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THE LIFE HISTORY IN CULTURE OF *PETROCELIS CRUENTA* J. AGARDH (RHODOPHYTA) FROM IRELAND

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Tetraspores of *Petrocelis cruenta* J. Agardh from County Waterford, Ireland gave rise to foliose, dioecious gametophytes in culture. Carpospores from this foliose phase gave rise to *Petrocelis*-like crusts that have not reproduced in culture. Anatomical and reproductive characteristics of the female gametophyte indicate that the naturally occurring gametophyte of *P. cruenta* is a species of *Gigartina* subgenus *Mastocarpus*. *Gigartina stellata* (Stackh.) Batt. is postulated to represent the naturally occurring gametophyte of *P. cruenta* in Ireland and possibly elsewhere. Field-collected sporophytes and cultured gametophytes of *P. cruenta* were compared with *P. middendorffii* (Ruprecht) Kjellman from the North Pacific. Results of attempted crosses between gametophyte stages of *P. cruenta* and *P. middendorffii* indicate that these species are reproductively isolated. The available evidence supports the continued recognition of *P. cruenta* and *P. middendorffii* as distinct species.

Species of the crustose red algal genus *Petrocelis* may be divided into two groups: those that generally produce tetrasporangia in series and those that generally produce solitary tetrasporangia. *Petrocelis hennedyi* (Harvey) Batters and *P. anastomosans* Dawson constitute the first group [*Petrocelis haematis* Hollenberg has been transferred to *Erythrodermis* by Denizot (1968)]; these species will not be considered further here. *P. ascendens* Dawson, *P. cruenta* J. Agardh, *P. franciscana* Setchell & Gardner and *P. middendorffii* (Ruprecht) Kjellman are species of the second group. Culture studies have demonstrated that *P. franciscana* (West, 1972) and *P. middendorffii* (Polanshek & West, 1975) from the North Pacific alternate with foliose, dioecious gametophytes in heteromorphic sexual life histories. When sporophytic crusts (the *Petrocelis* stage) of these species were compared, the taxonomic criteria originally used to separate them were not confirmed. Hybridization experiments demonstrated the interfertility of gametophytes derived from tetraspores of *P. franciscana* from California with those of *P. middendorffii* from Amchitka Island, Aleutian Islands, Alaska (Polanshek & West, 1975). After examination of isotype material of *P. middendorffii*, Polanshek & West (1975) proposed that *P. franciscana* be reduced to a synonym of *P. middendorffii*.

Our studies of *Petrocelis* species with solitary tetrasporangia continue with a report of the culture life history of *P. cruenta* J. Agardh, the type species of the

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genus, from the south coast of Ireland. Pybus (1975) previously attempted to culture tetraspores of *P. cruenta* from County Galway, Ireland, but with little success.

MATERIALS AND METHODS

Fertile specimens of *Petrocelis cruenta* were collected at the Curragh, County Waterford, Ireland in January 1975, placed in plastic bags containing seawater-moistened paper towelling in an insulated container and sent by refrigerated air freight to San Francisco. Large numbers of tetraspores were released from crusts placed in crystallizing dishes containing 30‰ sterile seawater. Spores were collected by pipette, resuspended in a test tube containing 30‰ sterile seawater, and filtered through 20 µm Nitex screen. The resulting spore suspension was diluted and inoculated by pipette into 50 or 90 mm crystallizing dishes containing Provasoli's Enriched Seawater (McLachlan, 1973) and either 22 mm² cover glasses or glass plates. Cultures were maintained under photoperiods of LD 16:8 and LD 8:16 at 10 and 15°C. Light intensities varied from 1500 to 2500 lx cool white fluorescent lighting. Germanium dioxide and Penicillin G were used as described previously (Polanshek & West, 1975; West, 1972). Some cultures contained several plants per dish whereas others contained individual plants derived from single tetraspores.

