

A Revision of the Species of the Algal Genus *Porphyra* Occurring on the Pacific Coast of North America¹

V. KRISHNAMURTHY²

THE GENUS *Porphyra* was created by C. Agardh (1824) to include the species of "*Ulva*" which possessed red pigment. Since then a number of authors have added to our knowledge of the different species of the genus throughout the world. A perusal of the literature, however, shows a number of taxonomic uncertainties which need to be cleared up. One of the problems in the taxonomy of this genus is the evaluation of criteria which will be reliable in the recognition of the different species.

One of the earliest criterion to be established was the number of layers of cells composing the leafy thallus and J. G. Agardh (1882) distinguished between monostromatic and distromatic species. Kjellman (1883) named the distromatic species as *Diploderma* whereas de Toni (1897) named them *Wildemannia*. The latter name has been dropped by subsequent authors. Rosenvinge (1893) united *Diploderma* under *Porphyra* pointing out that the distromatic species may frequently be monostromatic in portions of the frond and they could hardly be distinguished in such stages. However, he retained the name *Diploderma* at a subgeneric level. This has been supported by Hus (1902). However, the distromatic nature of the frond in such species is more constant than it was held to be by these earlier authors.

In this connection, it may be pointed out that J. G. Agardh (1882) listed under the "Monostromaticae" such forms as *P. miniata* and under "Distromaticae," forms such as *P. umbilicalis*, *P. perforata*, *P. columbina*, *P. linearis*, and *P. amethystea*. These species are monostromatic, whereas *P. miniata* is distromatic. De

Toni (1897) followed J. G. Agardh and listed *P. miniata* under *Porphyra* and the rest under *Wildemannia*. Rosenvinge (1893) pointed out in a footnote to *P. umbilicalis* J. Ag. that J. G. Agardh had included this species incorrectly under "distromaticae," probably because he did not recognize the fruiting portion of the thallus. However, this does not explain the other species referred by Agardh to the "Distromaticae"; there was probably an error in printing or in the manuscript.

The account of the species of *Porphyra* found on the Pacific coast of North America by Hus (1902) marked an important advance in our knowledge of the genus. The significance of the mode of division of reproductive cells of the frond in the diagnosis of species was first realized by this author and he gave formulas for the modes of division leading to formation of "carpospores" and "antherozoids." He described four types based on these formulas. He also pointed out that the first division leading to the formation of carpospores is perpendicular to the surface of the thallus, a fact very frequently overlooked by authors describing the morphology of the genus. The second division is also perpendicular but occurs at right angles to the first in each of the two sister cells. These two divisions are designated "cruciate division" by Hus. He considered the corresponding divisions leading to the formation of spermatia as vegetative, however, and stated that four antheridia are formed corresponding to one sporocarp. In each antheridium, according to him, the first division is *parallel* to the surface of the thallus.

Hus considered "cruciate" and "parallel" divisions as occurring alternately in the mother cell of a sporocarp or a group of antheridia until the characteristic number of "carpospores" or "antherozoids" was reached. If the mother cell were considered as a cube, there would be three planes of division—two across the surface

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² Friday Harbor Laboratories, Friday Harbor, Washington 98250. Present address: Marine Algal Research Station, Mandapam, Tamilnadu, India.

of the thallus and one across the height of the cell. If the sides of the mother cell are designated a , b (surface) and c (height), the spore formula will indicate the number of divisions along each side, for example: $a/2$, $b/2$, $c/2 = 8$ or $a/4$, $b/4$, $c/2 = 32$. On the other hand, the first "cruciate" division of "antherozoids" is considered vegetative, so the sides a and b of an antheridium will be just half the corresponding sides of a sporocarp. The formulas will then be: $1/2a/4$, $1/2b/4$, $c/8 = 128$, etc. Later authors seem to have dropped the $1/2$ in the formulas for spermatia and considered each spermatangium as a unit; this eliminates a possible complication, but I have not seen anywhere an explanation of this change. Tanaka (1952) lays great emphasis on the spore formula to the exclusion of all other criteria in determining specific limits. This has been followed by a number of workers, notably from Japan. Dawson (1944, 1952) also made use of this criterion. However, a close examination of the mode of division of sporogenous cells in different species of *Porphyra* shows that the spore formula can not be used strictly in determining the mode of formation of the spores and, ultimately, the number of spores obtained from one mother cell.

