THE TAXONOMIC IMPLICATIONS OF GENETIC AND ENVIRONMENTALLY INDUCED VARIATIONS IN SEAWEED MORPHOLOGY[1]

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ABSTRACT

Morphological characters are the most widely used criteria for the discrimination of seaweed taxa. Even so, many examples of extreme phe-

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notypic plasticity are known. Thus, several phycologists have recently initiated studies to evaluate the phenotypic range of taxa under varied conditions as well as to explore the degree of genetic control of individual characters. Several experimental techniques have been employed to enumerate the significance and basis of phenotypic plasticity in seaweeds, including culture studies, detailed seasonal observations of in situ populations, reciprocal transplantation of plants to diverse habitats, statistical analysis of character variations, and evaluation of genetic affinities. Obviously, the taxonomic status of seaweeds should reflect their genetic relationships. Three primary approaches are outlined including electrophoretic studies, quantitative genetic evaluations, and hybridization studies. A detailed summary of these genetic studies, as well as the other experimental field and laboratory techniques, is given in order to critically assess traditional taxonomic criteria and to aid in the search for new ones.

An evaluation of the relative merits of morphological and biochemical characters in species delimitations is also outlined. It is suggested that there should be no tacit assumption that biochemical features are in some way more fundamental than morphological ones. Thus, even seemingly trivial morphological features may be of great adaptive value, even though not apparent to the taxonomist. A good taxonomic character is constant, readily observable, and the plant should survive identification. If obscure characters are used to delimit species, strenuous efforts should be made to correlate these characters with more readily observable ones.

ZUSAMMENFASSUNG

Morphologische Eigenschaften sind die meistgebrauchten Kriterien fur die Unterscheidung der benthischen Meeresalgen. Dennoch sind viele Beispiele von extrem phenotypischer Plastizität bekannt. Also haben einige Phycologen Studien begonnen, um die phenotypische Reichweite der Taxen unter verschiedenen Umstanden zu bestimmen, gleichfalls den Grad der genetischen Kontrolle der individuellen Eigenschaften zu erforschen.

Verschiedene Versuchsmethoden wurden angewendet, um die Bedeutung und Basis der phenotypischen Plastizität von Meeresalgen aufzuzählen. Unter diesen waren Kulturstudien, detaillierte periodische Beobachtungen der in situ Populationen, gegenseitige Umpflanzung der Pflanzen in diverse Umweltsbedingungen, statistische Analyse der Variationen der Eigenschaften, und Bewertung der genetischen Verwandtschaften. Der taxonomische Eben der Meeresalgen soll offensichtlich ihre genetische Verhaltnisse zeigen. Drei primäre Methoden werden herausgestellt. Diese sind: elektrophoretische Studien, quantitätive genetische

Wertungen und Kreuzungsversuche. Eine detaillierte Zusammenfassung dieser genetischen Studien sowohl der anderen Versuchsmethoden der Verfahren im Freiland und im Labor wird gegeben, um die traditionellen taxonomischen Kriterien kritisch zu bewerten, und bei der Suche nach neuen zu helfen.

Eine Bewertung der relativen Werten der morphologischen und biochemischen Eigenschaften in der Bestimmung der Arten wird auch beschreibens. Es wurde vorgeschlagen, dass es nicht tacit angenommen wird, dass die biochemischen Eigenschaften irgendwie grundlicher als die morphologischen sind. Also dürfen auch scheinbar triviale morphologische Eigenschaften grossen Anpassungswert haben, auch wenn das dem Taxonomen noch nicht ersichtlich ist. Ein zuverlassiger taxonomischer Eigenschaft ist konstant, leicht zu beobachten, und die Pflanze soll die Bestimmung überleben. Wenn obskure Eigenschaften bei der Abgrenzung der Art gebraucht werden, dann soll energisch versucht werden, die mit anderen, leichter zu beobachten Eigenschaften zu korrelienen.

I. INTRODUCTION

All is not well with the taxonomy of the algae. The apparent stability of the classification of the Rhodophyta may be largely illusory (Dixon, 1961) and the genera of Phaeophyta are not clearly circumscribed (Russell and Fletcher, 1975). Even in the well studied flora of the British Isles drastic taxonomic changes still occur. The species included in the genus *Ectocarpus* in Newton (1931) are at present dispersed in 11 genera (Parke and Dixon, 1976), but are likely to be reunited into a single genus in the forthcoming flora (Russell, pers. comm.). We are still unable to satisfactorily discriminate species in intractable genera such as *Pterocladia* and *Gelidium* (Dixon and Irvine, 1977).

There are several reasons for these difficulties. Firstly, the type method encourages specific recognition of any entity preserved on a herbarium sheet without any knowledge of the range of forms encompassed by a population of the living plant. There is now increasing awareness that precocious fertility confers a spurious air of maturity on some plants long before development of the plant's ultimate form. Fertility of juveniles occurs most commonly in annual plants such as the members of the Ectocarpales whose specific characteristics are mostly subtle morphological differences (Russell, 1978) whose development is dependent upon environmental factors (Ravanko, 1970, 1975). Both Russell and Ravanko emphasize that many of the supposed species discriminated solely on morphological grounds may simply represent developmental stages or environmentally induced forms.

Dixon (1970) claims that variation in thallus form and structure under

different habitat, seasonal or geographical conditions is one of the major sources of difficulty in algal taxonomy. Russell (1978) notes that habitat linked characters are more prevalent in perennial plants than in annuals and cites the members of the Fucales as exhibiting a variety of variable morphological features that have lead to taxonomic problems.

Morphological characters remain the most widely used criteria for discriminating algal species. However, so many examples of extreme phenotypic plasticity have now been described (Norton et al., in press), and so many entities that formerly seemed quite distinct are now known to overlap in taxonomically critical features (Norton, 1978) that many of our concepts regarding valid taxonomic characters are changing.

In recent years phycologists aware of the dangers of relying so heavily on morphological characters have attempted to investigate the phenotypic range of individual taxa under varied conditions and to begin to explore the degree of genetic control of individual characters. It is the results of these studies, the critical assessment of traditional taxonomic criteria and the search for new ones, that concern us here.

