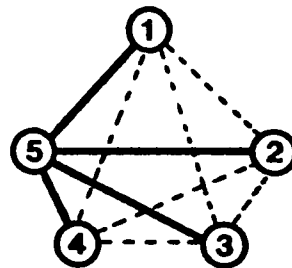
Internodal length

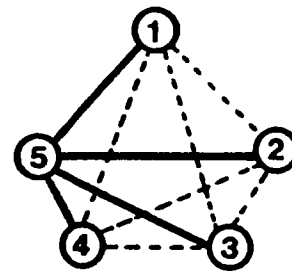Internodal diameter

Nodal length

Nodal diameter

No. of cortical cell rows

No. of dichotomies

No. of adventitious

branches

Fig. 3.5   Comparison of morphological characters among artificially-grown tetrasporophytes and field collected plants of <u>Ceramium</u> sp.1. Solid lines indicate significant differences (P< 0.0001, Kruskal-Wallis test, one-way analysis of variance) between plants, broken lines indicate that no significant differences were detected, circled numbers represent the growth conditions: (1) 36-61 uE m^{-2} s^{-1} (direct light), (2) 22-35 uE m^{-2} s^{-1} (light I), (3) 17-25 uE m^{-2} s^{-1} (light II); (4) natural daylight; and (5) field plants.
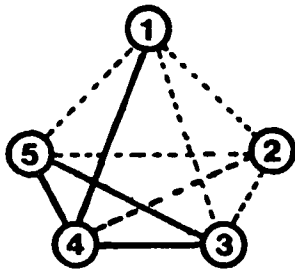
Internodal length

Internodal diameter

Nodal length

Nodal diameter

No. of cortical cell rows
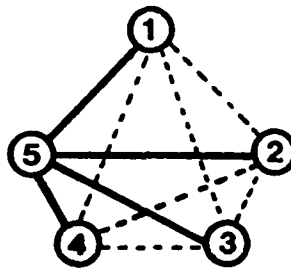
No. of dichotomies
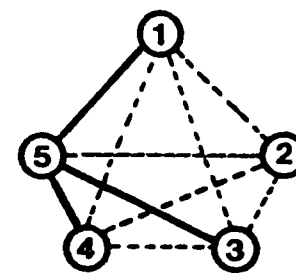
No. of adventitious branches

Fig. 3.6   Comparison of morphological characters
            among artificially-grown plants of <u>Ceramium</u>
            sp. 1 under 8:16 h LD daylength with
            different nutrient and water movement
            conditions. Solid lines indicate
            significant differences (P< 0.0001,
            Kruskal-Wallis test, one-way analysis of
            variance) between plants; broken lines
            indicate that no significant differences
            were detected; circled numbers represent
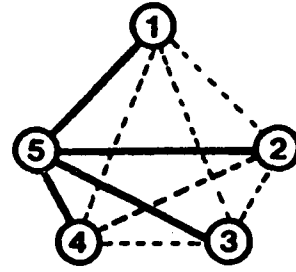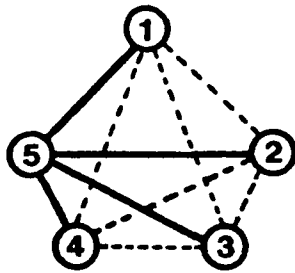   the growth conditions specified in Table
            7.

Internodal length   Internodal diameter   Nodal length
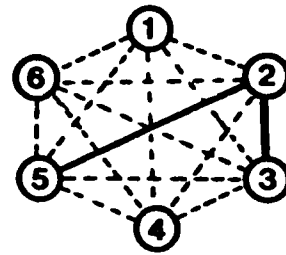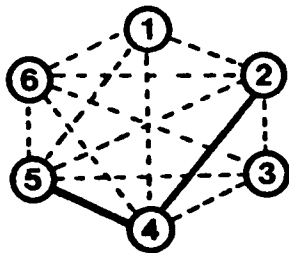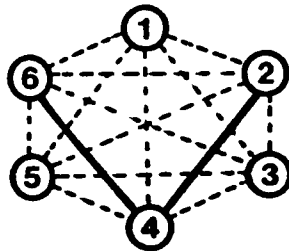
Nodal diameter   No. of dichotomies   No. of adventitious

branches

Distance between

dichotomies

Internodal length

Nodal length
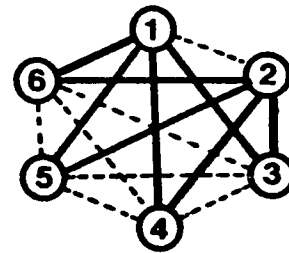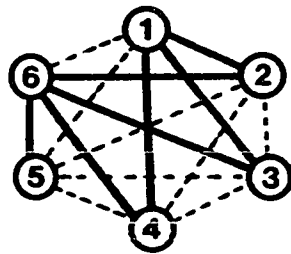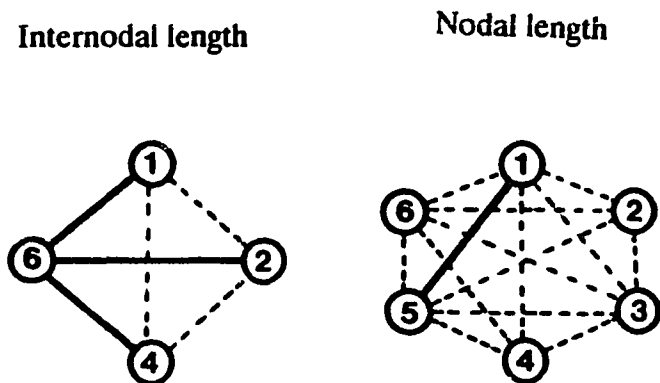
Fig. 3.7   Comparison of morphological characters
           among artificially-grown plants of _Ceramium_
           sp. 1 under 12:12 h LD daylength with
           different nutrient and water movement
           conditions. Solid lines indicate
           significant differences (P< 0.0001,
           Kruskal-Wallis test, one-way analysis of
           variance) between plants; broken lines
           indicate that no significant differences
           were detected; circled numbers represent
           the growth conditions specified in Table
           7.

Internodal length

No. of cells between
dichotomies

Distance between
dichotomies
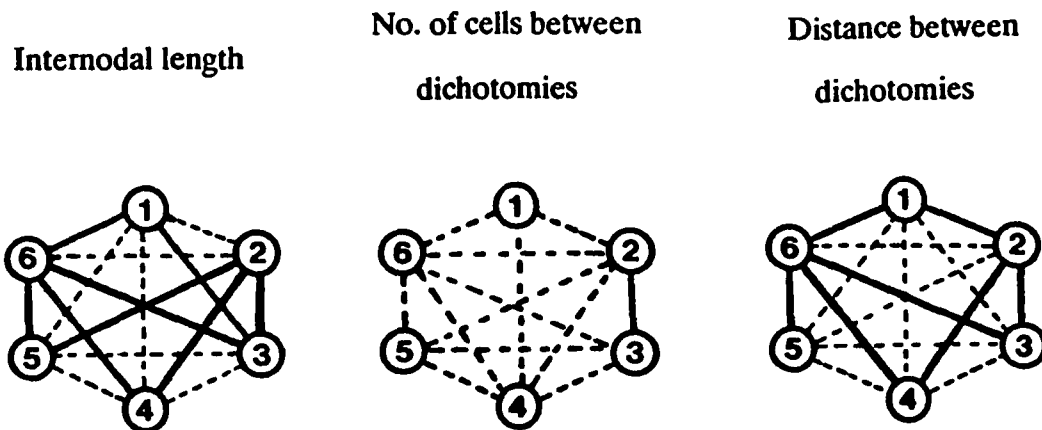
Fig. 3.8   Comparison of morphological characters
among artificially-grown plants of <u>Ceramium</u>
sp. 1 under 16:8 h LD daylength with
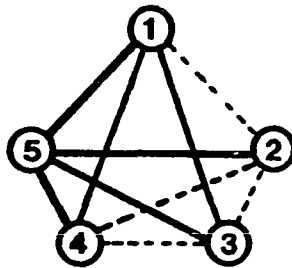different nutrient and water movement
conditions. Solid lines indicate
significant differences (P< 0.0001,
Kruskal-Wallis test, one-way analysis of
variance) between plants; broken lines
indicate that no significant differences
were detected; circled numbers represent
the growth conditions specified in Table
7.

