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### Polymorphism of selected marine Chaetophoraceae (Chlorophyta)

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## POLYMORPHISM OF SELECTED MARINE CHAETOPHORACEAE (CHLOROPHYTA)

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The effect of variations in light-intensity and temperature on morphology, and the formation of setae as a function of nitrate and phosphate concentrations were determined for ten species of epiphytic, endozoic and epizoic marine Chaetophoraceae. Pronounced morphological plasticity, e.g. production of laxly branched or discoid thalli, occurred in the genera *Ochlochaete* and *Ectochaete* and branched, discoid or sarcinoid-like thalli in *Pseudoclonium*. *Bolbocoleon* was not variable under a wide range of environmental conditions. Setae were always formed by two taxa, *Bolbocoleon piliferum* and *Ectochaete ramulosa*, but were never formed by *Pseudoclonium submarinum*, *Pseudulvella heterotricha*, *Pseudulvella prostrata* or *Entocladia testarum* under variable nitrate and phosphate concentrations. In media deficient in nitrogen and phosphorus, algae that normally did not produce setae had long delicate bulbous setae, e.g. *Entocladia viridis* and *Entocladia flustrae*. The phenotypic plasticity of the marine Chaetophoraceae demands combined field and laboratory studies for correct identification.

Trainor, Rowland, Lylis, Winter & Bonanomi (1971) have described numerous examples of polymorphism in freshwater diatoms, green and blue-green algae. Berthold (1882) demonstrated that weak light caused *Bryopsis* germlings to produce prostrate filaments instead of the normal, feather-like thallus and increased the formation of rhizoids on branches of the thallus. Oltmanns (1922) reported that certain red and brown algae had a reduced number of hairs in low light intensities and decreased branching. On the otherhand, Uspenskaia (1936) noted that an increase in light intensity and in the concentration of nitrates in the medium suppressed the development of hairs in *Stigeoclonium tenue* (Ag.) Kütz. Abbas & Godward (1963) observed that there was a corresponding increase in the number of branches in *Stigeoclonium amoenum* Kütz. and *Draparnaldia plumosa* (Vauch.) Ag. with increased temperatures. Wynne (1969) reported that environmental conditions controlled reproduction and morphology in *Petalonia fascia* (O. F. Müll.) Kuntze; plants that were cultured under cool, short daylengths tended to produce a greater percentage of blades, whereas those cultured under long days and warm temperatures formed higher percentages of *Ralfsia*-like crustose stages. The production of hairs and setae and the degree of branching is affected by nutrient depletion. Godward (1942) working with *Stigeoclonium amoenum*, Moewus (1949) with *Ectochaete* spp., and Moestrup (1969) with *Bolbocoleon piliferum* Pringsheim reported that old cultures, which were probably nutrient deficient, produced hairs and setae abundantly. Nielsen (1972) observed that *Phaeophila dendroides* (Crouan frat.) Batt., when transferred from nutrient medium into seawater, produced hairs. The production of hairs was induced by decreasing the concentration of nitrates and suppressed in young cultures with adequate nitrate in *Stigeoclonium farctum* Berth. (Reynolds, 1950) and in four species of *Aphanochaete* in axenic culture (Tupa, 1974). Uspenskaia (1936) reported that increased levels of nitrates in the cultural

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media caused *Stigeoclonium tenue* to become excessively branched and small. Butcher (1951) noted abundantly branched *Stigeoclonium nanum* (Dillw.) Kütz. in high nitrate media and long unbranched filaments in media with excess phosphates.

Cultural studies have been instrumental in resolving many taxonomic problems in algae. The need for further collaborative investigations of field and cultural material has been stressed by several phycologists (Pringsheim, 1967; Bold, 1970; and Trainor, 1970). Confusion exists in the circumscription of many genera of the family Chaetophoraceae. Earlier descriptions were based entirely on field material, and the tremendous phenotypic plasticity of the organism that may occur was not appreciated. For example, in certain isolates the following morphological features are variable depending on altered environmental conditions in culture: discoid to branched thallus, presence or absence of erect filaments, and the presence or absence of setae (hair-like outgrowths of vegetative cells that lack a nucleus). Recent studies of Chaetophoraceae by Printz (1964) Bourrelly (1966), South (1968, 1969), Nielsen (1972), Wilkinson & Burrows (1972), and Tupa (1974) illustrate the confusion that persists. A detailed taxonomic treatment of the algae cultured in the present study has been published elsewhere (Yarish, 1975). Studies of both freshwater (Tupa, 1974) and marine representatives (Nielsen, 1972; Yarish, 1975) correlate field and cultural observations for many of the inadequately defined taxa.