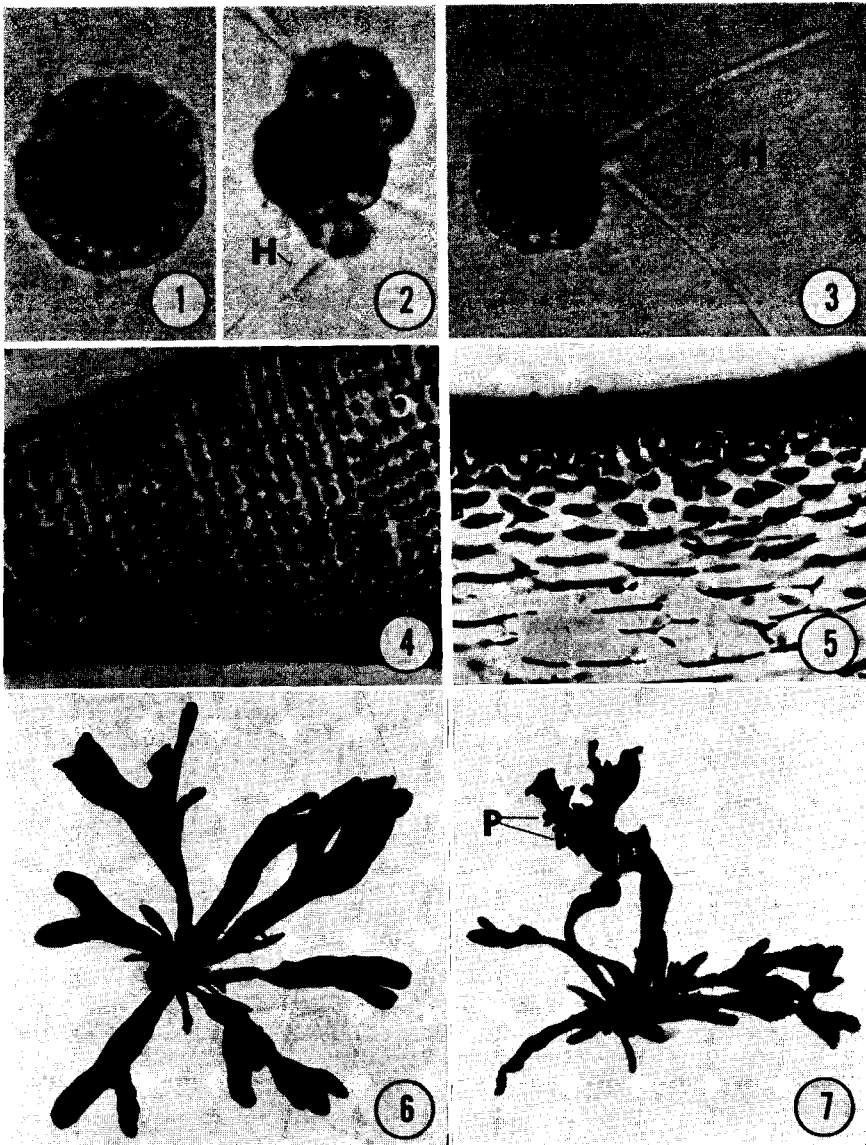
The conditions under which crosses of male and female blades were maintained and the preparation of semi-permanent slides for anatomical observations were described previously (Polanshek & West, 1975). Voucher material of the *Petrocelis cruenta* used in this study, consisting of dried specimens and semi-permanent slides, has been deposited in the Herbarium of the University of California, Berkeley (UC).

Male and female gametophytes of *P. middendorffii* used in this study were obtained by culturing tetraspores from plants collected at the following localities: Agua Blanca, Baja California; Rockaway Beach, California (West, 1972); Agate Beach, California; The Bodega Marine Laboratory, California; Simpson Reef, Oregon and Amchitka Island, Alaska (Polanshek & West, 1975).