II. CULTURE STUDIES

As noted by Boney (1978), culture studies have contributed greatly to the resolution of many taxonomic problems; in addition, they have also raised a variety of questions regarding concepts of algal taxonomy. For example, several pleomorphic life histories have been documented (Dring, 1974; Moss, 1974; Wynne, 1969), which link morphologically distinct entities as components of a single life history. In addition plant forms can sometimes arise in culture that bear no resemblance to existing taxa. Thus, collaborative field and culture studies are necessary to provide a better understanding of a plant's phenotype (Nielsen, 1979; Yarish, 1976).

Several recent culture studies with green algae have demonstrated the usefulness of this approach to morphological-taxonomic problems. For example, Hanic (1979) cultured *Prasiola meridionalis* and *Rosenvingiella constricta* through eleven generations over a six-year period, and concluded that the two were distinct genera. Wilkinson and Burrows (1972) found that at least six species of green shell-boring algae have been confused under the name *Gomontia polyrhiza*. Yarish (1975, 1976) and Nielsen (1978, 1979) note that several of the morphological criteria used to distinguish members of the Chaetophoraceae are variable and unreliable (e.g., presence or absence of setae, shape of thalli, and size and shape of cells), while others (e.g., germination patterns) are valid characters (Nielsen, 1980). Van den Hoek (1963) similarly used culture techniques to determine character stability in his monographic treatment of *Cladoph-*

ora. The taxonomic status of *Chaetomorpha atrovirens* and *C. linum* was tested by culture (Blair et al., in press) which showed both morphological variability and discontinuity of the two species based upon their length/width ratios. In *Rhizoclonium* spp. the abundance of rhizoids, which is a prime characteristic of the genus, can be controlled by temperature, salinity and irradiance (Price, 1967).

Barilotti (1970) cultured *Caulerpa prolifera* and found that many of the morphological characters used for the delineation of subspecific taxa (i.e., blade width and proliferations) were significantly altered by environmental factors such as temperature, salinity and illumination. Calvert (1976) similarly used culture studies to evaluate morphological variations in several other *Caulerpa* spp. due to reduced illumination. Colinvaux et al. (1965) showed that several taxonomic characters employed for species separation in *Halimeda* were variable in culture.

Bliding (1963), De Silva and Burrows (1973), Kapraun (1970), Pringle (1975), and Tanner (1977, 1978, 1979) have employed culture studies to critically evaluate the morphological variation and taxonomy of ulvacean algae. Fries (1975), Bonneau (1977) and Provasoli (1958) have shown that the bacterial microfloras on *Ulva* and *Enteromorpha* are responsible for considerable morphological variability. In addition, Bonneau (1977) has shown that the range of morphological potential exhibited by *U. lactuca* includes a configuration identical to that of *Enteromorpha,* and he has questioned the validity of separating the two genera. Similarly, Pringle (1975) noted that *E. linza* and *E. intestinalis* have the potential to be both partially tubular and distromatic, while Alexander (1970) reported flattened and tubular plants of *E. linza* in culture. Thus, both of the species may exhibit morphologies transitional between *Enteromorpha* and *Ulva.* Lastly, Chihara (1968) has shown that the mode of spore germination can be used to distinguish different species of *Ulva* that are morphologically similar, while Tanner (1978, 1979) has distinguished a new ulvaceous genus (*Chloropelta caespitosa*) with a different developmental pattern than *Ulva.*

A few examples of culture studies with brown and red algae may be cited as having clarified taxonomic problems. For example, Clayton (1978) employed culture studies, in conjunction with detailed field observations, to show that variation amongst different populations of *Scytosiphon lomentaria* was of a continuous nature, and that the species should not be further divided into infraspecific taxa. Similarly, Burrows (1964) evaluated several taxonomically important characters of *Laminaria saccharina* in culture. She found that the shape of the blades was a function of growth rate and that it was of little taxonomic value. In addition, the degree of mucilage duct development was a function of temperature. Similarly, temperature also seems to modify the degree of bullation,

thickness of blades, and cell sizes. Wynne (1972) cultured *Colpomenia sinuosa* f. *deformans* sensu S. et G. from the Gulf of California and found that it was morphologically different than a similar taxon, *C. bullosus*. Fletcher (1978) emphasizes that culture studies have demonstrated a variety of morphological, developmental and life history differences within the Ralfsiaceae. Kuckucks (1960) records four stages in the development of *Spongonema tomentosum*, each of which is fertile and has a distinctive morphology. That is, plants designated as *Ectocarpus luteolus*, *E. minimus*, *E. terminalis*, and *E. tomentosus* in Newton (1931) all belong within the same life history of *S. tomentosum* (=*E. tomentosus*).

Intraspecific variation within ectocarpoid brown algae has also been demonstrated by culture studies. That is, different populations of the marine fouling alga *Ectocarpus siliculosus* have been shown to possess strain specific variation in their tolerances to copper (Russell and Morris, 1970). According to Hall and associates (1979) this intraspecific variation may be associated with membrane and intracellular changes. In essence, the plants may appear morphologically identical but they are physiologically distinct.

Boney (1972) and White and Boney (1969, 1971) have noted pronounced form variation of endophytic and endozoic *Audouinella* in culture and have suggested a variety of taxonomic implications. Garbary et al. (1978) have recently evaluated the taxonomic status of *Ceramium rubrum* and *Ceramium rubriforme* based upon culture investigations. Both plants showed considerable phenotypic variation, which was primarily a response to daylength and temperature. Thus, completely corticated plants (i.e., *C. rubrum*) resulted from short daylengths, while plants with long, bare internodes and distinct bands grew under long daylengths (i.e., *C. rubriforme*). A number of taxonomic criteria used to delimit species of *Ceramium* (e.g., the degree and type of cortication) would thus appear to be unreliable. Accordingly, they suggest that *C. rubriforme*, *C. areschougii* and *C. pedicellata* in the northwest Atlantic are probably synonymous with *C. rubrum*. Additional culture studies of red algae have shown that many characteristics previously used to separate taxa of acrochaetioid algae (Knaggs, 1966; Stegenga and Mulder, 1979; Stegenga and Van Erp, 1979; Stegenga and Van Wissen, 1979), *Eucheuma* (Cheney and Dawes, in press), *Heterosiphonia* (West, 1970), and *Polysiphonia* (Taylor, 1966) may vary due to environmental parameters and/or life history stages. Ngan and Price (1979) have employed culture studies to evaluate the systematic significance of spore size in the Rhodophyta. Considerable variation in spore size was observed and it was concluded that it was not a useful taxonomic character at the species level.

