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THE LIFE HISTORY OF *PETROCELIS FRANCISCANA*

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Tetraspores from *Petrocelis franciscana* Setch. et Gardn. collected at Rockaway Beach, San Mateo County, California, 11 January 1971 were isolated into unialgal culture with Provasoli's enriched seawater medium at 10° and 15° C, 16:8 daily photoregime, 2000–2500 lx cool white fluorescent lighting. The germlings developed as crustose discs with marginal meristems until about 300–500 μm in diameter when erect multiaxial blades were established. The erect plants grew to reproductive maturity in 15° C but not in 10° C. By the fifth month of growth the erect axes flattened and branched dichotomously. At the end of 7 months the plants were reproductively mature. These cultured plants were morphologically similar to *Gigartina agardhii* Setch. et Gardn. (subgenus *Mastocarpus*) which occurs abundantly at Rockaway Beach. Male plants were non-papillate with spermatangia forming on the entire blade surface except at the growing tip and near the stipe. The female plants developed papillae which bore many procarps. Many of these procarps were penetrated and seemingly destroyed by intrusive filaments from adjacent vegetative branches but apparently a number were functional since a number of cystocarps developed on plants in both stationary and shake culture after 5 months. Some viable spores were released and germinated.

Along the Pacific coast of North America there are five species of *Petrocelis* (Dawson, 1961a, 1961b), a genus of crustose red algae customarily placed in the family Cruoriaceae* of the order Gigartinales. These species are known only in the tetrasporophytic phase. No gametophytes have been reported. *Petrocelis franciscana* Setch. et Gardn. is the most common of these species in California and it forms extensive patches in the intertidal zone. It is a perennial species which produces intercalary tetrasporangia primarily during the winter months (November–March).

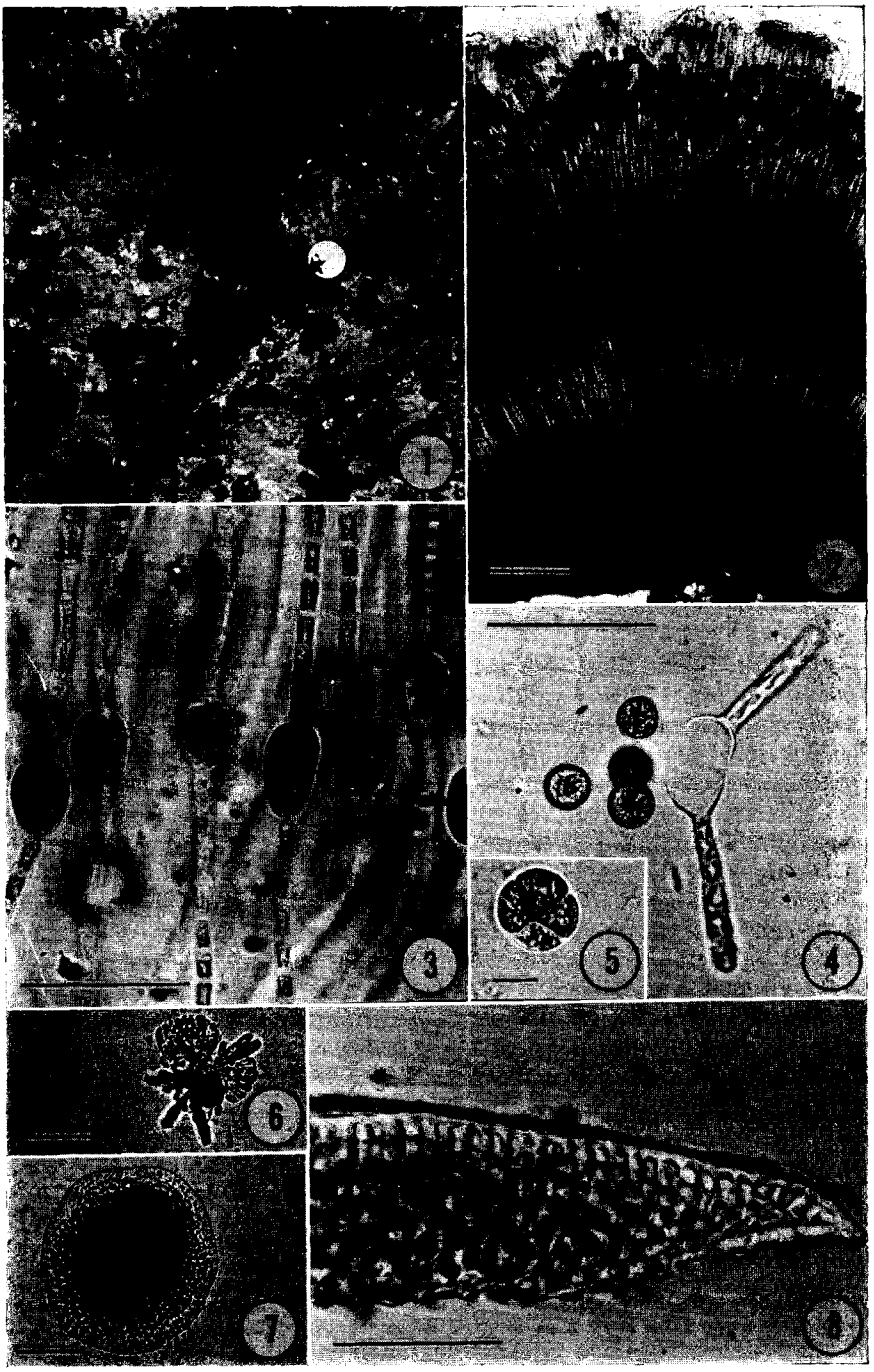
Gigartina agardhii Setch. et Gardn. and *G. papillata* (C. Ag.) J. Ag. are species of the subgenus *Mastocarpus* (Setchell & Gardner, 1933) which is characterised partially by the apparent absence of a tetrasporophyte. These perennial species are very common in California, occurring often in the same localities (Fig. 1) and at the same tidal levels as *Petrocelis*. Cystocarps are present throughout the year.