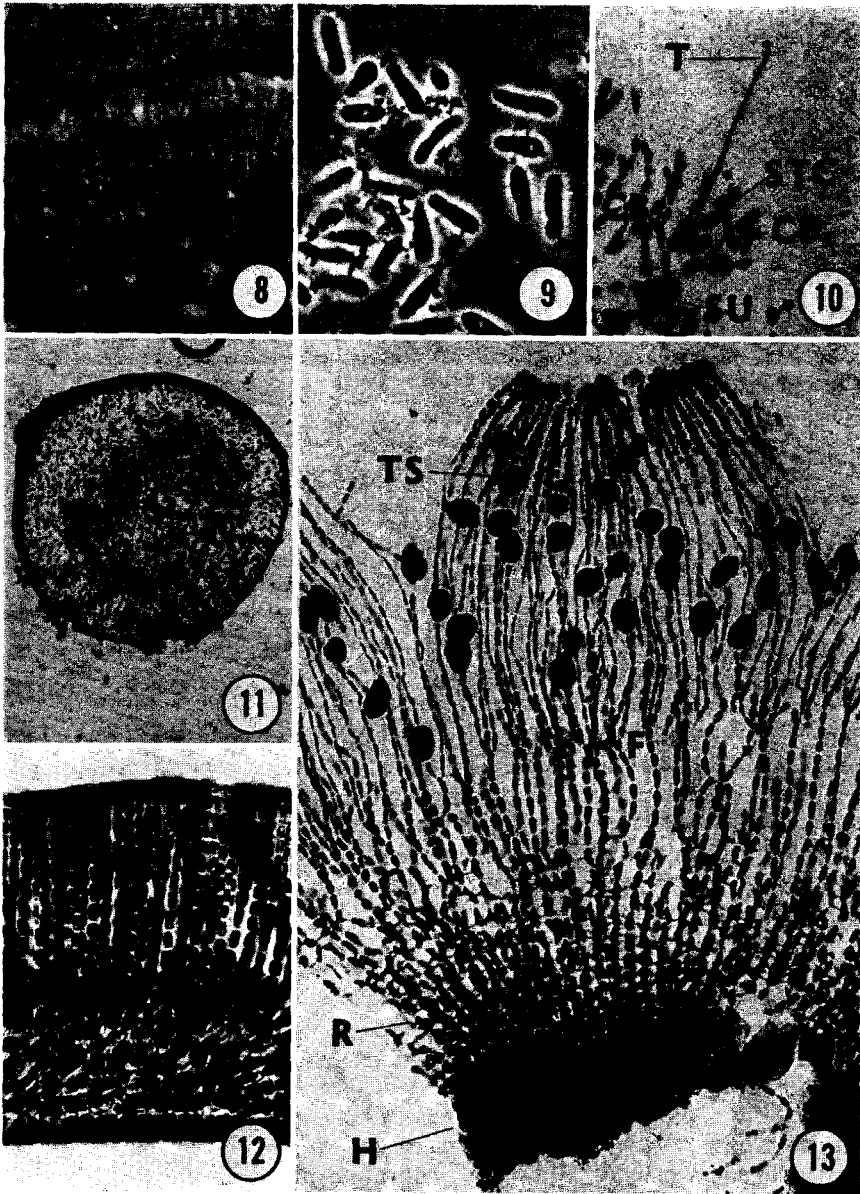
RESULTS

Tetraspores of *Petrocelis cruenta* averaged 13 µm diameter. Tetraspore germination and early germling development were similar to those described for *P. franciscana* (West, 1972) and *P. middendorffii* (Polanshek & West, 1975) and for carpospores of *Gigartina* subgenus *Mastocarpus* (Chen et al., 1974; Polanshek, 1975) and resulted in both discoid and spherical germlings (Figs 1, 2). Some germlings produced hyaline, unicellular hairs at 2 weeks (Figs 2, 3), a phenomenon described previously for *Chondrus crispus* Stackhouse (Chen & McLachlan, 1972; Prince & Kingsbury, 1973) but not for species of *Petrocelis* or *Gigartina* subgenus *Mastocarpus*. Further growth resulted in basal discs composed of a basal layer of cells and vertical filaments of cells with numerous secondary pit connections between cells of adjacent filaments (Fig. 4). By 6 weeks about half of the plants (average diameter 350 µm) had produced a single erect blade from the centre of the basal disc. Additional blades were produced subsequently as the area of the basal discs increased. Anatomically, blades were composed of a filamentous medulla and a cortex of dichotomously branched filaments of small, pigmented cells (Fig. 5), and were similar to *Gigartina*-phase gametophytes cultured from tetraspores of *P. middendorffii* (Polanshek & West, 1975; West, 1972). Blades, 15 mm in length, branched dichotomously after 5 months; with further growth blades became two to three times dichotomous (Fig. 6). Individual plants derived from single tetraspores of *P. cruenta* were either male or female (Figs 6, 7).