III. ECOLOGICAL FIELD STUDIES

Detailed seasonal observations of in situ populations may also help to elucidate a variety of morphological-taxonomic problems. For example, Sears and Wilce (1970) evaluated the systematic criteria used to distinguish species of *Derbesia,* based upon extensive subtidal observations in New England. Abbott (1972) evaluated the validity of several morphological characters used to delineate Pacific Coast species of *Iridaea.* She noted that thallus thickness and blade coloration were largely dependent upon exposure, while blade shape was primarily correlated with elevation. Such observations cast doubt on the validity of many characters used to delineate *Iridaea* species, and Abbott reduced 18 species to seven plus two varieties, with the majority of taxa being placed in synonymy with *I. cordata.* Similarly Munda (1979) found that several subspecific taxa of *Chordaria flagelliformis* were growth forms caused by varying environmental conditions and/or maturation stages. Mathieson (1965) observed pronounced morphological variations of in situ populations of *Phaeostrophion irregulare* occupying different vertical positions on the shore, as a result of enhanced dehydration because of the change in sequence of night to daytime low tides. The seasonal and spatial morphological variations within *P. irregulare* overlapped with that of *P. australe,* and it was synonymized under the first name.

Widdowson's (1965) taxonomic revisions in the genus *Hedophyllum* were also based upon detailed field insights. He noted that *H. subsessile* was incorrectly based upon a form variation of *H. sessile,* during the second summer of its life. Russell (1967) noted that a morphological transformation of *Ectocarpus fasiculatus* and the appearance of *E. distortus* and *E. landburgii* occurred in a seven week period which approximated the time of the mid-summer removal of *E. fasiculatus* and *Himanthalia* from the shore. He concluded that *E. distortus* and *E. landburgii* are free-floating ecads of *E. fasiculatus* which result from profuse branching. Steffensen (1976) found that specimens of *Ulva lactuca* from the Avon-Heathcote Estuary (New Zealand) represented a single population, which included four forms previously recognized as distinct taxa. Similarly, Tanner (1977, 1979) found that most species of *Ulva* from the Northeast Pacific showed seasonal variation in blade thickness and cell dimensions; accordingly six taxa recognized from the area were reduced to synonyms of other species.

An understanding of the life span and regenerative capacity of an alga is important in interpreting its morphology, and ultimately its taxonomy. For example, the morphology of perennial species, particularly pseudo-perennials (sensu Knight and Parke, 1931), is related to the size of the surviving fragment, the number, disposition, and growth potential of new

apices. An evaluation of such morphogenetic information can help to differentiate between different taxa as well as seasonal growth forms (Dixon, 1960, 1963, 1966; Stewart, 1976).

IV. TRANSPLANT STUDIES

Chapman (1978) suggests that reciprocal transplantion of seaweeds may help to evaluate interpopulation phenotypic variation. That is, it can provide a vehicle to evaluate the morphology of plants in a new habitat as compared to controls. He and Russell (1978) cite a variety of transplant studies of laminarian algae (Chapman, 1974; Druehl, 1965; Markham, 1969, 1972; Norton, 1969; Sundene, 1962a, 1962b, 1964; Svendsen and Kain, 1971) which have helped to interpret phenotypic variation and/or taxonomic decisions. Three further transplant studies of kelps should be noted (Gerard and Mann, 1979; Kato and Nakahisa, 1962; Sanbonsuga and Torii, 1974), as they have contributed to an understanding of phenotypic variation. In two studies by Sundene (1962a, 1964), he transported exposed coastal populations of *Laminaria digitata* (known as f. *stenophylla*) to sheltered areas which resulted in a modified morphology (f. *digitata*) typically found in sheltered conditions. He concluded that the forma *stenophylla* was a growth form conditioned by strong water movement. Norton (1969) and Svendsen and Kain (1971) recorded a similar experimental induction of cucullate (i.e., hood-shaped) lamina when populations of *Saccorhiza polyschides* and *L. hyperborea*, respectively, were transplanted to sheltered sites. Norton (1969), in agreement with Sundene (1962a, 1964), did not feel that such forms merited separate taxonomic status. In contrast, Svendsen and Kain (1971) used comparable results on *L. hyperborea* to describe a new taxon, f. *cucullata,* to replace a former species, *L. cucullata.*

Contrary to the above transplant studies, Chapman (1974) found that when two populations of *Laminaria* from eastern Canada (i.e., *L. longicruris* and *L. saccharina* in Taylor, 1957) were reciprocally transplanted between exposed and sheltered sites, no significant changes in stipe length and hollowness occurred. Markham (1969, 1972) similarly found that *L. longipes* and *L. sinclairii* populations did not change their anatomical characteristics (i.e., the presence or absence of mucilage ducts) upon transplantation and he concluded that the two were distinct species.

In addition to the laminarian algae, transplant studies have been initiated with dictyotalean (Hoyt, 1939) and fucoid brown algae (Gail, 1918; Hatton, 1938), as well as with various green and red algae. Hanic and Pringle (1978) and Pringle (1975) review much of the earlier work. For example, in one of the earliest transplant studies dealing with green algae, Tandy (1932, 1934) found that many of the characters used for recognition

of infraspecific taxa of *Caulerpa racemosa, C. cupressoides* and *C. sertularioides* could be varied by transplant experiments. He also noted that *C. peltata* and *C. fastigiata* were growth forms of *C. racemosa*, while *Halimeda opuntia* var. *opuntia* could proliferate the var. *triloba* and *H. tridens* could proliferate *H. monile* (as *H. monilis*). Pringle (1975) outplanted laboratory grown germlings of *Enteromorpha prolifera, Enteromorpha linza* and *E. intestinalis* to a wide variety of natural environments. He found that the morphology of each of the three taxa was plastic, varying with both the environment and the onset and extent of reproduction. All three species have the potential to branch and branching in *E. prolifera* increases significantly with depth and age. Miura (1975) similarly outplanted laboratory grown sporelings of *Porphyra yezoensis* f. *narowensis* ("Nara-susabinori") having the same genetic line and found a variety of width and length characteristics in different localities.

In a biosystematic study of the red alga, *Eucheuma* (Cheney, 1975; Cheney and Dawes, 1973, In press), extensive reciprocal transplantation experiments between species resulted in the typifying of several taxa and the recognition of shallow and deep water ecotypes. Although transplants of *Eucheuma* from deep to shallow waters showed an increase in lateral branches, they remained distinct even after a year. In addition, Dawes et al. (1974) found that the morphology and life history of *Eucheuma* were modified by vertical and horizontal transplantations.