In this report I shall consider the possible relationship between *Petrocelis franciscana* and *Gigartina agardhii* as based on culture studies of *Petrocelis* tetraspore germlings.

MATERIAL AND METHODS

On 11 January 1971 several specimens of *Petrocelis* were chipped off the rocks at the south end of Rockaway Beach (San Mateo County, California). The rock fragments were transported to the laboratory dry in plastic bags on ice. Specimens collected generally fit the description of *P. franciscana*, the only species recorded for central California. Segments of the tetrasporophytic crust (Figs 2, 3) were sliced off the rocks with a razor blade and immersed in sterile 30‰ seawater overnight at 10° C in the dark. Re-immersion of the dry thalli apparently caused the spores to be liberated (Fig. 4). In the morning spores were pipetted into several 35 × 50 mm crystallising dishes with 22 mm square coverslips on the bottom. Provasoli's enriched

* Denizot (1968) established the family Petrocelidaceae to accommodate *Petrocelis*.



seawater medium adjusted to 30‰ was used for all culturing. The germlings were grown at 10 and 15° C, 16:8 daily photoperiod and 2000–2500 lx cool white (General Electric) fluorescent lighting. The coverslips were examined weekly and photographed as the germlings developed. To eliminate diatoms GeO_2 was added to a final concentration of 5 mg/l (West, 1970). Blue-green algal contaminants were eliminated by the addition of 50 mg Penicillin G/l. Other contaminating algae were scraped off the coverslip with a microdissection scalpel. When the plants reached reproductive maturity several were placed on a continuous rotary shaker operating at 100 rpm in an attempt to achieve fertilisation.