Male plants with spermatangial sori covering much of the blade were observed after 8 months (Fig. 8). Large numbers of elongate spermatia were released



FIGS 1-7. Plants cultured from tetraspores of *P. cruenta*. Fig. 1. Discoid germling at 33 days. $\times 650$. Fig. 2. Spherical germling with unicellular hairs (H) at 33 days. $\times 700$. Fig. 3. 33 day germling with hairs (H). $\times 500$. Fig. 4. Radial section through basal disc. $\times 400$. Fig. 5. Longitudinal section through blade. $\times 512$. Fig. 6. Male gametophyte at 9 months. $\times 1.8$. Fig. 7. Female gametophyte with papillae (P), 9 months. $\times 1.8$.



FIGS 8–11. Plants cultured from tetraspores of *P. cruenta*. FIG. 12. Plant cultured from carpospores of cultured gametophyte. FIG. 8. Section through old spermatangial sorus showing spermatangia (S). $\times 800$. FIG. 9. Released spermatia. Phase optics. $\times 800$. FIG. 10. Procarp. Supporting cell (SU); carpogonial branch cells (CB₁, CB₂); sterile cells (STC); trichogyne (T). Squash preparation. $\times 320$. FIG. 11. L.S. of mature cystocarp illustrating gonimoblast (G) and lack of specialized inner pericarp. $\times 120$. FIG. 12. Radial section through second generation *Petrocelis*-like crust. $\times 256$. FIG. 13. Section through voucher specimen of *P. cruenta*, Karo preparation. Note that the hypothallium is incomplete. Hypothallium (H); reticulate zone of perithallium (R); free filaments of perithallium (F); tetrasporangia (TS). $\times 256$.

forming an opaque, white film around the blades. Spermatia (Fig. 9) were similar to those described previously for *P. middendorffii* (Polanshek & West, 1975).

Female plants produced papillate outgrowths from blade surfaces and margins (Fig. 7). Procarps (the female gametangial apparatus) similar to those described for the *Gigartina*-phase of *P. middendorffii* (Polanshek & West, 1975; West, 1972) and *G. stellata* (Chen et al., 1974; Edelstein et al., 1974) were produced in papillae of some plants after 9 months. Procarps (Fig. 10) consisted of a large supporting cell and a three-celled carpogonial branch. Sterile cells were borne on the first cell of the carpogonial branch and occasionally on the second. Far fewer procarps were present on the papillae of *P. cruenta* female gametophytes than on papillae of *P. middendorffii*. Reproduction occurred less regularly in these *P. cruenta* gametophytes than in those of *P. middendorffii* from the Pacific. Frequently, after a short period of spermatangium or carpogonial branch formation the blades again became vegetative and failed to reproduce further. In squash preparations the procarps, particularly the carpogonium, were often in a state of decomposition. Cells of the procarp were occasionally penetrated by filaments from the surrounding cortex as was described previously for *P. franciscana* (West, 1972).

After 10 months cystocarps were observed on one female plant in a mixed culture of male and female plants. Mature cystocarps lacked a specialized inner pericarp (Fig. 11). A tissue resembling a pericarp was observed in one old, discharged cystocarp. Female plants established in single culture did not produce cystocarps while isolated. Carpospores gave rise to *Petrocelis*-like crusts (Fig. 12), now (May, 1976) up to 9 mm diameter.