Munda (1977) transplanted *Halosaccion ramentaceum* from northern Iceland to Helgoland and evaluated the plant's growth under varying temperature regimes. Floc'h (1969) similarly conducted transplant studies of *Chondrus crispus* to evaluate the plant's morphological variability; no morphological alterations were found after seven months. As noted by Chapman (1978), when plants exhibit no response to transplantation, the results are ambiguous, and it may mean that the phenotypic differentiation observed has a high genetic component. Thus, sufficient time must be allowed for morphological changes to occur with slow-growing plants. In addition, the possibility of developmental canalization or epigenesis cannot be discounted if adult plants are employed.

V. STATISTICAL ANALYSIS

Several investigators have applied statistical analysis of character variations in order to delineate taxonomically difficult seaweeds and to check for species overlap. For example, Chapman (1977) studied the morphological variation of six populations of *Gracilaria tikvahiae* (as *Gracilaria* sp.) from the Gulf of St. Lawrence to New Jersey, employing seven vegetative characteristics. As no significant interpopulation variation was observed and the range of variability of the samples overlapped, he con-

cluded that only one highly variable species was present. Stewart (1968) employed similar statistical analysis of ten morphological criteria to evaluate the variation and taxonomic affinities of seven Pacific Coast species of *Pterocladia*, as well as *P. capillacea* from Europe. All of the Pacific taxa were conspecific with *P. pyramidale*, which in turn was indistinct from *P. capillacea*. Widdowson (1971) gave a detailed statistical evaluation (i.e., by discriminant and distance function analyses) of morphological variation in *Alaria* and noted considerable variation due to environmental factors; subsequently he reduced 108 taxa to 14 species. Searles (1978) evaluated the blade and general morphological characteristics of *Lessonia* populations in Chile and Argentina and concluded that there were three distinct species, even though each species showed phenotypic variation in response to wave action and vertical position. Bergquist (1959) employed statistical analyses of morphological characters to evaluate ecological variations in 85 samples of *Hormosira banksii*. Clayton (1975) studied morphological and anatomical variations in Australian species of *Colpomenia*, using a hybrid index method and analysis of variation. Some of the characteristics commonly used to distinguish the species were variable and provided no basis for taxonomic discrimination. Chapman (1972a, 1972b) and Goodband (1971) evaluated the taxonomy of several other brown algae based upon similar statistical analysis of character variation. Two recent studies by Blair et al. (In press) and Price (1967) investigated morphological variability within the unbranched Cladophorales. For example, Blair and associates (In press) found a statistically significant discontinuity of cell lengths and widths between *Chaetomorpha atrovirens* and *C. linum*, using the average length/width ratios of the plants.

A few recent applications of numerical taxonomy should be noted. For example, Russell and Fletcher (1975) and Pankhurst and Tittley (1978) have demonstrated the usefulness of computers to classify and identify brown algae, respectively. According to Pankhurst and Tittley (1978), the main problems in numerical taxonomy are the standardization of data, the accurate delineation of characters and incomplete data. In addition, it should be emphasized that numerical taxonomic methods are only successful if a wide variety of characters are employed. Prud'Homme van Reine (1978) has proposed a systematic classification of the Sphacelariales based upon the same numerical taxonomic methods employed by Russell and Fletcher (1975); that is, most weight was given to morphological characters.

Three other recent numerical taxonomic studies should be noted. Foremost, Russell and Garbary (1978) circumscribed generic delineations within the Ectocarpaceae by computer-based analyses of similarity coefficients and cluster analysis techniques. Bolton (1979) conducted a nu-

merical taxonomic investigation of *Pilayella littoralis* using computer clustering techniques on 71 morphological and ecological characters with 164 plants from a wide range of habitats within the British Isles. Lastly, Garbary (1979) employed numerical taxonomic techniques to evaluate generic circumscription within the Acrochaetaceae.

VI. GENETIC AFFINITIES

In addition to morphological similarities, the taxonomic status of seaweeds should reflect their genetic relationships. Three primary approaches have been employed to assess genetic affinities: (1) direct measures of genetic similarity using electrophoresis, (2) quantitative genetic studies, (3) an evaluation of reproductive isolation or interfertility (i.e., hybridization studies).

Few investigators have employed electrophoretic techniques to determine taxonomic relationships of seaweeds at or below the congeneric species level, and evaluations of natural populations are rare. Even so the technique may provide an important tool, in conjunction with morphological and culture studies, to define algal taxa. For example, a study by Cheney and Babbel (1978) dealing with species of *Eucheuma* showed a high degree of genetic similarity between *E. isiforme* and *E. nudum* (90.4%) and between *E. gelidium* and *E. acanthocladum* (85.7%), but a very low similarity between these two pairs of species. Thus, their electrophoretic results confirmed other studies (Cheney and Dawes, 1973, In press) that recommended the removal of *E. gelidium* and *E. acanthocladum* from the genus *Eucheuma* and suggested the possible conspecificity of *Eucheuma isiforme* and *E. nudum,* as well as *E. acanthocladum* and *E. gelidium.* Blair et al. (In press) assessed the possible conspecificity of *Chaetomorpha atrovirens* and *C. linum* by starch gel electrophoresis. A low genetic similarity was found between *C. atrovirens* and *C. linum* based upon field and culture materials and the two taxa were considered to be distinct, which confirmed earlier described culture studies. Cheney and Mathieson (1979) showed that populations of *Chondrus crispus* from New England and the Canadian Maritimes exhibited considerable genetic differentiation within relatively short distances, particularly when populations from different habitats (estuarine, coastal, intertidal, subtidal) were compared. Innes and Yarish (1979) report pronounced differences of isozyme patterns between *Ulva lactuca* and *Enteromorpha intestinalis,* as well as within different species of *Enteromorpha.* Lastly, Miura et al. (1978) have evaluated the isozyme composition from different species of *Porphyra.*

Rogers (1977) and associates (1977, 1980) have surveyed for the presence of haemagglutinins in seaweeds, while Blunden et al. (1978) have

reviewed their possible taxonomic value in seaweeds. Few general patterns were noted by Blunden et al. (1978), except that haemagglutinic activity was generally greater in the more advanced orders of the red and brown algae, while the lower orders showed no activity. The possible applications of hemagglutinins in evaluating the phylogenetic status of *Polyides rotundus* and the morphological distinction of *Plumaria elegans* and *Ptilota plumosa* are discussed. Fenical and Norris (1975) further outline the role of chemical separation (chemotaxonomy) with some *Laurencia* species. That is, species separation within the genus is complicated by a high degree of morphological variation, which can be elucidated by chromatographic comparisons of their halogenated compounds.