Nodal diameter   No. of dichotomies
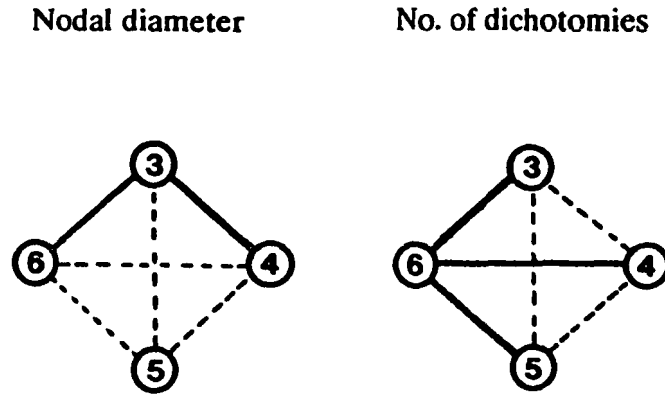
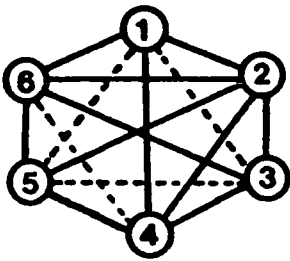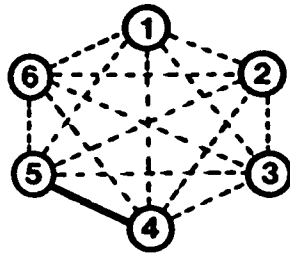Fig. 3.9   Comparison of morphological characters
                 among artificially-grown plants of C.
                 flaccidum under 8:16 h LD daylength with
                 different nutrient and water movement
                 conditions. Solid lines indicate
                 significant differences (P< 0.0001,
                 Kruskal-Wallis test, one-way analysis of
                 variance) between plants; broken lines
                 indicate that no significant differences
                 were detected; circled numbers represent
                 the growth conditions specified in Table
                 7.

Fig. 3.10   Comparison of morphological characters
             among artificially-grown plants of _C.
             flaccidum_ under 16:8 h LD daylength with
             different nutrient and water movement
             conditions. Solid lines indicate
             significant differences (P< 0.0001,
             Kruskal-Wallis test, one-way analysis of
             variance) between plants; broken lines
             indicate that no significant differences
             were detected; circled numbers represent
   the growth conditions specified in Table
   7.
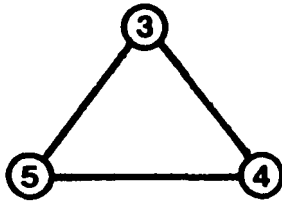
Internodal length   **Internodal diameter**   **Nodal length**
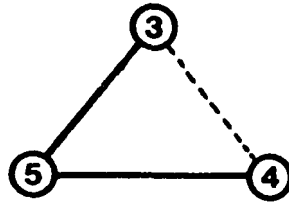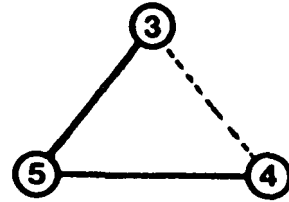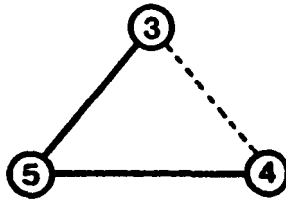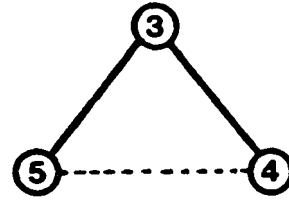
Nodal diameter   **No. of cortical cell rows**   **No. of dichotomies**
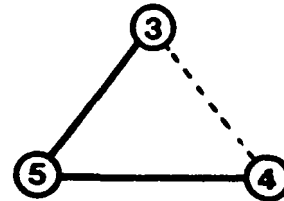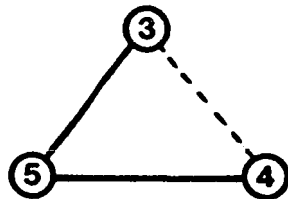
Distance between dichotomies   **No. of cells between dichotomies**
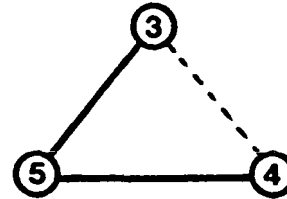
Plate XI.   Results of the first set of cultures of C. clarionensis under 16:8 LD (original material collected at Sans Souci Beach, Waikiki). R-number before scale refers to microscope slide on which specimen is found.

Fig. 1.   Prostrate sterile specimen. R-98 (Scale = 500 um).
Fig. 2.   Male gametophyte. R-98(2) (Scale = 500 um).
Fig. 3.   Female plant showing subterminal cystocarps. R-104 (Scale = 500 um).
Fig. 4.   Upper portion of tetrasporophyte. R-162 (Scale = 500 um).
Fig. 5.   Close-up of sterile specimen with unusual nodal structure. R-98 (Scale = 100 um).
Fig. 6.   Close-up of male plant showing spermatangia. R-98(2) (Scale = 100 um).
Fig. 7.   Nodal structure of female plant. R-104 (Scale = 100 um).
Fig. 8.   Nodal structure of tetrasporophyte. R-162 (Scale = 100 um).
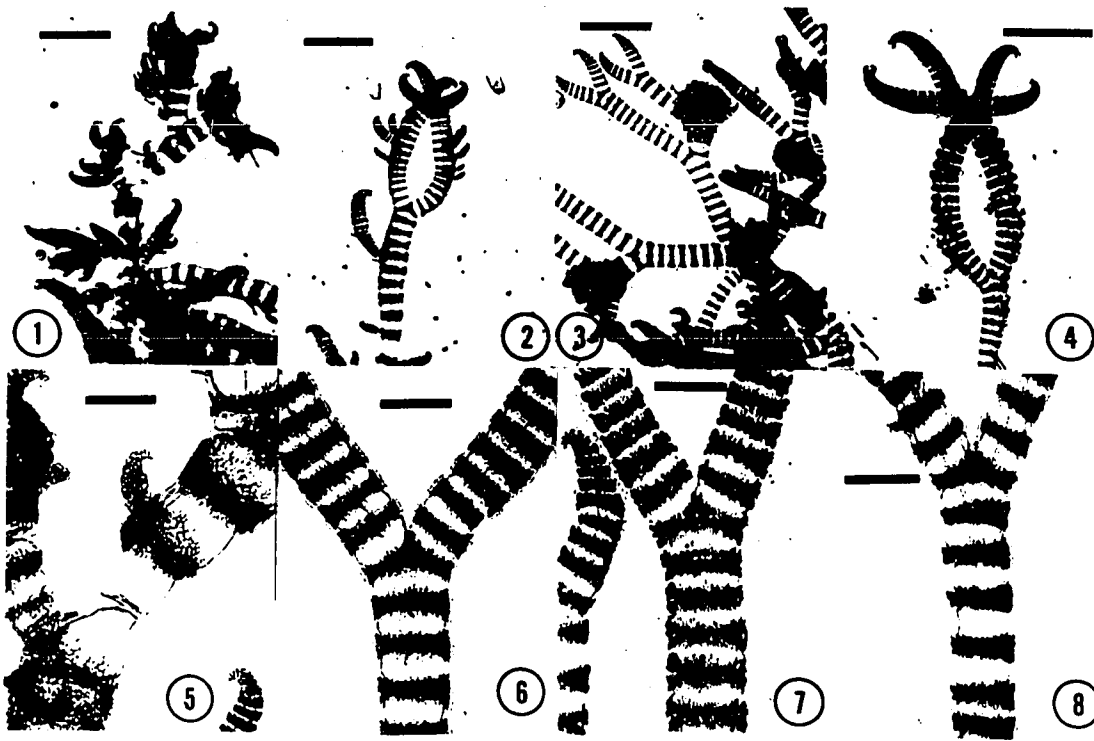
Plate XII. Results of the second set of cultures of C. clarionensis under 16:8 LD (original material collected at Sans Souci Beach, Waikiki). R-number before scale refers to microscope slide on which specimen is found.