The present study was undertaken because of difficulty in identifying isolates. Occasionally, phenotypic plasticity was so great that positive identification was impossible. A recurring problem was the formation of setae by isolates that were at first devoid of them, which thus invalidated the initial identification. This communication presents the results of a series of experiments to test the effects of variations in light intensity and temperature on selected epiphytic, endozoic and epizoic marine Chaetophoraceae. The range of morphological variation was determined and the formation of setae as a function of nitrate and phosphate concentrations was investigated.

## MATERIALS AND METHODS

Approximately 60 unialgal isolates of marine Chaetophoraceae from Australia, Florida and Texas were examined. After a preliminary study the following 10 isolates, which demonstrated a diverse array of characteristics, were chosen for more intensive study: *Bolbocoleon piliferum* Pringsheim, epiphytic on *Caloglossa*, Brisbane, Australia, 17 June 1971; *Entocladia testarum* Kylin, endozoic in oyster shell, Redfish Bay, Nueces Co., Texas; *Entocladia viridis* Reinke, culture collection of algae at Indiana University, Bloomington, Indiana, L. B. 1430; *Entocladia flustrae* (Reinke) Taylor, epizoic on shell fragments, Sarasota, Sarasota Co. Florida, 16 April 1972; *Ectochaete ramulosa* L. Moewus, epizoic on snail shell, Redfish Bay, Nueces Co., Texas, 17 January 1972; *Pseudendoclonium submarinum* Wille, epizoic on shell fragments, Sarasota, Sarasota Co., Florida, 16 April 1972; *Ectochaete taylori* Thivy, epizoic on shell fragments, Sarasota, Sarasota Co., Florida, 16 April 1972; *Ochlochaete hystrix* Thwaites in Harvey, epizoic on oyster shell, Biscayne Bay, Dade Co., Florida, 16 April 1972; *Pseudovella prostrata* (Gardner) Setchell et Gardner, growing on plastic, Redfish Bay, Nueces Co., Texas; and *Pseudovella heterotricha* Yarish, epizoic on oyster shell, Copano Bay, Aransas Co., Texas, 27 February 1972. The life histories of these isolates were reported by Yarish (1975). Stock cultures were maintained in von Stosch's enriched seawater medium as cited by Ott (1966) at  $22 \pm 1^\circ\text{C}$ , on a 12 h photoperiod with daylight fluorescent illumination of  $3800 \pm 100 \text{ lx}$ ; the medium was changed every three weeks. Inocula for all experiments were prepared as follows: transfers were made from stock culture tubes to fresh medium to obtain young, actively growing cultures; the tubes were agitated for several minutes to dislodge cells attached to the walls of the tubes;

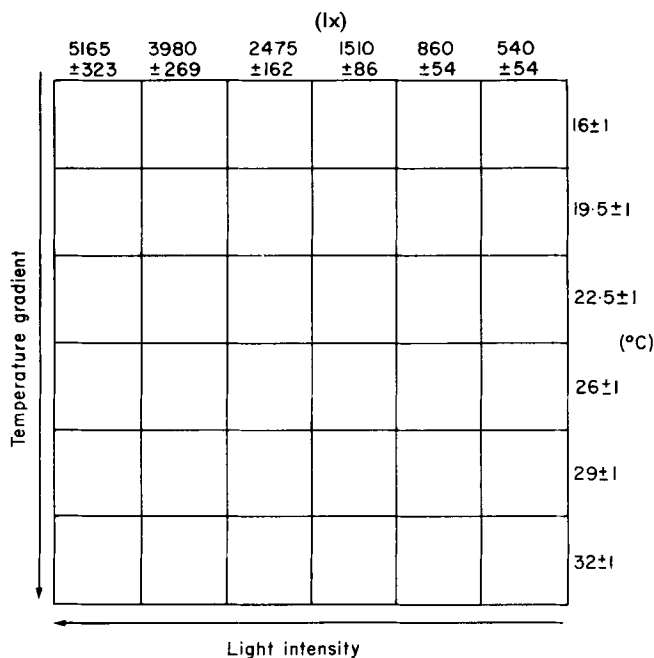


FIG. 1. A diagrammatic representation of the crossed light-intensity and temperature gradients.

sonication of the tubes dissociated the material into 1–3 cell fragments; 0.25 ml of the uniform suspension was added to each Petri dish. The crossed light-intensity and temperature gradient apparatus as described by Edwards & Van Baalen (1970) was used. Figure 1 is a diagrammatic representation of the 36 combinations of light-intensity and temperature employed. The salinity of the seawater, determined by a Goldberg Refractometer, was  $30 \pm 2\%$ . A daylength of 12 h was employed and the duration of all experiments was 14 days. The cultural medium was renewed weekly.