It has already been pointed out by Hus (1902) that the division of a spore mother cell is frequently irregular, particularly in sporocarps, so that the total number of spores per sporocarp may vary within wide limits (e.g., eight to 32 or even 64 in *P. perforata* J. Ag.). Also, transverse or vertical divisions may really be oblique to the long axis of the cell, thereby obscuring the mode of division of the mother cell. This has also been reported by Krishnamurthy (1959) for *P. umbilicalis* var. *laciniata*. In addition to these complications, there is also the fact that only in mature sporocarps and spermatangia can the number of spores and spermatia be ascertained. In such mature stages, it is often difficult, especially in sporocarps, to observe the pattern of division. Very often the spores in a sporocarp become rounded up and form a more or less spherical mass. The pattern of division in spermatangia can be followed more easily. Even in spermatangia do oblique divisions take the place of the so-called "paral-

lel" divisions and the spore formula in such cases becomes doubtful. However, a cross section of the thallus in the sporocarpic or spermatangial region shows that the spores or spermatia are arranged in a definite number of horizontal tiers, these being more constant, easily recognized, and often characteristic of the species.

The above considerations show that the criteria used so far in the delimitation of species of *Porphyra* are not as reliable as they have been considered to be by earlier authors and a need does exist for new criteria. An extensive study of the species of *Porphyra* from the Pacific coast of North America indicated the existence of such criteria and it was found that these could be used in separating the species from one another. In the following account I propose to use these criteria.

Notwithstanding Rosenvinge's opinion (1909) that distromatic species often show a monostromatic condition, especially along the margin, my experience has been that the distromatic species of the Pacific coast of North America are constant in this character and the delegation of such species to the subgenus *Diploderma* is quite valid.

Tokida (1935) established a new subgenus *Diplastida* for *Porphyra onoi* Ueda in which certain parts of the thallus are monostromatic with two eccentrically placed chromatophores. It has also been pointed out that other parts of the thallus are distromatic and, in these regions, the cells contain single chromatophores. It would appear, therefore, that the subgenus *Diplastida* is really not valid. However, there are species of *Porphyra* on the Pacific coast in which the thallus is monostromatic and the cells contain two chromatophores each. The first such species to be described was *P. lanceolata* by G. M. Smith (Smith and Hollenberg, 1943) and two other species, *P. pulchra* (Smith and Hollenberg, 1943) and *P. smithii* (Hollenberg and Abbott, 1968) have since been added. To accommodate these species, I propose to recognize Tokida's subgenus *Diplastida* in an amended form even if *Porphyra onoi* Ueda, for which the subgenus was erected, is not to be included in it.

Thus one can distinguish three subgenera

under *Porphyra*, viz. *Euporphyra*, *Diplastida*, and *Diploderma*, and representatives of all three subgenera are to be found on the Pacific coast of North America.

Within each genus, the occurrence of sporocarps and spermatangia on the same thallus or on different thalli has been recognized as a criterion by several workers (Hus, 1902; Kjellman, 1883, 1889, 1897; Smith and Hollenberg, 1943; Dawson, 1944, 1952; Tanaka, 1952). However, it was pointed out by Rosenvinge (1909) that the so-called dioeciousness in *Porphyra* is not always true and that some species may be producing spermatangia in the younger stages and sporocarps when mature. Cases have been reported where sporocarps and spermatangia occur in well-defined parts or segments of the thallus in species commonly showing dioeciousness. Such intersex plants (called andro-dioecious by Tanaka, 1952) occur in *P. purpurea*, *P. amplissima*, *P. variegata* sensu Tanaka, *P. helena*, etc. But the presence of such intersex plants does not negate the occurrence of dioeciousness. A number of species of *Porphyra* from the Pacific coast of North America are dioecious without any evidence of intersex plants: *P. lanceolata*, *P. pendula*, *P. hollenbergii*, *P. linearis*, *P. schizophylla*, and *P. norrisii*. Other species in this area are, by inference, dioecious: *P. sanjuanensis*, *P. variegata*, *P. occidentalis*. Therefore, it is possible to distinguish between three groups of species on the basis of this criterion: (1) monoecious species, (2) dioecious species, and (3) dioecious species with frequent occurrence of intersex plants. In the last group, however, the plants are predominantly dioecious.