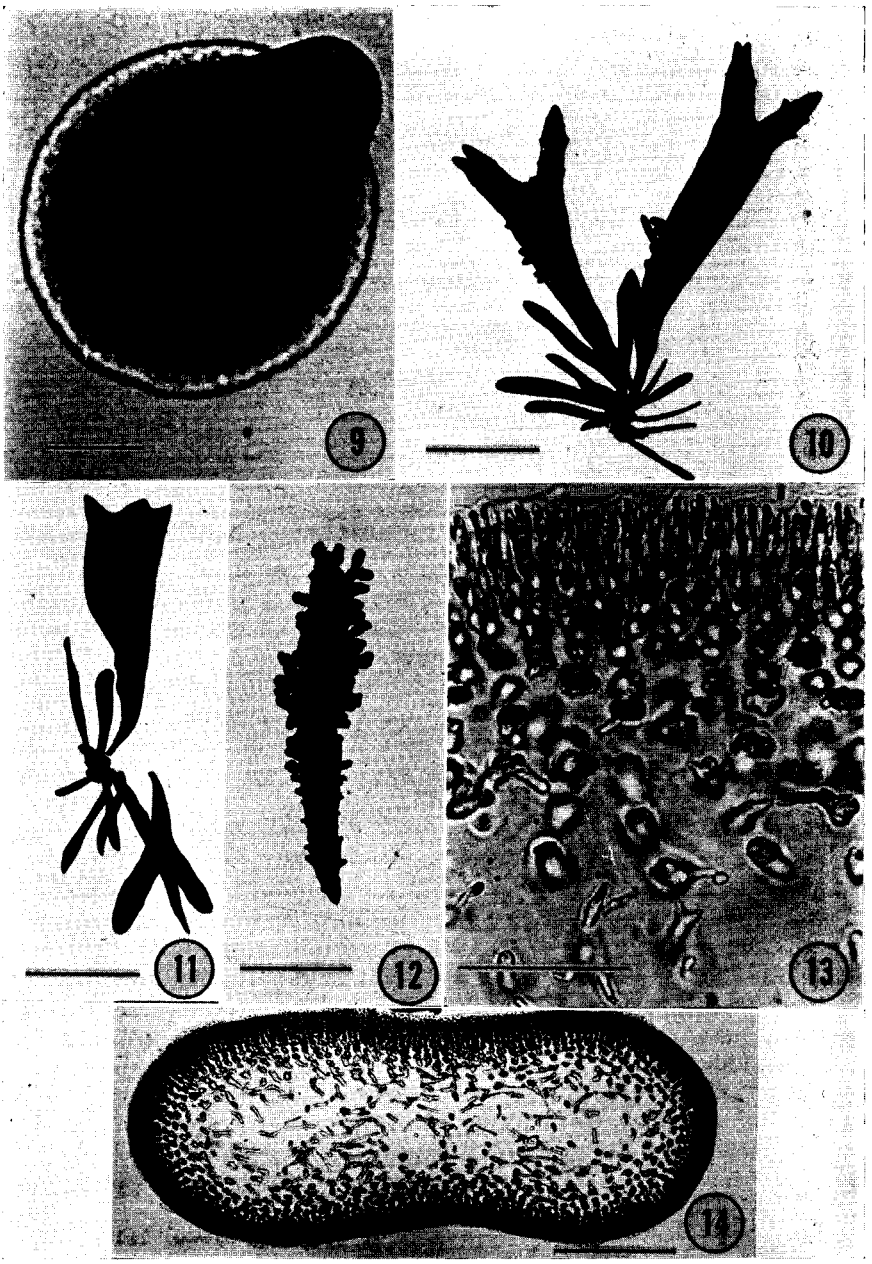
OBSERVATIONS

The liberated tetraspores were about 12–14 μm in diameter. Germination occurred in two different ways. Most spores divided several times (Fig. 5) without significant enlargement to form a compact crustose multicellular disc with a marginal meristem (Fig. 7). Other spores divided to form an irregular mass of cells from which several elongate multicellular rhizoids extended. After several days one or more of the rhizoids made contact with the substrate and initiated the formation of a disc similar to that formed directly (Fig. 6). Both paths of development resulted in the formation of mature plants of similar morphology. It appears that early germination patterns have little significance in the life history. The causes of the two germination paths are not apparent. Both occurred in close proximity in a single culture dish. Perhaps initial substrate contact by the spore was the primary controlling factor.