Two experiments were conducted in which the concentrations of nitrate and phosphate were varied. Experiments were conducted in Ott's synthetic seawater (Ott, 1966) modified to obtain the following concentrations of the two ions: 0%, 50%, 100% and 200% of those normally found in the medium. The levels of nitrate and phosphate were increased by doubling the  $\text{NaNO}_2$  and  $\text{Na}_2\text{HPO}_4$ , respectively. To obtain solutions in which the nitrate and phosphate concentrations were halved, half of the required  $\text{NaNO}_3$  or  $\text{Na}_2\text{HPO}_4$  was added and appropriate amounts of  $\text{NaCl}$  were added to adjust for  $\text{Na}^+$  ion concentrations. A solution which lacked nitrate and phosphate entirely was prepared by substituting equal amounts of  $\text{NaCl}$  for  $\text{NaNO}_3$  or  $\text{Na}_2\text{HPO}_4$ . Eight isolates were cultured in duplicate. Morphological observations were made after 1, 2 and 4 weeks.

## RESULTS

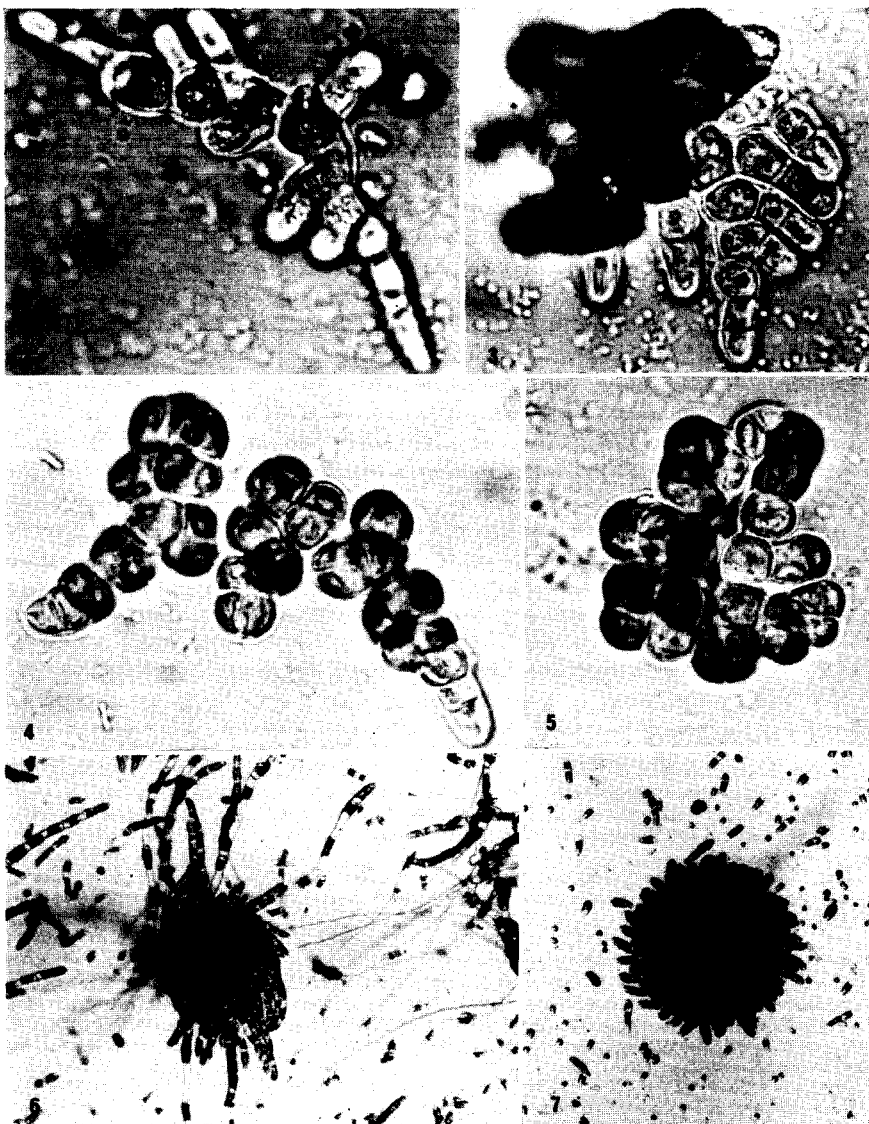
The results of the cultural experiments are presented under two categories: crossed-temperature and light-intensity gradient studies, and nutritional experiments.