Fig. 1. Sterile plant. R-136 (Scale = 500 um).
Fig. 2. Male specimen. R-168 (Scale = 500 um).
Fig. 3. Female plant. R-172 (Scale = 500 um).
Fig. 4. Nodal structure of sterile plant with adventitious outgrowths. R-136 (Scale = 150 um).
Fig. 5. Close-up of male specimen showing spermatangia. R-172 (Scale = 150 um).
Fig. 6. Nodal structure of female plant. R-172 (Scale = 150 um).
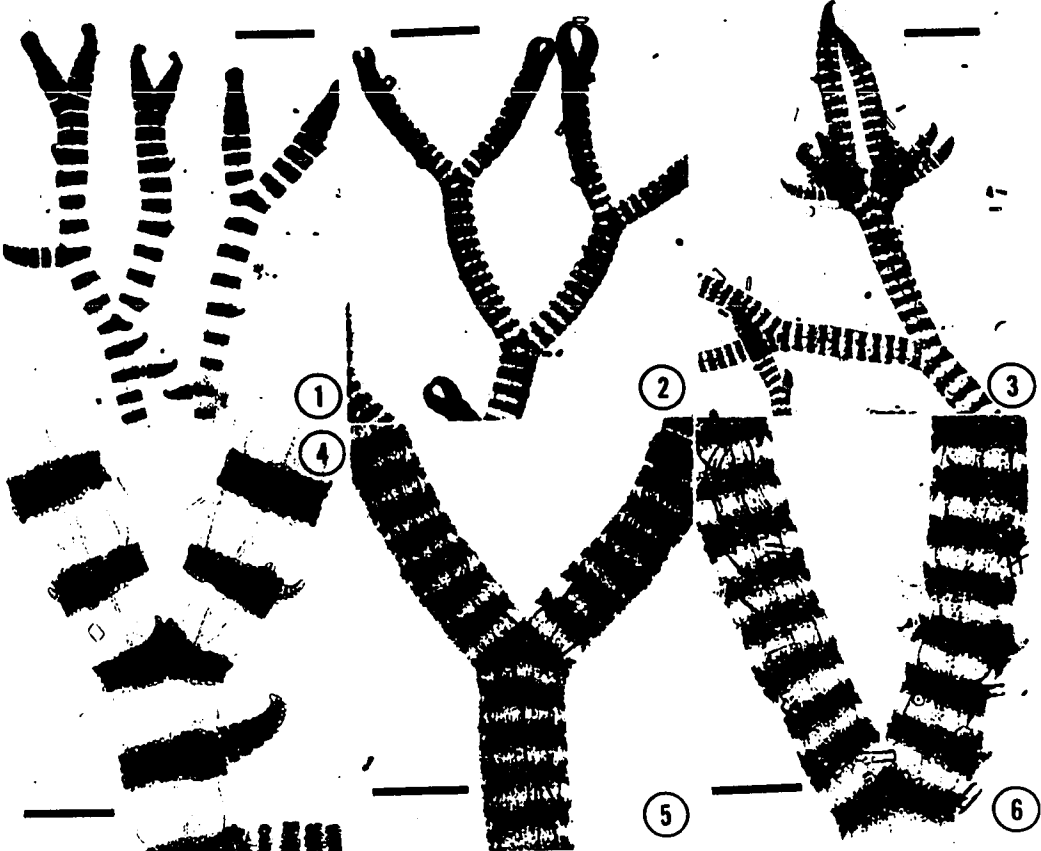
Plate XIII. Results of cultures of C. clarionensis under natural light conditions (original material collected at Sans Souci Beach, Waikiki). R-number before scale refers to microscope slide on which specimen is found.

Fig. 1. Sterile specimen. R-116 (Scale = 500 um).
Fig. 2. Male plant. R-117 (Scale = 500 um).
Fig. 3. Female plant with cystocarps and some germinating carpospores. R-119 (Scale = 500 um).
Fig. 4. Close-up to node structure of sterile plant. R-116 (Scale = 150 um).
Fig. 5. Nodal structure of male plant with some spermatangia. R-117 (scale = 150 um).
Fig. 6. Nodal structure of cystocarpic plant. R-119 (Scale = 150 um).
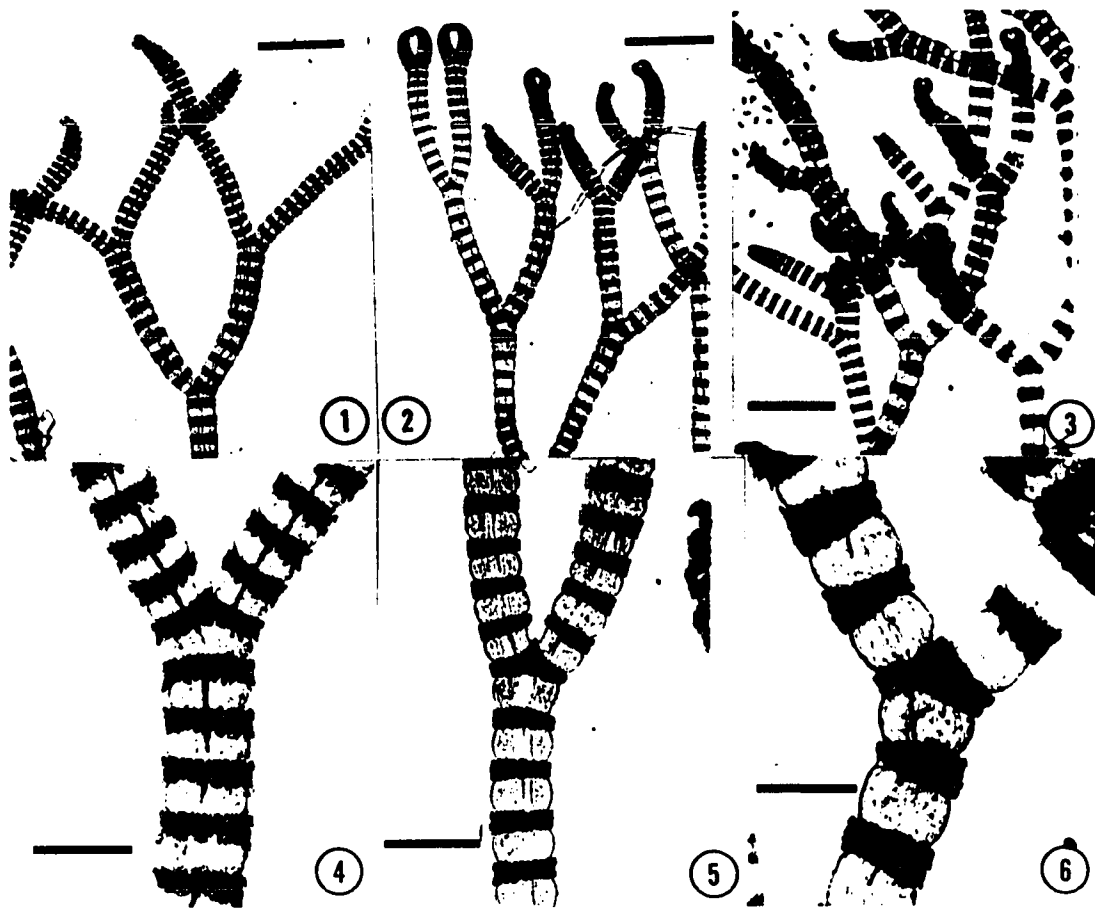
Plate XIV.   Plants obtained from the culture of branches
             of <u>Ceramium</u> sp. 1 (originally collected at
             Kaneohe Bay). R- number before scale refers
             to microscope slide on which specimen is
             found.

Fig. 1.   Upper part of a plant showing rhizoids
          originated along the entire length of the
          thallus. R-214 (Scale = 300 um).
Fig. 2.   Plant showing occasional condensation of nodes.
          R-214 (Scale = 200 um).
Fig. 3.   Typical structure of narrow thallus with poorly
          developed nodes. R-845/846 (Scale = 150 um).
Fig. 4.   Typical structure of plants grown in culture
          under any set of conditions. R-1899/1901 (Scale
          = 250 um).
Fig. 5.   Occasional morphologically divergent plants
          obtained in culture. R-555/556 (Scale =
          150 um).
Fig. 6.   New adventitious growth originating from dying
          branches. R-1899/1901 (Scale = 500 um).