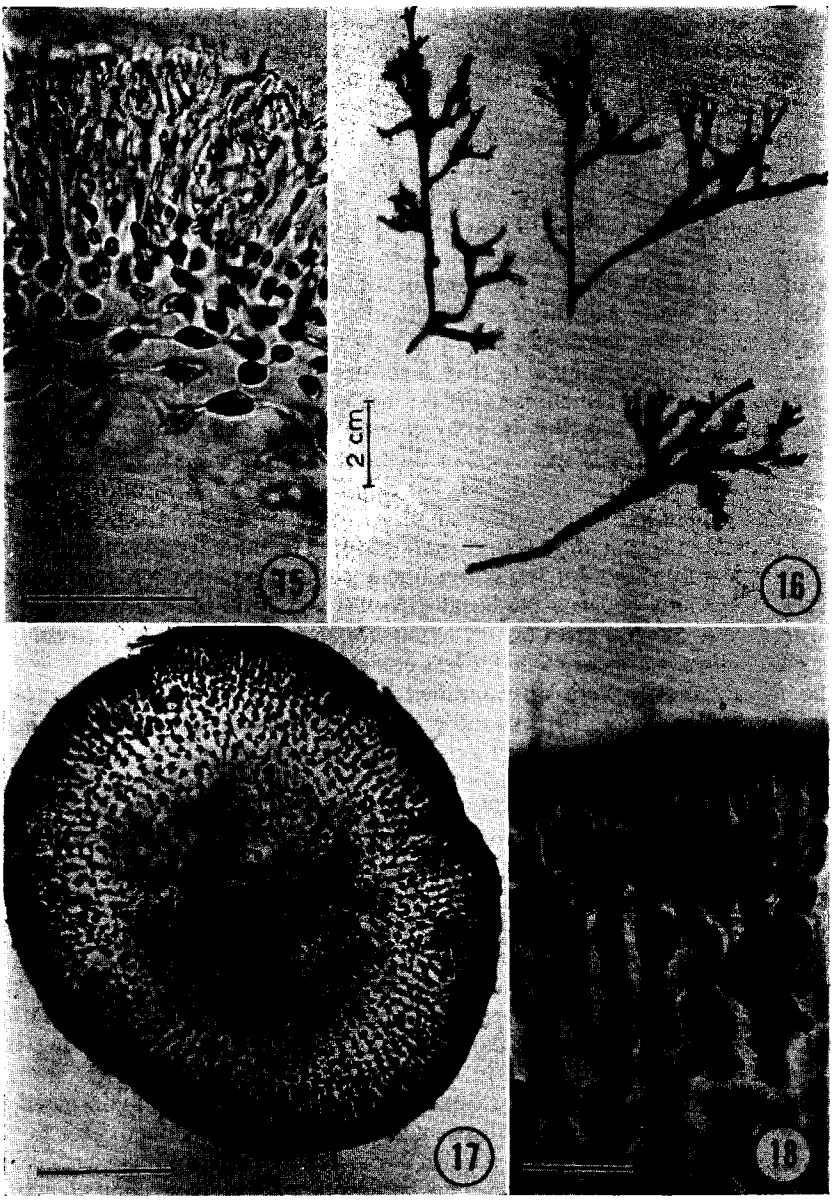
The enlarging disc became polystromatic throughout except at the margin (Fig. 8). The surface cells of the erect filaments were smaller, less vacuolate and less densely pigmented than the lower cells, suggesting that they were meristematic. Secondary pit connections were evident between the cells of adjacent filaments.

The basal discs grew in diameter and initiated erect axes much more rapidly at 15 than at 10° C (Fig. 20). The establishment of erect axes (Fig. 9) was correlated with a decrease in the growth rate of the basal discs. This was evidently due to a shift in the mitotic activity from the marginal meristem of the disc to the multiaxial meristem of the erect axis. Initially, one or two erect axes arose from a single disc. Many additional axes developed from the same discs later. The erect axes remained cylindrical until about 1–2 mm long at which point there commenced a perceptible flattening. The blade subsequently elongated and increased in width. The internal anatomy of the blade as seen in cross sections at this stage is clearly similar to that of the Gigartinaceae (Fig. 14). The cortex is composed of dichotomously branched filaments of 5–8 spherical to ellipsoidal, deeply pigmented cells decreasing in diameter toward the surface. The outer medulla is composed of lightly pigmented somewhat stellate cells and the inner

FIGS 1–8. Fig. 1. *Petrocelis franciscana* (irregular dark patches) intermixed with *Gigartina papillata* and *G. agardhii* Rockaway Beach. Fig. 2. Section of tetrasporangiate *Petrocelis* crust. Sporangia borne in a zone about 10–30 cells from upper surface. Scale = 200 μm. Fig. 3. Nearly mature intercalary tetrasporangia borne singly on filaments. Scale = 50 μm. Fig. 4. Tetrasporangium liberating 4 spores. Scale = 50 μm. Fig. 5. Early stage in spore germination leading to disc formation. Scale =10 μm. Fig. 6. Germling developed as irregular cell mass which produced rhizoids that are initiating a basal disc. Scale = 50 μm. Fig. 7. Germling developed directly into a basal disc. Scale = 50 μm. Fig. 8. Median longitudinal section through a five-week-old disc, showing the monostromatic margin and polystromatic centre with meristematic surface cells. Scale = 50 μm.