### CROSSED-TEMPERATURE AND LIGHT-INTENSITY GRADIENT STUDIES

Five isolates were studied with the crossed-gradient apparatus.

#### PSEUDENDACLONIUM SUBMARINUM

The amount of growth increased with an increase in light-intensity and was



FIGS 2-5. *Pseudodoctonion submarinum*; effects of crossed-gradient experiments on morphology. Fig. 2. Heterotrichous thalli developed at optimal conditions of light intensity and temperature.  $\times 1600$ . Fig. 3. Discoid thallus grown at very high light intensities and  $32^{\circ}\text{C}$ .  $\times 1600$ . Fig. 4. Compact filamentous thalli grown at light intensity of  $1510 \text{ lx}$ .  $\times 1600$ . Fig. 5. Compact plants that resembled "*Pleurococcus*" grown at  $540 \text{ lx}$ .  $\times 1600$ .

FIGS 6-7. *Ochlochaete hystrix*; effects of crossed-gradient experiments on morphology. Fig. 6. Discoid thalli with free peripheral branches grown at optimal light intensity and temperature.  $\times 210$ . Fig. 7. Compact discoid thallus grown at high temperatures.  $\times 210$ .

optimal at 3980 lx and 22.5 °C. Heterotrichous thalli with zoosporangia in the central cells developed under optimal conditions (Fig. 2). Disc-like thalli were formed at very high light intensities as the temperature increased to 32 °C (Fig. 3). The cells became rounded and the branched filamentous thalli appeared more compact as the light-intensity decreased to 1510 lx (Fig. 4). At 540 lx the plants resembled *Pleurococcus* (Wille, 1901) colonies (Fig. 5). No setae or hairs were produced.

#### OCHLOCHAETE HYSTRIX

The amount of growth increased with increasing light intensity and was optimal at 5165 lx and 29 °C. Plants at optimal light-intensity and temperature were discoid with free peripheral branches and produced numerous setae (Fig. 6). As the temperature increased, the laxly branched thalli became more compact and discoid (Fig. 7). Plants at 32 °C were all discoid and had a peripheral gelatinous sheath, regardless of the light-intensity, and thus bore a remarkable resemblance to *Pringsheimiella scutata* (Reinke) Höhnelt (Fig. 8). Plants at lower temperatures (Fig. 9) resembled *Ochlochaete hystrix*, while those at the optimum temperature of 29 °C resembled *O. ferox* Huber and *O. lentiformis* Huber (Fig. 6). The degree of branching was not noticeably affected by the variation in light-intensity, although the plants demonstrated a strong positive orientation to the light source. Most plants died at the lowest temperature tested. The production of setae was stimulated by an increase in light-intensity (Fig. 9) but at high temperatures the frequency of setae decreased tremendously (Fig. 8).