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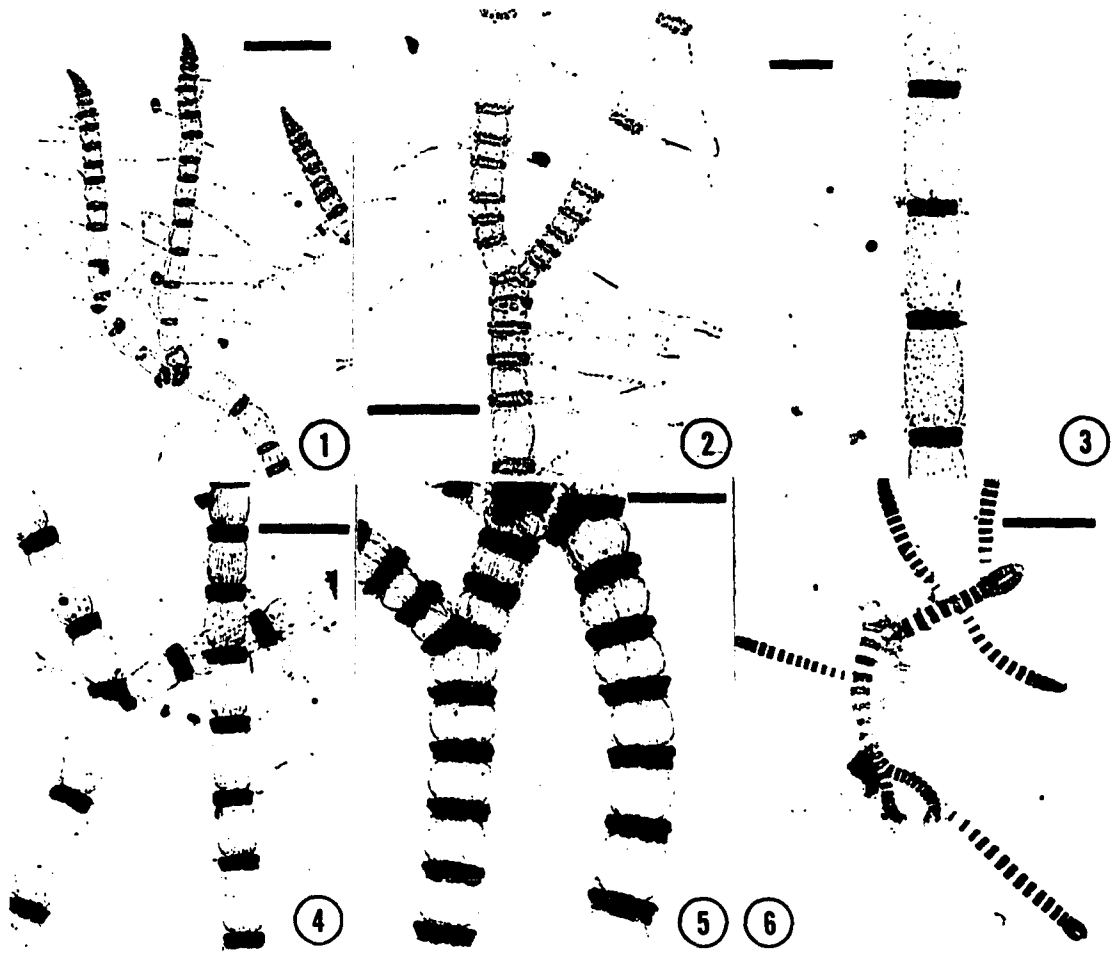
Plate XV.   Plants of C. **flaccidum** obtained in culture
            (original material collected at Kaalawai
            Beach). R- number before scale refers to
            microscope slide on which specimen is found.

Fig. 1.   Young plants emerging from disintegrating algal
          material. R-1870/1879 (Scale = 500 um).
Fig. 2.   Typical alternate branching pattern in plants
          grown in culture. R-1246/1251 (Scale = 500 um).
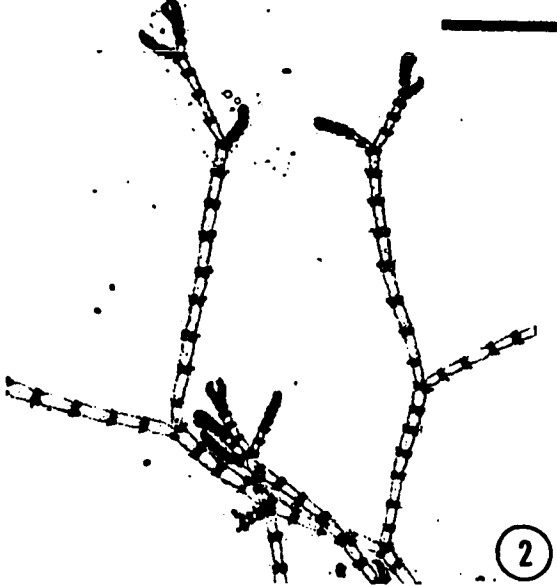
Literature cited

Abbott, I.A. 1985. New species of _Gracilaria_ Grev.
(Gracilariaceae, Rhodophyta) from California and
Hawaii. In: I.A.Abbott & J.N.Norris (eds.), _Taxonomy_
of Economic Seaweeds. Calif. Sea Grant Progr. Publ.
Univ. Calif., La Jolla, California, pp. 115-121.

------ 1988. Some species of _Gracilaria_ and _Polycavernosa_
from Thailand. In I.A.Abbott (ed.), _Taxonomy of_
economic seaweeds. Vol. II. Calif. Sea Grant Progr.
Publ. Univ. Calif., La Jolla, California, pp.137-150.

Dawson, E.Y. 1950. A review of _Ceramium_ along the Pacific
coast of North America with special reference to its
Mexican representatives. _Farlowia_ 4:113-138.

Dixon, P.S. 1960. Studies on marine algae of the British
Isles: the genus _Ceramium_. _J_. _Mar_. _Biol_. _Assoc_. _U.K_.
39: 331-374.

Feldmann-Mazoyer, G. 1940. _Recherches sur les Ceramiacees_
de la Mediterranee Occidentale. Imprimerie Minerva,
Alger. 510pp. 4 pls.

Garbary, D., Grund, D.W. & McLachlan, J. 1978. The
taxonomic status of _Ceramium rubrum_ (Huds.) C.Ag.

(Ceramiales, Rhodophyceae) based on culture experiments. _Phycologia_ 17: 85-94.

----- 1980. Branching patterns and life history stages in _Ceramium_ _rubrum_ (Huds.) C.Ag. _Nova_ _Hedwigia_ 33: 249-260.

Hannach, G. & Santelices, B. 1985. Ecological differences between the isomorphic reproductive phases of two species of _Iridaea_ (Rhodophyta; Gigartinales). _Mar_. _Ecol_. _Progress_ _Ser_. 22: 291-303.

Levring, T. 1937. Zur Kenntnis der Algenflora der norwegishen Westkueste. _Lunds_ _Univ_. _Arsskr_. _N_._F_. _Avd_. 2, 33: 1-148.

Luxoro, C. & Santelices, B. 1989. Additional evidence for ecological differences among isomorphic reproductive phases of _Iridaea_ _laminarioides_ (Rhodophyta; Gigartinales). _J_. _Phycol_. 25: 206-212.

McLachlan, J., 1979. Growth media-marine. _In_: J.R.Stein (ed.), _Handbook_ _of_ _Phycological_ _Methods_. _Culture_ _Methods_ _and_ _Growth_ _Measurements_. Cambridge Univ. Press, Cambridge. pp. 25-51.

Nakamura, Y., 1950. New _Ceramiums_ and _Campylaephoras_ from Japan. _Sci_. _Pap_. _Inst_. _Algol_. _Res_., _Hokkaido_ _Univ_. 3: 155-172.

 1954. The structure and reproduction of the genera
Ceramium and *Campylaephora* in Japan with special
reference to criteria of classification. *Sci. Pap.
Inst. Algol. Res., Fac. Sci. Hokkaido Univ.* 4: 15-62.

Setchell, W.A. & Gardner, N.L. 1930. Marine algae of the
Revillagigedo Islands expedition of 1925. *Proc. Calif.
Acad. Sci.* 19: 109-215.

Siegel, S. & Castellan Jr., N.J. 1988. *Non-parametric
statistics*. 2nd edition. McGraw-Hill, New York, 399
pp.

Suh, Y. & Lee, I.K. 1984. Morphology and reproduction of
some species of *Ceramium* (Rhodophyta) in culture.
Korean J. Bot. 27: 163-171.

Womersley. H.B.S. 1978. Southern Australian species of
Ceramium Roth (Rhodophyta). *Aust. J. Mar. Freshwater
Res.* 29: 205-257.

CHAPTER IV

SUMMARY OF RESEARCH AND CONCLUSIONS

Morphological vegetative and reproductive characteristics show some degree of variability in most orders of Rhodophyta. This variability is a major fact that affects the algal taxonomy when it is expressed by characters used as diagnostic. The genus _Ceramium_ is no exception. Species recognition in _Ceramium_ has been often obscured by the occurrence in nature of a range of forms separated into different species, but associated into "complexes" because of their conflicting morphological limits. A few culture studies have assessed the character variability of these species and correlated it with physical factors. From these studies it is evident that a certain number of diagnostic characters can be modified through the environment, to the extent of affecting drastically the separation of the species involved.