FIGS 9–14. Fig. 9. Six-week-old disc with erect axis developing. Scale = 100 μm. FIG. 10. Eight-month-old papillate female plant with secondary blades arising at the base. Plant grown in stationary culture. Scale = 1·0 cm. Fig. 11. Eight-month-old non-papillate male plant with secondary blades at base. Scale = 1·0 cm. Fig. 12. Eleven-month-old female plant grown for two months in shake culture. Papillae are shorter, broader and more lobed compared with those on plants in stationary culture. Some of these papillae bear immature cystocarps. Scale = 1·0 cm. Fig. 13. Cross-section of blade seen in Fig. 14 with characteristic cortex and medulla. Scale = 50 μm. Fig. 14. Cross-section of 3 mm long blade. Scale = 200 μm.



FIGS 15–18. Fig. 15. Cross-section of an old male plant. Cortex with a thick spermatangial layer. Scale = 50 μm. Fig. 16. Typical specimens of *Gigartina agardhii* from Rockaway Beach. Fig. 17. Cross-section of a papilla with the deeply stained supporting cells in the outer medulla. Medulla consists of stellate cells with thick walls. Compare this medulla with that of a vegetative plant (Fig. 13). Scale = 200 μm. Fig. 18. Two hypertrophied procarps penetrated by filaments derived from vegetative cells nearby. Scale = 25 μm.

medulla consists of elongate branched filaments most of which run parallel to the blade surface (Fig. 13). These blades vary in thickness from about 300–400 μm depending somewhat on their age. Plants grown in stationary and shake culture show little difference in blade thickness.

Plants held at 10° C reached a height of 2·0–3·0 mm and did not develop sexual cells after 12 months in culture. After six months of culture at 15° C the plants were 1·0–1·5 cm tall by 2·0–3·0 mm wide and several had developed a single dichotomy. At the end of seven months these plants reached reproductive maturity.

In the male plants (Fig. 11) a continuous spermatangial sorus covered the surface of the blade except near the stipe and the growing tips. Numerous colourless cylindrical spermatia 6–12 μm long and 2·0–2·5 μm in diameter were produced in a manner similar to that described by Grubb (1925) for *Chondrus crispus* Stackh. and by Hinchman (1964) for *Gigartina papillata*. Each male frond produced spermatia indefinitely after it reached sexual maturity. The spermatangial layer gradually increased in thickness until it was about 50 μm thick in the one-year-old plants (Fig. 15). No papillae or leaflets developed on the cultured male plants (Fig. 11), although males in the field often form flattened or conical leaflets in *G. papillata* (Hinchman, 1964). The male fronds outnumbered the female fronds about 3:1 in culture but it was not possible to determine the sex ratio accurately because the basal discs derived from individual spores became confluent. Several erect blades ultimately arose from each disc. In the field male plants always appear to be far less common than female plants.

The female plants were distinguished from the males by the presence of numerous papillae (Fig. 10). As the plants aged the papillae often developed secondary papillae. In stationary culture the papillae (Fig. 10) were generally elongate (up to 3 mm long) and cylindrical and in shake culture they were shorter, thicker and more spherical (Fig. 12). The internal anatomy of the papillae was different from that of the vegetative blades (Fig. 17). The medulla was constituted of stellate cells and lacked the elongate branched filaments present in the inner medulla of the blade. Procarps developed soon after the papillae were formed and were present only on the papillae. The supporting cells were derived from intercalary cells of the cortical filaments and were apparent as enlarged refractive cells (Fig. 17). The procarp consisted of a supporting cell and a three-celled carpogonial branch with a twisted configuration. The first and second cells of the carpogonial branch commonly bore one sterile cell (Fig. 19).