Another important character which is of considerable taxonomic significance is the pattern of distribution of sporocarps and spermatangia on the thallus. These tend to form (1) continuous marginal zones, (2) extensive but discontinuous marginal zones, (3) marginal patches and streaks, and (4) submarginal patches, streaks, and spots. In monoecious species, the spermatangia may form patches, streaks, and spots which are distributed in a general zone of sporocarps. In some species, both sporocarps and spermatangia form a mosaic of small

patches intermingled with vegetative cells. These different patterns of distribution of reproductive cells constitute a good criterion in the recognition of several species.

Of minor taxonomic importance are the nature of the attaching organ and the nature of the thallus margin which may be smooth or toothed or crenulate or strongly ruffled. In one species, *P. torta*, the thallus shows a strong midrib about which it is twisted and, in section, shows internal rhizoids in the midrib portion.

The first record of *Porphyra* from North America is that of Harvey (1841) under the name of *P. vulgaris* C. Ag. This same alga was later assigned to *P. perforata*. Subsequently Ruprecht (1852) recorded *P. umbilicata* from the northern part of the Pacific Ocean.

It was Hus (1900, 1902) who gave a detailed account of 15 species of *Porphyra* occurring on the Pacific coast of North America. Various amendments and additions have been made since then. Smith (Smith and Hollenberg, 1943) raised the status of *P. perforata* f. *lanceolata* and described *P. lanceolata*, while Hollenberg (Smith and Hollenberg, 1943) described *P. pulchra* and *P. schizophylla*. Hollenberg (1959) erected a new genus, *Smithora*, for *Porphyra naiadum* Anderson. Dawson (1944) described *P. thuretii* Setchell & Dawson based on specimens referred earlier by Hus (1902) to *P. leucosticta* Thur. He also described two new species, *P. pendula* and *P. hollenbergii* (Dawson, 1952). Hollenberg and Abbott (1968) found that some specimens earlier referred to by Smith (1944) as *P. pulchra* were really quite different and for these they created a new species *P. smithii*. Hollenberg and Abbott (1966) also placed *P. variegata* sensu Hus under *P. occidentalis* Setchell & Hus.

Thus, when this study was made, 17 species of *Porphyra* already had been recorded from the Pacific coast of North America.

When I first began collecting the species of *Porphyra* from the San Juan group of islands, I observed that there were several undescribed species on these shores. Also, some of the described species showed characters which indicated their being distinct. Hence I undertook

a revision of the species of *Porphyra* on the Pacific coast of North America and the following account is based on this work.

Specimens of *Porphyra* were collected from various islands of San Juan archipelago, Seattle, San Francisco, Pacific Grove, Carmel Bay, and La Jolla. A number of specimens were examined from the herbaria of the University of British Columbia, Vancouver; University of Washington, Seattle; University of California at Berkeley, where most of the specimens used by Hus in his studies are located; John Hopkins Marine Station, Pacific Grove; Scripps Institution of Oceanography, La Jolla; and Smithsonian Institution, Washington, D.C. Specimens from the Pacific coast of North America were also seen in the Agardh Herbarium at Lund and these were critically examined. Dr. Richard E. Norris kindly placed a collection of *Porphyra* from the state of Washington at my disposal.

In all, about 800 specimens of *Porphyra* were examined critically in determining the species occurring on this coast.