This research project consisted of the collection and examination of _Ceramium_ species around the island of Oahu and the comparison of these species with the _Ceramium_ flora of other tropical and subtropical

regions in the North Pacific. The morphological
variability of three of the most common species was
examined between generations, natural populations and
different culture conditions in order to evaluate the
reliability of their morphological characters.

Hawaiian species of _Ceramium_ were studied on the
basis of four working hypotheses. The first of these
hypotheses stated that "the species of _Ceramium_ present
in the Hawaiian islands, are of common occurrence in
other subtropical locations". Based on the
identification of the species recorded on Oahu and, to a
lesser extent in other Hawaiian islands and the
comparison of these species to geographical records from
other subtropical regions, this hypothesis was accepted.
With the exception of _C. flaccidum_ (Kuetzing) Ardissone
sensu Womersley (1978) (but excluding _C. fimbriatum_)
which is distributed worldwide, and five species of
Ceramium not previously identified, the remaining five
species have been recorded for tropical and subtropical
areas mainly in the North Pacific Ocean.

It has been previously mentioned that _Ceramium_
is structurally simple, the characters upon which species
distinction can be based, are few. Throughout this
study, each of the species examined, with the exception

of <u>Ceramium</u> sp. 2 and <u>C</u>. <u>fimbriatum</u>, showed variability
in its characteristic features to a greater or lesser
extent. In the case of <u>Ceramium</u> sp. 2, the uniformity of
its morphological components may well be artificial since
the plant was not frequently collected and therefore the
small number of individuals was not sufficient to
indicate the real variability in natural populations. On
the other hand, the specimens examined were collected
from several localities where the prevailing
environmental conditions are different and morphological
differences would be
expected in the plants. Conversely, <u>C</u>. <u>fimbriatum</u> was
often found in abundance and the individuals collected at
different sites do not show large differences in their
morphological characters.

Modifications in morphological characters
displayed in other species may be found in different
branches of the same individual or between individuals.
<u>Ceramium</u> <u>aduncum</u> can have strongly forcipate to entirely
straight apices in the same plant, <u>C</u>. <u>affine</u> occasionally
produces swollen branches whose dimensions are out of the
characteristic range for individuals of this species. <u>C</u>.
<u>hamatispinum</u> and <u>C</u>. <u>affine</u> each can be clearly separated
into two morphological groups. Characters which include

the degree of nodal development, number of cells in spines, spine shape and internodal (axial cells) dimensions are distinct enough in C. hamatispinum to separate it into two distinct forms. In C. affine, the two forms are separated on the basis of their distinctions in size, branching pattern and nodal development. Finally, species such as C. clarionensis display such a variability in node appearance due to the variation of cortical cell sizes and number of cortical cells rows that some specimens can be easily confused with C. aduncum.

The culture of species under laboratory conditions confirmed the idea that if variability is found in field-collected plants it may be reproduced in artificially grown specimens. Interestingly, some variations in morphology which were not observed in field plants were expressed under laboratory conditions. At the same time not all species show the same degree of variability. Ceramium clarionensis grows with the same vigor as plants of this species in the field, but displays morphological distinctions among sexual plants and tetrasporophytes. These distinctions include degree of nodal development, node structure, internodal and nodal dimensions. These features are modified depending

on the conditions under which the plants are grown. _Ceramium_ sp. 1 also shows significant deviations from field plants but the differences between reproductive stages are not so pronounced as in C. _clarionensis_. The latter species even produced a generation of individuals which differ entirely from any of the reproductive phases either collected in the field or grown in culture.

Because of the restricted local distribution and the reduced number of individuals that were found in most of the species, the extension of their phenotypic variability is difficult to study in the field. However, C. _flaccidum_ is abundant and common enough to facilitate this type of study. The phenotypic variability includes distinct morphological characters that not only change from population to population but, also with the spatial distribution within a population and to a less degree throughout time in the same population. Although the characters that are modified in C. _flaccidum_ by field and culture conditions are essentially the same modified as those by culture conditions in _Ceramium_ sp. 1, the extent to which these changes are shown by the two taxa results in recognition of two entities. Moreover, while specimens of _Ceramium_ sp. 1 cultured under laboratory conditions can be easily considered as a distinct species

from specimens in the field, C. flaccidum retains its specific characteristics under both field and culture conditions.

Based on the results gathered from culture experiments as well as field collections of the different species, the hypothesis stating that "different species of Ceramium have different degrees of variability of the morphological attributes used as diagnostic characters" is hereby accepted.

Differences in the degree of variability of taxonomic features thus depends upon the species under evaluation. Ceramium aduncum and C. clarionensis overlap to some extent since plants of C. clarionensis may develop similar nodes to those of C. aduncum under certain conditions, while the distinctive gland cells of C. aduncum could be absent making the similarity more obvious. The variability of nodal and internodal dimensions in most species can lead to identity of different forms of the same taxon as different species. This is the case of C. hamatispinum and C. affine whose descriptions ought to include the two clear morphological types found for both species during this study. The original description of Ceramium sp. 1, which was based on field-collected plants, requires major changes

including the variety of forms that were obtained in culture experiments. Some of these forms resemble the otherwise very distinctive variety peninsularis of C. affine Dawson. C. flaccidum, in spite of its broad variability, is well-defined on the basis of its cortical arrangement. Since this particular character is stable in this species, it allows its recognition within the entire phenotypic range of variability for the other characters.

In brief, most of the original descriptions of species in this study have been modified to include the variability that they show in their diagnostic characters. In other words, we accept the hypothesis that states that "the knowledge of the morphological variability of the Hawaiian species will result in a reevaluation of the taxonomic limits in several species".

Characters such as nodal and internodal dimensions, size of plants and branching pattern in C. flaccidum are significantly different in plants collected from different populations from different localities. Water turbulence, light intensity and substrate are a few of the abiotic factors in which these localities differ. The characteristics of plants within each population at a particular time are fairly uniform. Tall plants with few branches and with long and narrow internodes are

characteristic from Kahala Beach, an open reef area where
C. flaccidum grows saxicolous on pieces of dead coral.
Short and bushy plants with short internodes grow at
Kaalawai Beach epiphytic on Acanthophora in an area
protected from direct wave exposure. Epiphytic plants
collected at Kualoa Point show intermediate
characteristics from the other two populations. This
indicates that the morphology of each population is
associated with the environmental characteristics of the
locality in which plants grow.

A more direct result that implies a correlation
between environmental conditions and phenotypic
variability derives from the evaluation of characters in
plants grown under culture conditions. The morphological
characteristics of C. clarionensis, Ceramium sp. 1 and C.
flaccidum change significantly from the field to the
laboratory. In addition to the production of specimens
entirely aberrant in comparison to field plants and whose
morphology was never found in field equivalents,
individuals of C. clarionensis treated under different
conditions of light formed noticeably different plants.
Light regimes, which probably include light intensity and
photoperiod as well as light quality, have a fundamental
effect upon the nodal degree of development, the

internodal dimensions and the branching patterns of the plant. Evidently these modifications are not only induced by the prevailing conditions but arise as an interaction with the ploidy level of the plant under treatment.

The stable and possibly extreme conditions supplied by the culture medium, controlled light regime and temperature in the closed system of a Petri dish results in significant differences between plants of Ceramium sp. 1 grown under these conditions and their counterparts in the field. The phenotypic plasticity of these plants is such that major changes occur within a week during the lifetime of an individual plant. There exists an intrinsic variability which contributes to the overall variation in morphological characters of different progenies. Despite this variability, the changes induced by the culture conditions are significant and the resulting plants are easily distinguishable from field material. Culture conditions, regardless of the combination of light regime, nutrient concentration and water movement conditions always produce thin plants with a fragile appearance and poorly developed nodes in comparison to field plants. There are no specific or clear trends in the results that indicate a direct

correlation between a particular change in morphology and a specific combination of factors. The variability obtained in cultures somehow suggests that these are rather stressful conditions for the plants to grow.

Similarly, a great range of variability in characters obtained from cultures of C. flaccidum and, as in Ceramium sp. 1, a proportion of this variability is intrinsic to the individual and the rest is clearly induced by the conditions in which it is growing. Again, no specific trends are detected, but a general decrease in nodal development and the formation of gland cells are the most notable of the deviations from field plants.

In view of the field and experimental results, the hypothesis that "the degree of variability of diagnostic characters can be correlated with the degree of environmental variability" is accepted.