Quantitative genetic studies can be employed to evaluate morphological variation of seaweeds (Chapman, 1978), for their primary aim is to delineate the genetic versus environmental components of phenotypic variation. Such methods have been used by Chapman (1974, 1975) to estimate the genetic and environmental components of phenotypic variation of stipe structure and mucilage duct anatomy, which are important taxonomic criteria for non-digitate *Laminaria* species in eastern Canada. The degree of mucilage duct development was found to have a low heritability in Newfoundland populations, while a high genetic component was found in Nova Scotian populations with respect to stipe length and the development of hollow stipes.

Chapman (1978) suggests that crossability tests are an effective way to evaluate genetic and taxonomic affinities of seaweeds and he summarizes a variety of hybridization studies with kelps. The primary conclusion from these studies is that where species are easily distinguished morphologically, there is usually reproductive isolation. Morphologically confused species are interfertile. The recent crossing studies of *Laminaria longicruris* and *L. saccharina* (Lüning et al., 1978) is a documentation of the genetic complexities within closely related species, i.e., the *Simplices* section of *Laminaria* in the North Atlantic.

In evaluating biosystematic approaches to the taxonomy of red algae, Rueness (1978) emphasizes that although breeding characteristics are a useful and contributory tool, they should not be overemphasized as a criterion, as sexual incompatability may develop between morphologically indistinguishable populations—e.g., *Ceramium strictum* from America and Scandinavia. Morphologically, these two *C. strictum* isolates are indistinguishable and they have more features in common than does either with *C. tenuicorne* or *C. tenuissimum*. Even so, *C. strictum* from Norway and *C. tenuicorne* from the Baltic are interfertile, while *C. tenuissimum* is clearly distinct and sexually isolated. He designates the Baltic strain of *C. tenuicorne,* which differs genetically in various morphological and physiological features, as an ecotype and treats it taxo-

nomically as a subspecies of *C. strictum* (subsp. *tenuicorne*). Thus, specimens differing markedly in genetically determined morphological characters may be completely interfertile. Chapman (1978) reports the same phenomenon in brown algae and rejects the viewpoint that internal reproductive isolation provides the best evidence for the erection of species (Ling and Tyler, 1974). He emphasizes that although reproductive isolation often corresponds to morphologically well defined species, crossability is not an all or nothing criterion (e.g., Bolwell et al., 1977; Saito, 1972). Futhermore, meiotic aberrations that might prevent species crossability may not be manifested until the F_2 generation.

As noted earlier, the questions of whether morphological differences in seaweeds are due to phenotypic plasticity (i.e., epigenetic) or genetic control are still largely unanswered. Chapman (1978), Fjeld and Løvlie (1976), and Rueness (1978) give detailed accounts of hybridization studies in various seaweeds and emphasize that an assessment of the capacity for hybridization between taxa is an effective means of evaluating the genetic (versus epigenetic) basis for their morphological differentiation.

In this context, several investigators have suggested that intergeneric and interspecific hybridization can occur in nature (Table I). For example, Neushul (1962, 1971) observed an intermediate form between *Macrocystis pyrifera* and *Pelagophycus porra* and inferred that it was an intergeneric hybrid. The development of improved culture techniques for isolating, holding, and breeding macroalgae under controlled conditions has provided the technological basis for evaluating such potential crosses, as well as testing the interfertility of a wide variety of other seaweeds. For example, Sanbonsuga and Neushul (1978, 1979) found that intergeneric hybrids between *M. angustifolia* and *P. porra,* although rare in nature, are comparatively easy to produce. The plants resulting from this intergeneric cross were intermediate in morphology, and although sori were formed, they never produced functional spores. Crosses between *M. angustifolia* and *Nereocystis luetkeana* were also attempted and some hybrids survived for a year. The hybrid sporophytes lacked vesicles, had corrugated blades, and produced no sporangia (Neushul, 1978).

Burrows and Lodge (1951, 1953, 1954) and Seoane-Camba (1966) found *Fucus* plants that displayed characteristics of two species and claimed they represented hybrids. Bolwell et al. (1977) studied the barriers to both intergeneric and interspecific cross-fertilization in *Fucus* and *Ascophyllum,* using ultraviolet microfluorescent techniques. They observed inherent interspecific and intergeneric barriers, but showed that fertilization could occur (Table I), following the breakdown of such barriers through the modification of appropriate membrane receptors in older eggs. Thus, their results contrast with several earlier investigations (Table I) which showed an abundance of hybrid forms on several shores and no

Table I
A summary of intergeneric and interspecific seaweed hybrids

Species	Comments	Authors
Phaeophyceae		
Agarum cribrosum (4 forms, *cribrosum, rugosum, rishiriense* and *yakishiriense*)	interfertile and with 32–96% occurrence of sporophytes	Nakahara and Yamada, 1974
Ascophyllum nodosum (male) × *Fucus vesiculosus* (female)	4% successful intergeneric hybrids, but plants were stunted and grew slowly	Williams, 1899
Ascophyllum nodosum (male) × *Fucus serratus* (female)	not successful with freshly collected plants; therefore an inherent interspecific and intergeneric barrier to fertilization	Bolwell et al., 1977
Ascophyllum nodosum (female) × *Fucus serratus*	not successful with freshly collected plants; therefore an inherent interspecific and intergeneric barrier to fertilization	Bolwell et al., 1977
Ascophyllum nodosum (female) × *Fucus vesiculosus* (male)	not successful with freshly collected plants; therefore an inherent interspecific and intergeneric barrier to fertilization	Bolwell et al., 1977
Ascophyllum nodosum (male) × *Fucus vesiculosus* (female)	not successful with freshly collected plants; therefore an inherent interspecific and intergeneric barrier to fertilization	Bolwell et al., 1977
Ectocarpus siliculosus (American strain) × *E. siliculosus* (European strain)	observed a genetical isolation of the two sexually reproducing groups	Müller, 1976