Male and female plants in shake and stationary culture were maintained together for as long as 7 months before mature cystocarps developed. One or two cystocarps developed on a fertile papilla. Most papillae did not form cystocarps. About 30–60 days after the cystocarps became apparent as swollen structures (Fig. 12) on the papillae the carpospores were released through lateral ostioles. The carpospores attached and germinated in a manner similar to that of *Petrocelis* tetraspores.

Trichogynes with spermatia attached were never observed nor was a connection seen between the carpogonium and the supporting cell. Other authors (Hinchman, 1964; Marshall, Newton & Orr, 1949; Mikami, 1965) were also unable to detect any connection between the carpogonium and the auxiliary

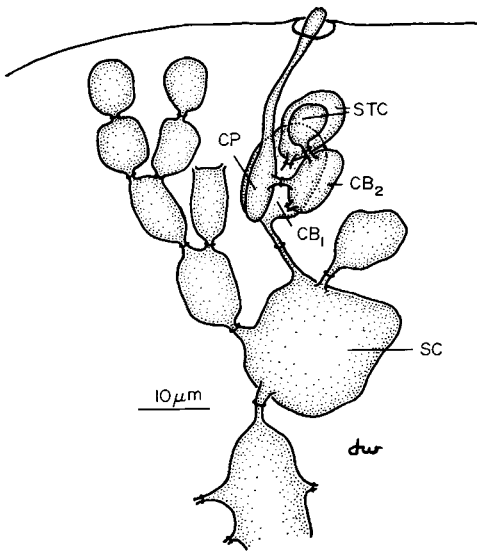


FIG. 19. Drawing of a typical procarp showing the supporting cell (SC) derived from an intercalary cell of cortical filament and the carpogonial branch with the carpogonium (CP) and two branch cells (CB_1, CB_2) each bearing a sterile cell (STC).

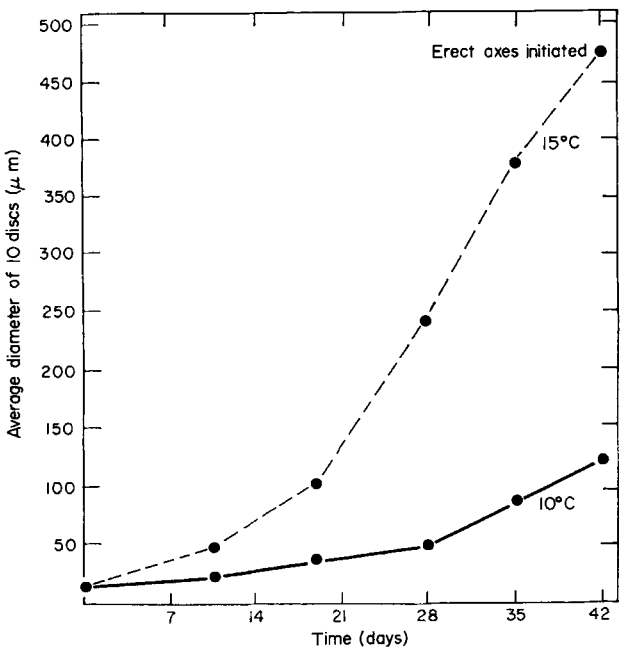


FIG. 20. Growth in diameter of discs at 10 and 15° C. Erect axes formed in 50% of plants at 15° C by 42 days. None was present at 10° C.

(supporting) cell although numerous stages of carposporophyte development from the auxiliary cell were reported by Hinchman and Mikami.

In many papillae examined most of the procarps became hypertrophied and were penetrated by small twisted filaments derived from adjacent vegetative medullary cells (Fig. 18). The cause of this process is not known but it resulted in the destruction of these procarps. The same phenomenon was observed occasionally by Hinchman (1964).

A morphological comparison of the plants in culture with *Gigartina* species present at Rockaway Beach shows that the closest similarity is with *G. agardhii* and *G. papillata*, both of the subgenus *Mastocarpus*. Neither is known to have a tetrasporophyte. The cultured plants are smaller than field-collected specimens of either species but it is common for red algae in culture to be smaller than in nature. The cultured plants have narrow dichotomously branched axes with slightly thickened margins like those of *G. agardii* (Fig. 16). *Gigartina papillata* is a much broader blade. The specimens in culture are therefore tentatively assigned to *G. agardhii*. Further culture studies will hopefully clarify this matter; it is possible that both species have a *Petrocelis* phase.