Many of the recorded species had to be studied critically with reference to type specimens. For some of the species, type had not been designated by the original author and a lectotype had to be selected. Type specimens were examined whenever possible. In cases where these were not available, authentic specimens were examined. Lectotypes were selected whenever necessary. In this work, I was greatly helped by my visits to various herbaria and institutions in Europe, particularly the British Museum (Natural History), London; Naturhistoriska Riksmuseet, Stockholm; University of Uppsala, Uppsala; Agardh Herbarium, University of Lund, Lund; Botanical Gardens, Copenhagen; Riksherbarium, Leiden; and Muséum (national) d'histoire naturelle, Paris.

KEY TO THE SPECIES OF *Porphyra* OCCURRING ON THE
PACIFIC COAST OF NORTH AMERICA

- I. Thalli monostromatic, with a single chromatophore in each cell Subgenus *Euporphyra*
- 1a. Plants monoecious 2
- 1b. Plants dioecious 12
- 2a. Spermatangia strictly marginal 3
- 2b. Spermatangia either submarginal or both marginal and submarginal 7
- 3a. Spermatangia in a continuous marginal zone 4
- 3b. Spermatangia in marginal patches 5
- 4a. Thalli without umbilicate base *P. purpureo-violacea*
- 4b. Thalli with umbilicate base *P. umbilicalis*
5. Spores up to 32 in packet, in continuous patches without areas of vegetative cells between them 6
- 6a. Thalli delicate scarlet, epiphytic on the larger subtidal brown seaweeds; spermatangia with spermatia in a single group *P. nereocystis*
- 6b. Thalli small, grey to reddish brown, intertidal; spermatangia with spermatia in two overlying groups *P. segregata*
- 7a. Spermatangia in streaks; spermatia in two overlying hemispherical groups 8
- 7b. Spermatangia in spots or irregular patches 9
- 8a. Spermatangial streaks narrow; plants a delicate red *P. thuretii*
- 8b. Spermatangial streaks broad; plants green to reddish brown *P. abbottae*
- 9a. Sporocarpic region generally continuous, without intervening areas of vegetative cells; spermatangia in spots *P. fucicola*
- 9b. Sporocarpic region mottled, with intervening areas of vegetative cells; spermatangia in irregular patches 10
- 10a. Spores in two tiers or occasionally four tiers 11
- 10b. Spores in more than four tiers; plants twisted with strongly ruffled margins *P. torta*

- 11a. Plants growing in lower intertidal; grey to reddish brown *P. perforata*
 11b. Plants growing at high intertidal; vegetative portions blue-green; sporocarpic margin scarlet *P. perforata* f. *patens*
 12a. Plants apparently dioecious, spermatangia not known *P. sanjuanensis*
 12b. Spermatangia in a yellowish continuous marginal zone 13
 13a. Thallus divided into several linear-lanceolate blades *P. hollenbergii*
 13b. Thallus undivided or rarely once divided at base 14
 14a. Thallus with unruffled margin, distinctly stipitate *P. linearis*
 14b. Thallus with ruffled margin *P. pendula*
- II. Thalli monostromatic, with two chromatophores in each cell Subgenus *Diplastida*
- 1a. Plants monoecious 2
 1b. Plants dioecious, occasionally monoecious with male and female portions clearly marked by a sharp line *P. lanceolata*
 2a. Sporocarpic region mottled, with intervening areas of vegetative cells; spermatangia in submarginal streaks *P. pulchra*
 2b. Sporocarpic region more uniform without intervening areas of vegetative cells; spermatangia in marginal and submarginal spots *P. smithii*
- III. Thalli distromatic Subgenus *Diploderma*
- 1a. Thallus always distromatic 2
 1b. Thallus monostromatic in marginal portions *P. abyssicola*
 2a. Plants monoecious 3
 2b. Plants dioecious 6
 3a. Spermatia in 16 tiers *P. papenfussi*
 3b. Spermatia in four tiers or less 4
 4a. Spermatia in four tiers *P. amplissima*
 4b. Spermatia in two tiers 5
 5a. Thallus 30 to 75 μ thick with crenulate margins *P. cuneiformis*
 5b. Thallus 35 μ thick, with smooth margins *P. tenuissima*
 6a. Gelatinous matrix of thallus with conspicuous line of separation between the two layers of cells 7
 6b. Gelatinous matrix of thallus without conspicuous line of separation between the two layers of cells 8
 7a. Cells pyriform, gelatinous matrix with eccentric stratifications internal to each cell *P. schizophylla*
 7b. Cells more or less rectangular, gelatinous matrix not stratified *P. norrisii*
 8a. Cells with stratified cell wall *P. variegata*
 8b. Cells with cell wall not stratified *P. occidentalis*