Table I
Continued

Species	Comments	Authors
Ectocarpus siliculosus × *E. siliculosus* (several continental European locations, Naples, Ville Franche, Roscoff)	interfertile	Müller, 1975
Ectocarpus siliculosus × *E. siliculosus* (several Mediterranean, North American and Australian strains)	European strains interfertile from Mediterranean to Norway; plasmogamy between strains from Florida, North Carolina and European clones. South Australian strain interfertile with most other strains. Local population related closely enough to permit plasmogamy on a world-wide basis, even though some local strains (Massachusetts and Florida), are in the process of isolating themselves from the original gene pool	Müller, 1979
Fucus distichus × *F. distichus* (two ecological forms)	interfertile; the resulting embryos were transplanted to the field	Pollock, 1969
Fucus serratus × *F. spiralis*	apparent hybrid found in nature	Burrows and Lodge, 1951
Fucus serratus × *F. spiralis* and *F. vesiculosus*	interfertile	Burrows, 1953; Burrows and Lodge, 1951, 1954
Fucus serratus × *F. vesiculosus*	apparent hybrids found in nature	Sauvageau, 1909; Burrows and Lodge, 1951
Fucus serratus (female) × *F. vesiculosus* (male)	0% interfertility during crossing tests	Thuret, 1854

Table I
Continued

Species	Comments	Authors
Fucus serratus (male) × *F. vesiculosus* (female)	fertile hybrids produced	Thuret, 1854
Fucus serratus (male) × *F. vesiculosus* (female)	4% fertile hybrids produced	Kniep, 1925
Fucus serratus (female) × *F. vesiculosus* (male)	2% fertile hybrids produced	Kniep, 1925
Fucus serratus (male) × *F. vesiculosus* (female)	99% fertile hybrids produced	Burrows and Lodge, 1951
Fucus serratus × *F. vesiculosus*	apparent hybrids found	Burrows and Lodge, 1951; Seoane-Camba, 1966
Fucus serratus (female) × *F. vesiculosus* (male)	not successful with freshly collected plants; therefore an inherent interspecific and intergeneric barrier to fertilization	Bolwell et al., 1977
Fucus serratus (male) × *F. vesiculosus* (female)	not successful with freshly collected plants; therefore an inherent interspecific and intergeneric barrier to fertilization	Bolwell et al., 1977
Fucus serratus (female) × *F. vesiculosus* (male)	low level of fertility (up to 20%) if eggs stored 5–7 days	Bolwell et al., 1977
Fucus serratus (male) × *F. vesiculosus* (female)	low level of fertility (up to 20%) if eggs stored 5–7 days	Bolwell et al., 1977
Fucus spiralis × *F. ceranoides*	apparent hybrids found	Gard, 1910; Sauvageau, 1908

Table I
Continued

Species	Comments	Authors
Fucus spiralis (male) × *F. vesiculosus* (female)	100% fertility during crossing tests	Kniep, 1925
Fucus spiralis (female) × *F. vesiculosus* (male)	70% fertility during crossing tests	Kniep, 1925
Fucus spiralis × *F. vesiculosus*	apparent hybrids found	Burrows and Lodge, 1951; Kniep, 1925; Sauvageau, 1909; Stomps, 1911
Fucus vesiculosus × *F. chalonii*	an apparent hybrid found	Parriaud, 1954
Laminaria cucullata × *L. hyperborea*	completely interfertile	Svendsen and Kain, 1971
Laminaria digitata (f. *digitata*, *stenophylla* and an unidentified form)	completely interfertile	Sundene, 1958
Laminaria hyperborea × *L. digitata* × *L. saccharina*	unsuccessful; no hybrids produced	Schreiber, 1930
Laminaria japonica × *L. ochotensis* × *L. religiosa*	interfertile	Yabu, 1964
Laminaria japonica × *L. diabolica*	interfertile	Yabu, 1964
Laminaria japonica × *L. japonica* (various strains)	extensive inbreeding, selection and X-ray procedures have increased plant production and iodine content of hybrids	Anon., 1975; Fang et al., 1962, 1963, 1965
Laminaria longicruris × *L. longicruris* (various strains)	fertile hybrids produced which showed a three-fold variation in alginate content	Chapman and Doyle, 1979
Laminaria longicruris × *L. saccharina* (two forms)	successfully crossed, but no sporangia produced in seven months	Lüning et al., 1978

Table I

Continued

Species	Comments	Authors
Laminaria saccharina (Helgoland, with smooth blade) × *L. saccharina* (Isle of Man, with bullate blade)	interfertile, F₁ hybrid bullate	Lüning, 1975
Laminaria saccharina subspecies *agardhii* × *L. longicruris*	completely interfertile	Chapman, 1974, 1975
Lessonia littoralis × *Macrocystis pyrifera*	an apparent hybrid described	Searles, 1978
Macrocystis angustifolia × *Nereocystis luetkeana*	hybrid produced; it was morphologically intermediate, with no vesicle formation and corrugated blades	Sanbonsuga and Neushul, 1978, 1979
Macrocystis angustifolia × *Pelagophycus porra*	hybrid produced; it was morphologically intermediate; sori were formed but sporangia were non-functional	Sanbonsuga and Neushul, 1978, 1979
Macrocystis pyrifera × *Pelagophycus porra*	an apparent hybrid found between two genera	Neushul, 1962, 1971
Saccorhiza dermatodea × *S. polyschides*	no normal sporophytes (hybrids) produced	Norton, 1972
Undaria peterseniana (female) × *U. pinnatifida* (male)	crossing successful; hybrids intermediate between parents both morphologically and ecologically	Migita, 1967
Undaria peterseniana × *U. pinnatifida* × *U. undarioides*	every crossing combination possible, but only 20–75% viability	Saito, 1966, 1972
Undaria peterseniana × *U. undarioides*	F₁ generation morphologically intermediate; 75% viability and no sporangia produced	Saito, 1972

Table I

Continued

Species	Comments	Authors
Undaria pinnatifida (type B) × *U. undarioides*	F₁ generation morphologically intermediate; 65% viability	Saito, 1972
Undaria pinnatifida (type B) × *U. peterseniana*	F₁ generation morphologically intermediate; hybrids did not mature due to insufficient growth; 20% viability	Saito, 1972
Rhodophyceae		
Antithamnion plumula (Plymouth strain) × *A. plumula* (Oslofjord strain)	unsuccessful	Sundene, 1959
Antithamnion plumula × *A. plumula* (13 strains), including var. *crispum* (Isle of Man) × var. *crispum* (Guernsey, Channel Islands)	some interfertile, others not	Sundene, 1975
var. *crispum* × var. *plumula*	interfertile	
var. *crispum* × var. *bebbii*	intersterile	
var. *plumula* × var. *bebbii*	intersterile	
	several strains interfertile	
Antithamnion plumula var. *plumula* × *A. plumula* var. *bebbii*	interfertile	Rueness and Rueness, 1975
Ceramium strictum × *C. strictum* (various Scandinavian strains)	interfertile	Rueness, 1978
Ceramium strictum (American strain) × *C. strictum* (Scandinavian strain)	intersterile	Rueness, 1978
Ceramium strictum (Norway strain) × *C. tenuicorne* (Baltic strain)	interfertile	Rueness, 1978