Crosses between male and female gametophytes of *P. cruenta* with those of *P. middendorffii* from the North Pacific proved negative. Most crosses were tried only once. The irregularity of reproduction of *P. cruenta*, particularly of the female gametophytes, has prevented a systematic approach to hybridization experiments. We have been unable to use the format described previously (Polanshek & West, 1975; Proctor et al., 1967) for checking gamete viability in hybridization experiments. These preliminary results suggest, however, that *P. cruenta* from Ireland is reproductively isolated from the North Pacific *P. middendorffii*.

During the course of this study we observed a yellow tinge in old *P. cruenta* cultures. Presumably the substance causing this coloration is produced by the alga. The substance reacts positively with Bentamine Fast 2G (Sieburth & Jensen, 1969) and may be a polyphenolic compound. Additional investigations into the chemical nature of this substance are in progress. A similar phenomenon was also observed in our cultures of *G. stellata*, but not in cultures of Pacific species of *Petrocelis* or *Gigartina* subgenus *Mastocarpus*.

DISCUSSION

We will address our discussion to two principal questions that arise from the demonstration of this life history. (1) What is the naturally occurring gametophyte of *Petrocelis cruenta*? (2) Do *P. cruenta* and *P. middendorffii* represent distinct species?

The gametophytes cultured from tetraspores of *P. cruenta* may be characterized as follows: the dichotomously branched blades arising from the basal holdfast are multiaxial with a filamentous medulla and a cortex of dichotomously branched filaments. Male plants bear spermatangia in continuous sori on both blade surfaces. The three-celled carpogonial branches have sterile cells and are borne only in papillate outgrowths from the blades of female plants. Mature cystocarps lack an inner pericarp. This combination of characters indicates that the naturally occurring gametophyte of *P. cruenta*, like that of *P. middendorffii* (including *P. franciscana*), is a species of *Gigartina* subgenus *Mastocarpus* as defined by Kim (1976).

Gigartina stellata is the only species of subgenus *Mastocarpus* recorded from Ireland. A survey of the literature shows that the European distributions of *G. stellata* and *P. cruenta* are similar, ranging from Morocco to Norway (Ardré, 1969; Feldmann, 1954; Gayral, 1958; Hauck, 1885; Newton, 1931; Kjellman, 1883). As with other species of subgenus *Mastocarpus*, tetrasporangial plants of *G. stellata* are unknown in nature. Both male and female plants have been reported for British populations of *G. stellata*, the species apparently being dioecious (Marshall et al., 1949). Although the dioecious nature of this species is circumstantial evidence of a sexual life history, culture studies of *G. stellata* from Nova Scotia (Chen et al., 1974; Edelstein et al., 1974) and from Scotland, Wales and Maine (West & Polanshek, 1975) showed that carpospores usually give rise to successive generations of cystocarpic plants in what is construed as an apomictic life history (Chen et al., 1974). However, in one instance, carpospores from *G. stellata* collected in Wales gave rise to both *Petrocelis*-like crusts and *Gigartina* plants (West & Polanshek, 1975).

The postulated apomixis in *G. stellata* does not eliminate the possibility of sexual reproduction in this species as well. Polanshek (1975), using cultures of carpospores and blade apices from individual field-collected plants, demonstrated that California populations of *G. papillata* consist of two types of cystocarpic (female) plants; some that give rise to successive generations of cystocarpic plants and others that alternate with *Petrocelis*-like crusts. An analogous situation may exist with respect to *G. stellata*. Hybridization experiments demonstrated the interfertility of field-collected male and female sexual plants of *G. papillata* with *Gigartina*-phase gametophytes cultured from tetraspores of *P. middendorffii*, linking *G. papillata* to the life history of *P. middendorffii* in central California. It should be possible to test the assumed relationship of *G. stellata* to the life history of *P. cruenta* using culture and hybridization studies.

Marshall et al. (1949) reported monoecious plants of *G. stellata*. At present we are unable to speculate on the origin or role of monoecious plants in the life history.