In summary, the morphological variability shown by red algae, and the fact that their taxonomy is based on morphological attributes, leads to a careful examination of the species in each genus in order to encompass this variability in their diagnosis. An example of this approach was attempted with the genus Ceramium in Hawaii. In trying to evaluate the variability and reliability of the specific diagnostic

characters, one encounters several constraints. One of them is the reduced availability and restricted local distribution of some of the species, a fact that could possibly be surpassed by more intense sampling. A second constraint that has been previously mentioned is the size of the specimens and the intricacy by which they are attached to the substrate. Nonetheless, once these difficulties are overcome, a large geographical analysis comparing the local flora of Ceramium with that of other localities in the North Pacific, shows that several species are in common with both east and west Pacific coasts. North Pacific islands probably share the specific flora of Ceramium representing a bridge between the two sides of the North Pacific.

Further studies at the experimental level with Ceramium species will probably confirm the differences in variability found in the species treated during this research project. None of the morphological characters were shown to be absolutely uniform by any of the species. It is probable, however, that culture conditions represent stressful conditions seldom present in the field, thus the variability obtained experimentally should be interpreted as potential and not representative for natural populations. An indication of

the phenotypic plasticity of the plants was given by the culture experiments; however, transplant experiments would certainly be a very adequate way of assessing changes in the field.

The collection of an abundant number of specimens and the careful examination of most characters proved to be taxonomically useful in this case and had the effect of focusing upon the morphological variation of the characters used for definition of each species.

APPENDIX

The following is a collection of tables, result
of the measurements of individual plants of Ceramium sp.
1, C. flaccidum and C. clarionensis during the course of
the experiments and observations reported in Chapter III.

Morphological characteristics of field plants,
gametophytes, tetrasporophytes and sterile branches from
experimentally-grown plants are expressed in ranges.
Ranges include the totality of specimens measured.
Numbers in parenthesis are the extreme values of the
ranges where fall values less than 15% of all those
recorded.

Tables in which the comparison of morphological
characteristics among individuals of different
reproductive stages, progenies or grown under distinct
sets of conditions are also included in this appendix. A
column indicating the pairs of groups compared is located
to the left of the table followed by a column indicating
the character evaluated, another with the critical value
of z calculated for that pair and the last column of the
right consists of the calculated difference between the

mean scores for that pair.   This last value has to be
higherthan the critical value of z in order to be
statistically significant.

Table A1

Morphological characteristics of C. flaccidum along a transect across Kahala Beach reef.

Distance from the shore (m)

	5	10	15	20	25
No. plants/m^2	40	30	40	50	38
Thallus length (mm)	5-10	4-9	5-14	4-15	4-11
Node length (um)	38-40(60)	36-60	36-48(60)	36-60	36-60
Node diameter (um)	48-72	(48)60-72(84)	48-72	60-84(96)	(48)60-84
Internode length (um)	(120)180-300(372)	(168)204-312	(180)192-384(444)	(192)216-360(432)	(204)240-336(480)
Internode diameter (um)	36-60(72)	(36)48-72	36-48(72)	36-60(84)	36-60(72)
No. of dichotomies	5-9	5-9	4-9	5-9(11)	5-8(9)
Distance between dichotomies (um)	500-3,600	750-1,600	600-1,600	600-1,300	650-2,150
No. cells between dichotomies	(4)5-6	5-6	5-6(8)	5-6(7)	5-7

Table A2. Morphological characteristics of gametophytes of C.clarionensis grown under 16:8 LD daylength (1st set of plants).

	Cystocarpic (n=15)	Spermatangial (n=15)	Sterile (n=15)
Length (mm)	3-8.4	3-5.6	3-6.5
Node diameter (um)	(120)132-144(168)	108-120(180)	(156)180-228(264)
Node length (um)	(48)60-72(84)	48-60(84)	(84)96-120(192)
Internode diameter (um)	(108)120-144(156)	96-120(180)	(132)168-204(252)
Internode length (um)	12-120(168)	24-48(72)	(12)24-36(48)
No.of cortical cell rows	5-6(8)	4-7(10)	(8)10-15(21)
No. of dichotomies	3-6(8)	2-6(7)	2-3(4)
No. of adventitious branches	(3)5-21	none-18	16-49

Table A3. Comparison among the three morphological types
of gametophytes of $\underline{C}$. $\underline{clarionensis}$ grown under
16:8 LD daylength. Results of Kruskal-Wallis
test (n = 90).

Character	DF	x^2	$P>x^2$
Node diameter	2	52.73	0.0001
Node length	2	62.52	0.0001
Internode diameter	2	50.44	0.0001
Internode length	2	17.27	0.0001
No.of cortical cell rows	2	60.84	0.0001
No. of dichotomies	2	43.60	0.0001

Table A4. Morphological characteristics of gametophytes of C. clarionensis grown under 16:8 LD daylength (2nd set of plants).

	Cystocarpic (n=36)	Spermatangial (n=6)	Sterile (n=28)
Length (mm)	4.5-8.3	2.7-4.9	4.6-8.4
Node diameter (um)	(120)132-204(228)	99-132(156)	(108)120-180
Node length (um)	60-108(120)	(24)36-60	48-96(120)
Internode diameter (um)	120-192(228)	108-120(168)	120-180(192)
Internode length (um)	(12)24-96	24-48	(12)24-84(108)
No. of cortical cell rows	(4)5-10(13)	3-7	4-9(12)
No. of dichotomies	3-6(7)	2-5	(3)4-5(6)
No. of adventitious branches	5-37	3-10	11-84

Table A5. Characters which show significant differences (P< 0.05) within
morphological types of gametophytes of C. clarionensis grown
under 16:8 LD daylength (2nd set of plants, n=70).

Pairs compared	Character	critical value of z	difference between mean scores
I - II	Node diameter	21.64	24.46
I - II	Node length	21.64	33.78
I - III	Internode diameter	22.08	26.37
I - II	Internode diameter	21.64	24.27
I - II	No. of cortical cell rows	21.64	30.03
I - III	No. of cortical cell rows	22.08	24.31
I - II	No. of dichotomies	21.64	22.95

(I)   cystocarpic plants.
(II) spermatangial plants.
(III) sterile plants.

Table A6. Morphological characteristics of gametophytes of C. clarionensis grown under natural conditions of daylength.

	Cystocarpic (n=22)	Spermatangial (n=18)	Sterile (n=4)
Length (mm)	4-9	4-8	5
Node diameter (um)	72-108(132)	(72)84-96(108)	96-108
Node length (um)	36-48(60)	(24)36-48	36
Internode diameter (um)	72-108(132)	(72)84-108	96
Internode length (um)	(36)72-120(132)	(36)60-96(120)	48-72
No. of cortical cell rows	2-3(4)	2-4(3)	3-4
No. of dichotomies	4-7(8)	(3)4-7	3-5
No. of adventitious branches	1-4(5)	1-3(18)	1-19

Table A7. Morphological characteristics of
        tetrasporophytes of *C*. *clarionensis* grown under
                16:8 h LD daylength.

Length (mm)	3.9-10.9
Node diameter (um)	(96)108-132(144)
Node length (um)	(36)48-60
Internode diameter (um)	(96)108-144(156)
Internode length (um)	(48)60-156(204)
No. of cortical cell rows	(3)4-5(7)
No. of dichotomies	(3)4-6(7)
No. of adventitious branches	2-20(44)

Table A8. Characters which show significant differences (P< 0.05) among gametophytes of C. clarionensis grown under laboratory conditions.

Pairs compared	Character	critical value of z	difference between mean scores	Number of observations
I - II	Internode diameter	53.90	61.72	94
I - III	Node diameter	57.62	143.20	74
I - III	Node length	57.62	149.16	74
I - III	Internode diameter	57.62	126.86	74
I - III	Internode length	54.75	71.99	74
I - III	No. of cortical cell rows	49.66	142.97	74

(I)   First set of plants cultured under 16:8 LD daylength.
(II) Second set of plants cultured under 16:8 LD daylength.
(III) Gametophytes cultured under natural daylength conditions.

Table A9. Characters which show significant differences (P< 0.05) among gametophytes and tetrasporophytes of C. clarionensis grown under the same laboratory conditions.

Pairs compared	Character	critical value of z	difference between mean scores	Number of observations
I - III	Node diameter	52.77	85.77	100
I - III	Node length	52.77	79.99	100
I - III	Internode diameter	52.77	53.74	100
I - III	Internode length	50.15	106.63	100
I - III	No. of cortical cell rows	45.50	74.88	100
II - III	Node diameter	42.16	202.35	134
II - III	Node length	42.16	130.24	134
II - III	Internode diameter	42.16	115.46	134
II - III	Internode length	45.69	113.36	134
II - III	No. of cortical cell rows	36.35	103.31	134

(I)   First set of gametophytes cultured under 16:8 LD daylength.
(II) Second set of gametophytes cultured under 16:8 LD daylength.
(III) Tetrasporophytes grown under 16:8 LD daylength.