Table I
Continued

Species	Comments	Authors
Ceramium tenuissimum × *C. strictum*	intersterile	Rueness, 1978
Ceramium tenuissimum × *C. tenuicorne*	intersterile	Rueness, 1978
Chondrus crispus (T4 strain) & *C. crispus* (nine European isolates)	interfertile	Guiry (in press)
Chondrus crispus (Bay of Fundy strain) × *C. crispus* (Gulf of St. Lawrence strain)	no fertile hybrids produced; the two strains remained distinct	Chen and Taylor (1980)
Gigartina agardhii × *G. agardhii* (isolates from various Pacific sites)	a high incidence of compatibility (94%) was evident among many isolates from British Columbia to Southern California. However, isolates from distant localities were less frequently compatible than from a single site	West et al., 1978
Gigartina sp. (Chile strain) × *G. papillata* (California strain)	interspecific hybrids produced	West et al., 1979
Gigartina agardhii (both male and female) × *Gigartina*-phase gametophyte from *Petrocelis middendorfii* (i.e. *G. papillata*)	intersterile; therefore *G. agardhii* is reproductively isolated from *G. papillata*/*P. middendorfii*	West et al., 1978
Gigartina ochotensis (Japan strain) × *G. stellata* (France and Portugal strains) and *G. papillata* (Alaska and California strains)	interspecific hybrids produced	West et al., 1979

Table I
Continued

Species	Comments	Authors
Gigartina pacifica (female) × *Gigartina*-phase (male) from *Petrocelis middendorfii* (i.e. *G. papillata*)	interfertile	Polanshek and West, 1975
Gigartina pacifica (Japan strain) × *G. stellata* (France and Portugal strains) and *G. papillata* (Alaska and California strains)	interspecific hybrids produced	West et al., 1979
Gigartina papillata (male or female) × *Gigartina*-phase gametophyte of *Petrocelis middendorfii* (i.e. *G. papillata*)	interfertile; therefore *G. papillata* is the naturally occurring gametophyte of *Petrocelis middendorfii*	Polanshek and West, 1977
Gracilaria tikvahiae × *G. tikvahiae* (as *Gracilaria* sp.)	fertile hybrids produced	van der Meer and Todd, 1977
Petrocelis middendorfii gametophytes (from Amchitka) × *P. franciscana* gametophytes (from California)	hybrid carpospores gave rise to crustose plants; life history and anatomical studies suggest that one species exists	Polanshek, 1975; Polanshek and West, 1975
Polysiphonia boldii × *P. denudata*	intersterile and with complete incrossability	Edwards, 1970
Polysiphonia boldii × *P. hemispherica*	obtained fertilization and carposporophyte, but reduced viability of tetrasporic germlings	Rueness, 1973
Polysiphonia ferulacea (North Carolina strain) × *P. ferulacea* (Bermuda strain)	plants were unable to hybridize	Kapraun, 1977
Porphyra angustata × *P. pseudolinearis* × *P. umbilicalis* (all = dioecious forms)	interfertile	Suto, 1963

Table I
Continued

Species	Comments	Authors
Porphyra tenera × *P. yezoensis* (monoecious forms)	interfertile	Suto, 1963
any of above monoecious × any dioecious	most died in young stages, and only a few survived	Suto, 1963
Porphyra yezoenis × *P. katadai*	a possible hybrid described	Fukuhara, 1971
Chlorophyceae		
Enteromorpha × *Enteromorpha* (many species)	many species tested, all showed a strict sterility barrier	Bliding, 1963
Enteromorpha clathrata × *E. lingulata* × *E. prolifera* × *E. salina* (all combinations)	intersterile	Kapraun, 1970
Enteromorpha intermedia × *E. prolifera, E. clathrata* and *E. kylinii*	intersterile	Bliding, 1955
Ulva curvata × *U. curvata* (various strains)	strains from North Carolina to New Jersey produced viable zygotes which germinated normally	Rhyne, 1973
Ulva curvata (north Carolina strain) × *U. rigida* & *U. lactuca* (Massachusetts strains)	intersterile	Rhyne, 1973
Ulva dangeardii × *U. curvata* (as *U. lactuca*)	intersterile	Dangeard, 1958
Ulva lactuca × *U. fasciata* × *Enteromorpha lingulata* (all combinations)	intersterile	Kapraun, 1970

Table I

Continued

Species	Comments	Authors
Ulva lactuca × *U. thuretii*	forms from the north (*U. lactuca*) and south (*U. thuretii*) of the English Channel did not interbreed	Føyn, 1955
Ulva mutabilis	crosses of various mutants e.g. branched, precocious, slender, long	Fjeld and Løvlie, 1976; Føyn, 1960, 1961, 1962
Ulva mutabilis × *U. lactuca* & *U. thuretii*	intersterile	Føyn, 1958
Ulva—eight species (*U. lactuca, U. rigida, U. scandinavica, U. gigantea, U. olivascens, U. rotundata, U. curvata* & *U. neopolitana*)	fertilization only occurred between intraspecific species	Bliding, 1968
Ulva scagelii × *U. californica*	viable zygotes produced and supporting information for the synonymization of *Ulva scagelii* with *U. californica*	Tanner, 1979

inherent sterility barriers. Such conflicting results suggest that further hybridization studies would be beneficial to clarify the role of cross-fertilization within fucoid algae, perhaps employing field desiccated plants to see if natural stress can break down sterility barriers.

Bliding (1955, 1963, 1968) conducted extensive experiments based on intra- and interspecific crosses, as well as intergeneric crosses, in *Ulva* and *Enteromorpha*. He found that strict intersterility barriers exist between species of the Ulvaceae (Table I). Kapraun (1970) confirmed Bliding's hybridization experiments and showed that intra- and interspecific crosses in *Enteromorpha* and *Ulva* gave non-viable zygotes. Such findings are surprising in view of several previously described culture-morphological studies which suggest that the two genera may be the same.