#### ECTOCHAETE TAYLORI

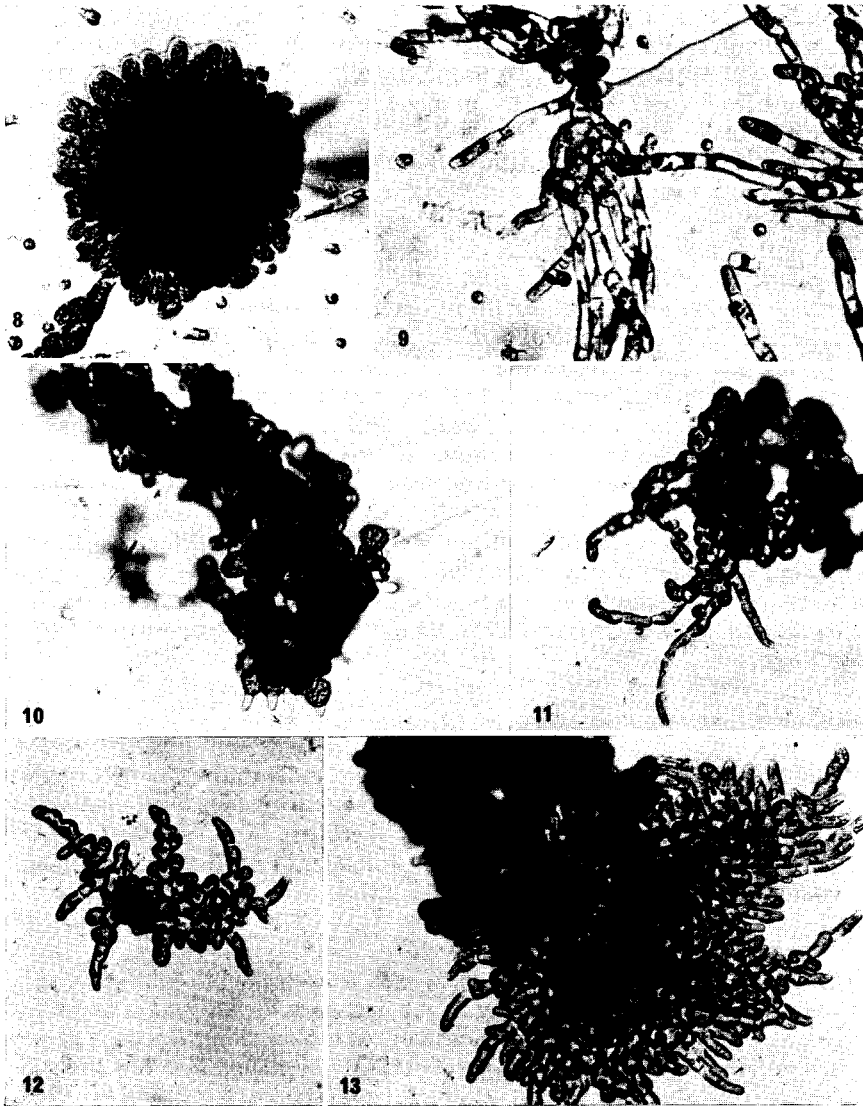
The amount of growth increased with increasing light-intensity and was optimal at 3980 lx and 26 °C. Plants which grew under optimal conditions were branched with an abundance of setae and zoosporangia (Fig. 10). Plants which grew at higher light intensities were mostly vegetative (Fig. 11). At 16 °C, there was an increase of discoid thalli, most of which had very few setae, formed by the lateral coalescence of filaments (Figs 12, 13).

#### ECTOCHAETE RAMULOSA

As the light-intensity increased there was a corresponding increase in the amount of growth up to 5165 lx (Fig. 14); a decline in the amount of growth was observed at 16 °C and at low light intensities. At low temperatures the algae were discoid and had setae (Figs 15, 16) or were laxly branched with few setae (Fig. 17). Fewer setae were produced at lower light intensities.

#### BOLBOCOLEON PILIFERUM

The amount of growth increased with an increase in light-intensity and was optimal at 5165 lx and 22.5 °C (Figs 18, 19); it was apparently unaffected by temperature variations. All plants died at 32 °C regardless of the light intensity. The cells at very low light intensities were filled with starch granules. At very high light intensities the algae were profusely branched, whereas at low light intensities branching was substantially reduced. Zoosporangia were observed under all conditions where growth occurred. The setae were more abundantly produced at the lower light intensities (860 lx or less).



FIGS 8-9. *Ochlochaete hystrix*; affects of crossed-gradient experiments on morphology. Fig. 8. Discoid thallus with a peripheral gelatinous sheath grown at the highest temperature of 32°C. × 420. Fig. 9. Laxly branched thalli with abundant setae grown at low temperatures and high light intensities. × 420.

FIGS 10-13. *Ectochaete taylori*, effects of crossed-gradient experiments on morphology. Fig. 10. Thallus which grew at the optimal conditions at 3980 lx and 26°C were irregularly branched and the cells had an abundance of setae and zoosporangia. × 420. FIG. 11. Thallus consisted of irregularly branched, vegetative filaments at lower light intensities. × 420.

FIGS 12, 13. Discoid thalli with few to so setae grown at 16°C. × 420.