Table A10. Characters which show significant differences between artificially cultured and field tetrasporophytes of <u>C. clarionensis.</u> Results of Wilcoxon-Mann-Whitney test (n=90).

Character	critical value of z	P>z
Node diameter	5.68	0.0001
Node length	5.92	0.0001
Internode diameter	4.90	0.0001
Internode length	4.29	0.0001

Table A11. Characters which show significant differences (P< 0.05) among tetrasporophytes and gametophytes of <u>C. clarionensis</u> grown under natural daylength conditions (n=114).

Pairs compared	Character	critical value of z	difference between mean scores
I - II	Node diameter	46.85	63.39
I - II	Node length	46.85	63.21
I - II	Internode diameter	46.85	73.12
I - II	No. of cortical cell rows	40.37	68.09

(I) Tetrasporophytes.
(II) Gametophytes.

Table A12. Morphological characters assessed in cultures of _Ceramium_ sp. 1 under different
light intensities. Measurements in micrometers.

Conditions	Node diameter	Node length	Internode diameter	Internode length	No. of adventitious branches	No. of cortical cell rows
GAMETOPHYTES						
Direct light	60-84(96)	24-48	(60)72-84(96)	216-504	4-50	2-4(5)
Light I	60-96	24-48(60)	(72)84-96(132)	(216)276-396(456)	1-15	2-4
Light II	(60)72-108	24-28	60-96(120)	144-420(600)	15-50	2-4(5)
Control	(60)72-108	24(36)-60	60-84(96)	(156)336-492	9-34	3-4
TETRASPOROPHYTES						
Direct light	(60)72-108	24-48	(60)72-120	(144)192-444	3-24	2-4
Light I	(60)72-96(108)	(24)36-48	(60)72-96(132)	(156)408-600(672)	6-72	2-3(4)
Light II	(12)60-108	(12)24-36	(48)60-96(132)	24-432	8-75	2-4(5)
Control	(12)60-108	24-60	60-120(132)	(84)252-612(624)	12-73	2-4(5)

Table A13. Morphological characters showing significant differences (P<0.05) among experimentally-grown gametophytes and field plants of Ceramium sp. 1 (n = 78).

Experimental pair	Character	critical value of z	difference in mean scores
F - L.I.	Internode length	30.32	32.36
F - D.L.	Internode diameter	29.05	76.51
F - L.I.	Internode diameter	30.32	70.96
F - L.II.	Internode diameter	29.05	70.86
F - C	Internode diameter	29.05	51.12
F - D.L.	Node length	29.05	73.90
F - L.I.	Node length	30.32	55.85
F - L.II.	Node length	29.05	72.43
F - C	Node length	29.05	73.90
L.I - L.II	Node diameter	12.64	67.44
F - D.L.	Node diameter	29.05	78.94
F - L.I.	Node diameter	30.32	66.44
F - L.II.	Node diameter	29.05	67.44
F - C	Node diameter	29.05	78.94
F - D.L.	No. of cortical cell rows	29.05	70.09
F - L.I.	No. of cortical cell rows	30.32	55.06
F - L.II.	No. of cortical cell rows	29.05	63.13
F - C	No. of cortical cell rows	29.05	80.67
F - D.L.	No. of dichotomies	29.05	50.10
F - L.I.	No. of dichotomies	30.32	69.00
F - L.II.	No. of dichotomies	29.05	64.40
F - C	No. of dichotomies	29.05	38.38
C - L.I.	No. of adventitious branches	13.02	45.94
C - L.II.	No. of adventitious branches	13.02	51.14
F - D.L.	No. of adventitious branches	29.05	50.13
F - L.I.	No. of adventitious branches	30.32	78.53
F - L.II.	No. of adventitious branches	29.05	83.73
F - C	No. of adventitious branches	29.05	32.59

D.L. = Direct light incidence (36-61 uE m^{-2} s^{-1})
L.I. = 22-35 uE m^{-2} s^{-1})
L.II.= 17-25 uE m^{-2} s^{-1})
C = Control (natural light incidence)
F = Field-collected gametophytes

Table A14. Morphological characters showing significant differences
(P<0.05) among experimentally-grown tetrasporophytes and field
plants of _Ceramium_ sp.1.

Experimental pair	Character	critical value of z	difference in mean scores
C - D.L.	Internode length	15.27	75.28
C - L.I.	Internode length	15.59	40.13
C - L.II	Internode length	12.81	103.61
C - F	Internode length	32.96	68.05
L.I. - L.II.	Internode length	13.19	63.48
C - L.II.	Internode diameter	15.27	37.15
C - F	Internode diameter	32.96	84.63
D.L. - L.II.	Internode diameter	12.81	43.27
D.L. - F	Internode diameter	40.37	73.17
L.I. - F	Internode diameter	34.12	88.49
L.II. - F	Internode diameter	32.96	121.78
C - L.II.	Node length	12.81	43.27
C - F	Node length	32.96	81.53
D.L. - F	Node length	40.37	91.34
L.I. - F	Node length	34.12	88.27
L.II. - F	Node length	32.96	124.79
C - F	Node diameter	32.96	88.49
D.L. - L.I.	Node diameter	15.59	38.48
D.L. - F	Node diameter	40.37	81.45
L.I. - F	Node diameter	34.12	92.47
L.II. - F	Node diameter	32.96	119.93
C - F	No. of cortical cell rows	32.96	94.92
D.L. - F	No. of cortical cell rows	40.37	96.67
L.I. - F	No. of cortical cell rows	34.12	87.08
L.II. - F	No. of cortical cell rows	32.96	111.28
C - L.II.	No. of dichotomies	12.81	19.95
C - F	No. of dichotomies	32.96	60.67
D.L. - F	No. of dichotomies	40.37	76.26
L.I. - L.II.	No. of dichotomies	13.19	46.78
L.II. - F	No. of dichotomies	32.96	80.62

Table A14. (Continued) Morphological characters showing significant
differences (P<0.05) among experimentally-grown
tetrasporophytes and field plants of <u>Ceramium</u> sp.1.

C - D.L.	No. of adventitious branches	15.97	50.37
C - F	No. of adventitious branches	32.96	100.07
D.L. - L.I.	No. of adventitious branches	15.59	61.89
D.L. - L.II.	No. of adventitious branches	15.27	58.93
D.L. -F	No. of adventitious branches	40.37	49.69
L.I. - F	No. of adventitious branches	34.12	111.58
L.II. - F	No. of adventitious branches	32.96	108.62

D.L. = Direct light intensities (36-61 uE m^{-2} s^{-1})
L.I. = 22-35 uE m^{-2} s^{-1}
L.II.= 17-25 uE m^{-2} s^{-1}
C   = Control (natural light incidence)
F   = Field-collected gametophytes

Table A15. Characters which show significant differences among plants of Ceramium sp. 1 grown under different daylengths. Results of Kruskal-Wallis one-way analysis of variance test (P<0.01).

Experimental pair	Character	critical value of z	difference in mean scores
I - II	Node diameter	69.22	229.13 *
I - III	Node diameter	70.54	83.30 *
II - III	Node diameter	38.40	312.43 *
I - II	Node length	69.22	289.45 *
II - III	Node length	38.40	267.15 *
I - II	Internode diameter	69.22	211.41 *
I - III	Internode diameter	38.40	266.69 *
I - II	Internode length	69.22	211.60 *
I - III	Internode length	70.54	198.23 *
I - II	No.of cortical cell rows	69.22	284.20 *
II - III	No. of cortical cell rows	38.40	262.97 *
I - II	No.of dichotomies	69.22	111.53 *
I - III	No.of dichotomies	70.54	234.39 *
II - III	No.of dichotomies	38.40	345.92 *
I - II	No.of cells between dichotomies	67.59	95.97 **
I - III	No.of cells between dichotomies	68.71	161.07 **
II - III	No.of cells between dichotomies	37.69	256.14 **
I - III	No.of adventitious branches	70.03	218.65 ***
II - III	No.of adventitious branches	38.12	151.44 ***
I - III	Distance between dichotomies	68.71	197.35 **
II - III	Distance between dichotomies	37.69	146.85 **

I -Plants grown under 8:16 LD; II -Plants grown under 12:12 LD; III-Plants grown under 16:8 LD; * n=694; ** n=676; *** n=689.