An evaluation of Table I shows that several other hybridization studies have been conducted, particularly with members of the Fucales, Laminariales, and Ceramiales. The pioneering work of Sundene (1958, 1959) on various forms of *Laminaria digitata* and several varieties of *Antithamnion plumula* should be noted, as he was one of the first to evaluate form variation and interfertility with modern culture techniques.

A few hybridization studies of domesticated marine crop plants should be mentioned. Suto (1963) has conducted breeding studies on *Porphyra,* which is farmed extensively in Japan. Saito (1962) studied the propagation of the brown alga *Undaria,* a Japanese marine crop plant. Suto (1972) has extended his pioneering studies, and initiated crosses between various varieties of *Porphyra,* producing plants that are intermediate between the parental types. The breeding of new varieties of *Laminaria japonica* (Anon., 1975; Fang et al., 1962, 1963, 1965) for higher production rates and iodine content has been achieved by inbreeding, selection and X-ray treatment in China. The work suggests that natural populations have a high level of genetic diversity and that through inbreeding and repetitive selection, new varieties can be developed. For example, since 1973 two new varieties of *Laminaria japonica* with higher production rates (8–40%) and iodine content (20–58%) have been perfected and adapted for enhanced farming in northern China (Anon., 1975).

Few investigators have evaluated the reproductive dispersal range and/ or gene flow in seaweeds (Table I). Müller (1979) evaluated the genetic affinities of *Ectocarpus siliculosus* from the Mediterranean, North Atlantic and Australia. Complete interfertility was found in European materials ranging from the Mediterranean to Norway. Plasmogamy was also found between strains from Florida, North Carolina and all European clones. Overall, local populations from each geography are closely related enough to permit plasmogamy on a worldwide basis. Even so, some local populations (e.g., Massachusetts and Texas) are in the process of isolating them-

selves from the original gene pool, as they are either fully or partially sterile with strains from other localities. West et al. (1978) found a high incidence of reproductive compatibility (94%) among many isolates of *Gigartina agardhii* obtained from collection sites extending from British Columbia to southern California. Accordingly, they postulate that *G. agardhii* is an "evolutionarily young" species with a high degree of genetic compatibility (i.e., gene flow) over a wide geographical distance. Guiry (In press) has found a similar interfertility between a single male clone (i.e., T4) of *Chondrus crispus* from Canada and nine European female isolates, although Chen and Taylor (1980) have observed distinct strains of the same species from the Gulf of St. Lawrence and the Bay of Fundy in Canada.

In contrast to the studies of Müller (1979), West et al. (1978) and Guiry (In press) described earlier, there are surprisingly short dispersal distances recorded for spores in some algae, like *Alaria esculenta* (Sundene, 1962b), *Gelidium robustum* (Guzmán del Proo and De la Campa de Guzmán, 1969), and *Postelsia palmaeformis* (Dayton, 1973; Paine, 1979), which could create genetic isolation. The potential spread of algae by the drifting of pieces of frond that are or become fertile in transit should also be noted (see Lewis, 1968). For example, De Valera (1962) has suggested that this may account for the isolated growth of *Bifurcaria bifurcata* around the north of Ireland, while Lewis (1968) notes that the scattered finds of *Cystoseira* in various parts of N.W. Scotland, which are well beyond their normal range, may have a similar explanation.

As noted previously, electrophoretic techniques have recently been employed to determine the genetic similarities of various seaweed populations. Such studies are of fundamental importance in determining the effective dispersal ranges and rates of gene flow in seaweeds and they will have a practical application in the future domestication of marine crop plants.

VII. DISCUSSION

As noted above, we see two heartening trends. Firstly, an abundance of attempts to explore the range of form variation in individual species, which has led to an appreciation of the extreme phenotypic plasticity of many species. Secondly, an increasing tendency to embrace cytological, ultrastructural and biochemical characters to supplement morphological ones. Additional diagnostic features such as these are particularly welcome where other characters are few or very susceptible to environmental modifications.

However, the undoubted benefits that will accrue from these trends must not blind us to their possible disadvantages. As traditional morphological characters fall into disrepute there will be an increasing tendency

to abandon them in favor of the newly available characters whose importance may become inflated far above their actual taxonomic value.

Let us examine the relative merits of morphological and biochemical characters at the level of species delimitation. This is the level at which taxonomy is utilized by, say, an ecologist wishing to identify the plants in his study area.

Firstly, there is no reason to believe the tacit assumption that biochemical features are in some way more fundamental than morphological ones. Even seemingly trivial morphological features may be of great adaptive value, even if this value is not yet apparent to the taxonomist.

Secondly, a good taxonomic character is simply one that is constant, irrespective of its genetic basis or its apparent trivial or fundamental nature—nor need a good character be unaffected by environmental factors. Even a feature susceptible to wide variation may be useful taxonomically, providing the extremes of its morphological range overlap little or not at all with those of the species with which it might be confused.

Thirdly, the fact that in general many algae seem to exhibit a very high degree of phenotypic plasticity does not mean that every species or every character of a species is equally prone to do so. Each character should be judged on its merits after suitable experimentation. Moreover, there is no reason to assume that ultrastructural or biochemical features are in some way immune from environmental influence. On the contrary, many obvious examples such as the effect of light and shade on leaf pigments demonstrate that they are not. At present we possess far too little knowledge of the variation in biochemical characters in seaweeds to evaluate its taxonomic significance.

Fourthly, the value of any individual character is dependent on the degree to which it correlates with the other features of a species. Our knowledge of biochemical characters often hinges on very limited investigations. In contrast, a traditional taxonomist during a single day's fieldwork may observe hundreds of plants and note the various correlations of characters that they exhibit.

Finally, it is well not to forget the requirements of the user in the search for taxonomic truth. Cytological, ultrastructural and biochemical tests are laborious, often requiring special skills and equipment and usually resulting in the destruction of the plant. To someone merely wishing to identify plants, traditional morphological characters have the overwhelming advantage that they are readily observed and the plants survive identification. If obscure or esoteric characters are to be used to delimit species, then it is vital that strenuous efforts are made to correlate these characters with more readily observable ones. If the taxonomist fails to do so, then far from stimulating research on that species, he will actively inhibit it.

VIII. ACKNOWLEDGMENTS

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