Polymorphism of marine Chaetophoraceae



FIGS 14–17. *Ectochaete ramulosa*; effects of crossed-gradient experiments on morphology. Fig. 14. Thallus consisted of branched, tufted filaments.  $\times 210$ . Figs 15, 16. Discoid thalli with setae grown at low temperatures. FIG. 15,  $\times 420$ ; FIG. 16,  $\times 210$ . Fig. 17. Irregularly branched thallus grown at low light intensities.  $\times 210$ . FIGS 18, 19. *Bolbocoleon piliferum*; effects of crossed-gradient experiments on morphology. Figs 18, 19. Thalli which grew under standard cultural conditions similar to ones grown under crossed-gradients of light intensity and temperature. Fig. 18,  $\times 210$ ; Fig. 19,  $\times 840$ .

In all cases of phenotypic plasticity in the crossed-gradient experiments, plants were re-incubated under standard cultural conditions; in every instance, the original growth form was restored.

#### NUTRITION EXPERIMENTS

Setae production as a response to varying nitrate concentrations is summarized in Tables I and II. These algae may be segregated into three groups: those that always produced setae or hairs, *Bolbocoleon piliferum* and *Ectochaete ramulosa*; those that never produced setae or hairs in high or low concentrations of nitrate or phosphate, *Entocladia testarum*, *Pseudulvella heterotricha*, *Pseudulvella prostrata* and *Pseudendoclonium submarinum*; and those that produced setae in low concentrations of nitrate and phosphate, *Entocladia viridis* and *Entocladia flustrae*.

TABLE I. Relative abundance of setae as a function of nitrate concentration after 2 weeks. F = frequent, T = trace, A = absent.

Isolate	Nitrate concentration			
	0%	50%	100%	200%
<i>Bolbocoleon piliferum</i>	F	T	T	T
<i>Entocladia testarum</i>	A	A	A	A
<i>Entocladia viridis</i>	F	A	A	A
<i>Entocladia flustrae</i>	F	A	A	A
<i>Ectochaete ramulosa</i>	F	F	F	F
<i>Pseudulvella heterotricha</i>	A	A	A	A
<i>Pseudulvella prostrata</i>	A	A	A	A
<i>Pseudendoclonium submarinum</i>	A	A	A	A

TABLE II. Relative abundance of setae as a function of phosphate concentration after 2 weeks. F = frequent, T = trace, A = absent.

Isolate	Phosphate concentration			
	0%	50%	100%	200%
<i>Bolbocoleon piliferum</i>	F	F	F	T
<i>Entocladia testarum</i>	A	A	A	A
<i>Entocladia viridis</i>	F	A	A	A
<i>Entocladia flustrae</i>	F	T	T	A
<i>Ectochaete ramulosa</i>	F	F	F	A
<i>Pseudulvella heterotricha</i>	A	A	A	A
<i>Pseudulvella prostrata</i>	A	A	A	A
<i>Pseudendoclonium submarinum</i>	A	A	A	A

#### DISCUSSION

The concentration of both nitrates and phosphates was important for setae production in some algae. Setae were always formed by two genera; *Bolbocoleon* and *Ectochaete*. In media deficient in nitrogen and phosphorous, algae that normally did not produce setae had long delicate bulbous setae, e.g. *Entocladia viridis* and *Entocladia flustrae*. In addition in these media, individual cells of the setae-producing algae had several setae. Tupa (1974) suggested that hairs were

produced by *Aphanochaete* in response to low concentrations of nitrogen to increase surface area for uptake of nitrate from the surrounding medium. The result of this investigation showed that the production of setae was variable for some algae and was in response to nitrogen and/or phosphorus depletion in the medium.

The variability exhibited by each species in culture was phenotypic and not genotypic since in all cases the initial growth form was re-established when plants were re-incubated under standard cultural conditions.

The phenotype of any alga is determined by the genome of that alga and the extent to which the expression of the genotype may be modified by the environment. If one relies on morphological attributes alone to delimit genera and species, those traits employed should be the least variable of those which characterize the organism. The most obvious morphological attributes—presence of setae and shape of thallus—have been shown by this investigation to be extremely variable for certain organisms. Trainor *et al.* (1971) has written, “if an organism has the genetic potential to alter its form in culture, some similar alteration might occur in nature.” Careful observations of morphological variation, both in field and in culture under a variety of environmental conditions are necessary to provide us with a better understanding of phenotypic plasticity in many algae. In the case of certain Chaetophoraceae it is essential to culture the organisms to obtain a correct identification. Many species described in the literature are probably ecophenes of a more limited number of species.

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