The type locality of *P. middendorffii* (the Okhotsk Sea) is in the North Pacific, but this species has also been reported from the North Atlantic (Collins, 1908; Kjellman, 1883; Taylor, 1957). Kjellman (1883) and Collins (1908) characterized specimens from the Polar Sea and from New England, respectively, as *P. middendorffii* primarily on the basis of a strongly developed basal layer. This layer constituted half to two-thirds of the thallus thickness in specimens from New England (Collins, 1908). We have not had the opportunity to study specimens from either the Polar Sea or Atlantic North America.

Petrocelis middendorffii from Amchitka Island and *P. cruenta* from Ireland are similar anatomically. Both consist of three tissue layers: a densely cellular hypothallium, a reticulate lower perithallium formed by secondary pit connections between the vertical filaments of cells and an upper perithallium of loosely coherent filaments of cells (Fig. 13; see also Denizot, 1968). In specimens of *P. middendorffii*, overall thallus thickness ranged from 250 μm to 1.1 mm; thickness of the hypothallium from 50 to 175 μm . The hypothallium constituted less than a quarter of the total thickness of the plant. In specimens of *P. cruenta* from Ireland total crust thickness was about 700–800 μm and thickness of the complete hypothallium was 300–400 μm , approximately half of the total crust thickness. Thus, contrary to the characterization of these species by Kjellman (1883) and Collins (1908), it appears that greater development of the hypothallium may be characteristic of *P. cruenta*, not of *P. middendorffii*. In terms of hypothallium development, plants from Atlantic North America and the Polar Seas appear to correspond more closely to *P. cruenta* than to *P. middendorffii*. At this time we are unable to assess the influence of environmental factors on the morphology and anatomy of *Petrocelis*.

If one accepts the following working hypothesis there is a good reason why specimens from the Polar Sea and from Atlantic North America probably represent *P. cruenta* rather than *P. middendorffii*. Previous studies indicate that *P. middendorffii* from the North Pacific alternates with species of *Gigartina* subgenus *Mastocarpus* in a sexual life history. *G. stellata* is the only species of subgenus *Mastocarpus* currently recognized in the North Atlantic. The relationship between *Gigartina coronopifolia* (Zoega) Silva from Iceland (Silva, 1952; Zoega, 1775) and *Gigartina stellata* from other regions of the North Atlantic cannot be resolved at present. We propose that *G. stellata* probably represents the naturally occurring gametophyte of *P. cruenta*. If this can be demonstrated, then the question is: what species of subgenus *Mastocarpus* represents the alternate phase of *P. middendorffii* if the latter occurs in the North Atlantic?

Having demonstrated the occurrence of foliose gametophytes in the life histories of *P. middendorffii* and *P. cruenta* we can make comparisons between the gametophytes cultured from tetraspores of these two species. In the case of *P. cruenta* it should be emphasized that we have cultured tetraspores of only one collection of plants from one locality. (1) Some tetraspore germlings of *P. cruenta* produce hyaline hairs while those of *P. middendorffii* do not. (2) Cultured gametophytes of *P. cruenta*, but not *P. middendorffii*, liberate a yellow substance into the culture medium. (3) Female gametophytes of *P. cruenta* produce far fewer procarys per papilla than do those of *P. middendorffii* grown under the same conditions. (4) Cultured gametophytes of *P. middendorffii* from the North Pacific develop surface calcification (aragonite) under certain conditions. Generally *P. cruenta* does not show the same tendency. That this may be indicative of genetic differences between the species seems to be confirmed by results of our preliminary hybridization experiments; we found no signs of interfertility between cultured gametophytes of *P. cruenta* and those of *P. middendorffii*. We believe that the differences between the gametophytes and sporophytes of the two species support the continued recognition of *P. cruenta* and *P. middendorffii* as distinct species.

Certain areas of future study are indicated. *P. cruenta* should be cultured

from throughout its known range, particularly from the type locality (Brest, France), to confirm the life history reported here. Variation in morphological, anatomical and reproductive characteristics should be determined more accurately to circumscribe the species. Hybridization experiments should be undertaken to evaluate the genetic continuity of the species. These studies are a necessary basis for a comparison of *P. cruenta* with those plants from Atlantic North America and the Polar Sea that have been attributed to *P. middendorffii*.

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