Porphyra abbottae sp. nov.

Figs. 1-2

Plantae saxicolae, sessiles, irregulariter expansae laciniataeque, basi cordata, margine multum corrugato. Plantae monoeciae, usque ad 60 cm long., usque ad 25 cm lat. Frons rubellow-brunnea, in parte media olivacea. Thallus monostromaticus, partibus in vegetativis 52-56 μ crass., in areis reproductivis 56-65 μ crass. Cellulae vegetativae a superficie visae polygo-

nales, usque ad 27 μ dimensione maxima; in sectione 35-38 μ alt, 17-27 μ lat. Chromatophorus singulus, pyrenoidem manifestam atque brachia tenuia quae usque ad periferiam cytoplasmatis extendunt et hic replicantur habens. Zona fertilis a apice margineque, plerumque usque ad 10 cm introrsus extensa. Spermatangia lineas magnas irregulares latas submarginales superficialesque apud sporocarpos efficientia. Cellulae vegetativae in zona fertili nullae. Sporae plerumque 8 in duobus ordinibus,

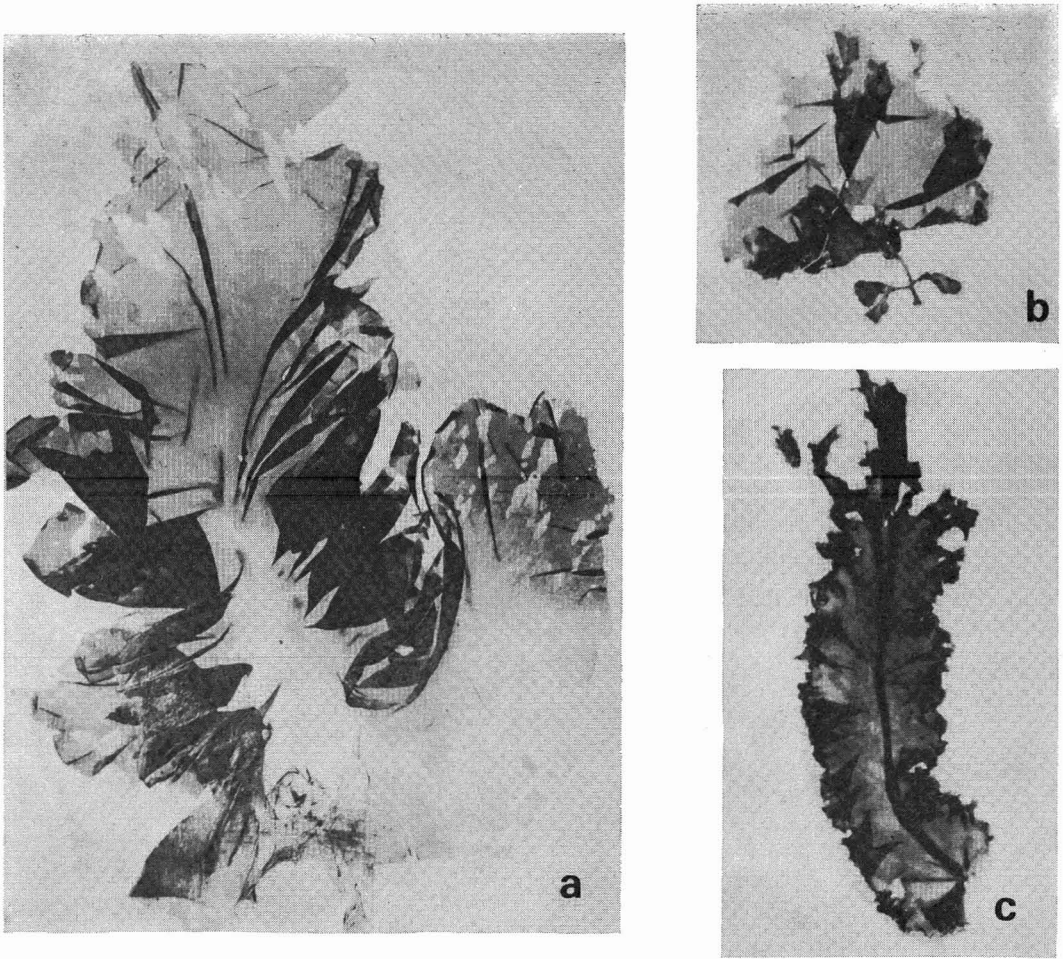


FIG. 1. a, *Porphyra abboitae*; b, *Porphyra fucicola*; c, *Porphyra torta*.

rarissime 16 per divisionem obliquam cellularum duorum ordinum effectae. Spermata plerumque 32, saepe 64, in 8 ordinibus, in duabus aggregationibus superiacentibus, omni e 4 ordinibus composita, dissepimento satis crasso seiunctis disposita.

Planta typica a Krishnamurthy (no. 11-00154) e loco Cattle Point, San Juan Island dicto, m. Mai, d. 26, 1968 lecta; in Herbario Departmenti Botanici Universitatis Washingtonensis, Seattle deposita.

Plants saxicolous, sessile, irregularly expanded and lacinate with a cordate base and much ruffled margin. Plants monoecious, up to 60 cm long, up to 25 cm broad. Color of the