Table A16. Characters which show significant differences among
experimentally-grown and control plants of C. flaccidum under
different daylengths. Results of Kruskal-Wallis one-way
analysis of variance test (P< 0.01).

Experimental pair	Character	critical value of z	difference between mean scores
I - II	Distance between dichotomies	43.92	70.94 *
II - III	Distance between dichotomies	68.12	97.30 *
II - C	Distance between dichotomies	56.95	64.88 *
I - C	Distance between dichotomies	42.63	135.82 *
III- C	Distance between dichotomies	67.70	162.18 *
II - III	Internodal diameter	62.15	107.28 **
I - III	Internodal diameter	49.22	176.18 **
I - II	No.of dichotomies	45.83	155.71 **
II - C	No.of dichotomies	60.18	89.79 **
I - III	No.of dichotomies	49.22	181.43 **
I - C	No.of dichotomies	46.70	65.91 **
III- C	No.of dichotomies	62.79	191.86 **
II - III	Internodal length	62.15	90.96 **
II - C	Internodal length	60.18	100.87 **
I - III	Internodal length	49.22	94.07 **
I - C	Internodal length	46.70	97.76 **
III- C	Internodal length	62.79	191.86 **
I - II	No.of cells between dichotomies	43.92	124.25 *
I - III	No.of cells between dichotomies	56.70	145.12 *
I - C	No.of cells between dichotomies	42.63	128.17 *
I - II	No.of cortical cell rows	45.83	178.67 **
I - III	No.of cortical cell rows	49.22	183.52 **
I - C	No.of cortical cell rows	46.70	190.71 **

Table A16. (Continued) Characters which show significant differences among experimentally-grown and control plants of C. flaccidum under different daylengths. Results of Kruskal-Wallis one-way analysis of variance test (P< 0.01).

I	-	II	Nodal length	45.83	135.85 **
I	-	III	Nodal length	49.22	183.37 **
I	-	C	Nodal length	46.70	140.79 **
I	-	II	Nodal diameter	45.83	111.93 **
I	-	III	Nodal diameter	49.22	152.03 **
I	-	C	Nodal diameter	46.70	143.18 **
I	-	II	No.of adventitious branches	33.68	143.51 ***
II	-	III	No.of adventitious branches	64.58	174.50 ***

I -16:8 LD daylength;
II -12:12 LD daylength;
III-8:16 LD daylength;
C -control under natural daylength.
*   n=310;
** n=372;
*** n=295.

Table A17. Characters which show significant differences among
experimentally-grown plants of Ceramium sp. 1 under different
nutrient concentrations, and water movement conditions at
8:16 h LD daylength (n=280). Results of Kruskal-Wallis
one-way analysis of variance test (P< 0.01)

Experimental pair*	Character	critical value of z	difference between mean scores
II - IV	Nodal diameter	42.93	47.40
IV - V	Nodal diameter	49.28	61.20
II - III	Nodal length	44.22	61.62
II - V	Nodal length	53.15	68.52
I - II	Internodal length	50.85	110.00
I - IV	Internodal length	46.83	64.20
I - VI	Internodal length	48.59	52.89
II - III	Internodal length	44.22	115.36
II - IV	Internodal length	42.93	45.80
II - V	Internodal length	53.15	133.70
II - VI	Internodal length	54.19	57.10
III- IV	Internodal length	47.53	69.60
III- VI	Internodal length	49.28	58.30
IV - V	Internodal length	49.28	87.90
V - VI	Internodal length	50.97	76.60
IV - V	Internodal diameter	49.28	68.10
I - II	Distance between dichotomies	50.85	68.50
I - III	Distance between dichotomies	45.86	61.18
I - IV	Distance between dichotomies	46.83	56.10
II - VI	Distance between dichotomies	54.19	76.97
III- VI	Distance between dichotomies	49.28	69.65
IV - VI	Distance between dichotomies	50.42	64.57
V - VI	Distance between dichotomies	50.97	54.57

Table A17. (Continued) Characters which show significant differences among experimentally-grown plants of Ceramium sp. 1 under different nutrient concentrations, and water movement conditions at 8:16 h LD daylength (n=280). Results of Kruskal-Wallis one-way analysis of variance test (P< 0.01)

II - IV	No.of dichotomies	42.93	79.26
IV - VI	No.of dichotomies	50.42	68.13
I - III	No.of adventitious branches	45.86	66.46
I - IV	No.of adventitious branches	46.83	96.40
I - V	No.of adventitious branches	47.53	97.26
I - VI	No.of adventitious branches	48.59	65.13
II - III	No.of adventitious branches	44.22	82.81
II - IV	No.of adventitious branches	42.93	112.73
II - V	No.of adventitious branches	53.15	113.51
II - VI	No.of adventitious branches	54.19	81.48

*   Explanations in Table 7.

Table A18. Characters which show significant differences among
experimentally-grown plants of <u>Ceramium</u> sp.1 under different
nutrient concentrations and water movement conditions at 12:12
LD daylength (n=54). Results of Kruskal-Wallis one-way
analysis of variance (P< 0.01).

Experimental pair*	Character	critical value of z	difference between mean scores
I - VI	Internodal length	16.23	31.17
II - VI	Internodal length	13.89	28.42
IV - VI	Internodal length	18.23	18.24
I - V	Nodal length	45.82	46.67

* Explanations in Table 7.

Table A19. Characters which show significant differences among
experimentally-grown plants of _Ceramium_ sp.1 under different
nutrient concentrations and water movement conditions at 16:8
LD daylength (n=256). Results of Kruskal-Wallis one-way
analysis of variance (P< 0.01).

Experimental pair*	Character	critical value of z	difference between mean scores
I - III	Internodal length	57.79	73.93
I - VI	Internodal length	45.59	46.62
II - III	Internodal length	59.52	116.98
II - IV	Internodal length	47.61	47.49
II - V	Internodal length	52.79	80.02
III- IV	Internodal length	51.89	64.49
III- VI	Internodal length	56.67	120.55
IV - VI	Internodal length	44.00	51.06
V - VI	Internodal length	49.56	83.59
I - II	Distance between dichotomies	33.89	38.57
I - VI	Distance between dichotomies	31.43	41.02
II - III	Distance between dichotomies	43.80	74.08
II - IV	Distance between dichotomies	33.38	45.41
III- VI	Distance between dichotomies	41.92	76.52
IV - VI	Distance between dichotomies	30.88	47.86
V - VI	Distance between dichotomies	34.90	38.16
II - III	No.of cells between dichotomies	43.80	44.07

* Explanations in Table 7.

Table A20. Morphological characters which show significant
differences among experimentally-grown plants of C. flaccidum
under different nutrient concentrations and water movement
conditions at 8:16 LD daylength (n=144). Results of Kruskal-
Wallis one-way analysis of variance test (P< 0.01).

Experimental pair*	Character	critical value of z	difference between mean scores
III- IV	Node diameter	21.24	31.33
III- VI	Node diameter	29.83	43.91
III- VI	No.of dichotomies	27.95	28.01
IV - VI	No.of dichotomies	21.19	28.85
V - VI	No.of dichotomies	14.75	21.93

* Explanations in Table 7.

Table A21. Morphological characters which show significant
differences among experimentally-grown plants of C. flaccidum
under different nutrient concentrations and water movement
conditions at 16:8 LD daylength. Results of Kruskal-Wallis
one-way analysis of variance test (P< 0.01).

Experimental pair*	Character	critical value of z	mean score difference	Number of observations
III- V	No.of dichotomies	19.21	43.77	101
IV - V	No.of dichotomies	19.84	51.21	101
III- V	Distance between dichotomies	21.72	45.92	93
IV - V	Distance between dichotomies	22.20	46.53	93
III- V	No.of cells between dichotomies	21.72	42.25	93
IV - V	No.of cells between dichotomies	22.20	50.52	93
III- IV	Internodal length	21.69	26.75	198
III- V	Internodal length	26.39	106.57	198
IV - V	Internodal length	27.45	79.82	198
III- V	Internodal diameter	26.39	29.56	198
IV - V	Internodal diameter	27.45	44.10	198
III- V	Nodal length	26.92	32.17	202
IV - V	Nodal length	27.99	42.20	202
III- V	Nodal diameter	26.92	45.71	202
IV - V	Nodal diameter	27.99	48.79	202
III- IV	No.of cortical cell rows	22.13	33.64	202
III- V	No.of cortical cell rows	26.92	36.57	202

* Explanations in Table 7.

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