Although *Gigartina* plants in nature are subject to frequent emersion this probably is not a requirement for survival or reproduction in nature or in culture because plants in culture grew comparatively well continually immersed and ultimately reached sexual maturity.

DISCUSSION

Deviations from the *Polysiphonia*-type of life history are not common among the Gigartinales (Dixon, 1970). Several species in the Phyllophoraceae show interesting modifications (Dixon, 1970) too extensive and complex to be considered here. In the Furcellariaceae *Halarachnion ligulatum* (Woodw.) Kütz. is known to have a *Cruoria*-like tetrasporophyte (Boillot, 1965) and *Neurocaulon grandifolium* Rodrig. is now known to have a small discoid tetrasporophyte (Codomier, 1969). South, Hooper & Irvine (1972) have also described a life history link between *Turnerella pennyi* (Harv.) Schmitz (Solieriaceae) and *Cruoria arctica* Schmitz in Rosenv. In the Gigartinaceae, *Chondrus*, *Iridaea* and *Rhodoglossum* appear to have *Polysiphonia*-type life histories. *Besa*, a rare crustose form which bears cystocarpic papillae, has no known tetrasporophyte. In *Gigartina*, which is the largest and most complex genus of the family, the majority of the species apparently exhibit the *Polysiphonia*-type life history. However, among the species of the subgenus *Mastocarpus* it has been carefully and repeatedly demonstrated that a tetrasporophyte is missing (e.g. Rosenvinge, 1931; Setchell & Gardner, 1933; Marshall, Newton & Orr, 1949; Hinchman, 1964; Mikami, 1965).

Hinchman (1964) speculated that three possible life histories might explain the apparent absence of a tetrasporophyte among the species of the subgenus *Mastocarpus* (he referred these species to the '*Gigartina papillata* complex'): (1) the tetrasporophyte exists as a phase different in morphology from the gametophytes; (2) a tetrasporophyte is absent and meiosis occurs following fertilisation during the formation of the carposporophyte; (3) meiosis does not occur—the known plants having an entirely non-sexual haploid cycle. For several reasons which appeared plausible at the time Hinchman decided that the third

explanation was the most likely. However, in view of the results presented here, the second and third possibilities now seem less likely, but they should not be excluded from consideration for two reasons also raised by Hinchman. First, in certain localities where *Gigartina papillata* is common, crustose species which might be the alternate stage are absent or very sparse. Second, he observed neither syngamy nor karyogamy. No connection was seen between the carpogonium and the auxiliary cell. These features suggest that an alternate obligate diploid stage does not exist in certain populations or species within the subgenus.

The subgenus is widely distributed throughout the temperate and cold waters of the northern hemisphere. In Japan *Gigartina pacifica* Kjellm., *G. ochotensis* (Rupr.) Rupr. and *G. mamillosa* (Good. et Woodw.) J. Ag. are not known to have tetrasproangia (Mikami, 1965). *Gigartina pacifica* is abundant at Amchitka in the Aleutian Islands (Weinmann, 1969) where *Petrocelis middendorffii* (Rupr.) Kjellm. is also common. *Gigartina stellata* (Stackh.) Batt. occurs on both sides of the North Atlantic and also lacks a known tetrasporophyte. *Petrocelis cruenta* J. Ag. or *P. middendorffii* may be an alternate stage for that species.

Before the systematic relationships among the many species of *Gigartina* subgenus *Mastocarpus* and among the species of *Petrocelis* can be clearly discerned it is evident that substantial field ecology and laboratory culture studies must be undertaken in a wide variety of geographic areas.

Among the Cryptonemiales and Gigartinales thus far studied in culture those cases in which the gametophytes and tetrasporophytes are not isomorphic show a constant pattern—the gametophyte is the erect macroscopic phase and the tetrasporophyte is the crustose (often microscopic) phase (Dixon, 1970; Scott & Dixon, 1971). The adaptive significance of this pattern is not yet apparent but it is interesting to note that at least one phase often has a clear seasonal pattern in its growth and reproduction. Careful field and laboratory studies should reveal the general development responses of each to ranges in physical and chemical factors.

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