frond reddish brown, olive green in the median portion. Thallus monostromatic, 52 to 56 μ thick in vegetative portions, 56 to 65 μ thick in reproductive areas. Vegetative cells in surface view polygonal, up to 27 μ in the greatest dimension, in section, 35 to 38 μ in height and 17 to 25 μ in width. Chromatophore single, with prominent pyrenoid and slender arms extending to and folded at the periphery of the cytoplasm. Fertile zone extending from the apex and margin inward, frequently up to 10 cm. Spermata forming large irregular and broad submarginal and superficial streaks among the sporocarps. No vegetative cells in the fertile zone. Spores usually eight in two tiers, very rarely 16 by oblique division of the cells of the

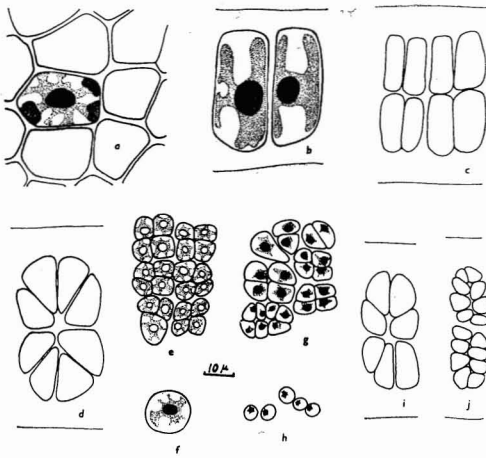


FIG. 2. *a-j*, *Porphyra abbottae* sp. nov. *a*, Surface view of frond showing details of structure in one cell; *b*, cells in vertical section of the frond; *c*, section through sporocarpic portion of the frond showing division into two layers of cells; *d*, further division in the sporocarpic cell, giving rise to eight spores; *e*, surface view of sporocarpic region of the frond; *f*, a single spore; *g*, surface view showing divisions leading to formation of a spermatangial sorus; *h*, spermatia; *i*, section of a spermatangium showing early divisions, the separation of spermatia into two groups being already evident; *j*, a fully developed spermatangium.

two tiers. Spermatia usually 32, frequently 64, in eight tiers, arranged in two overlying groups of four tiers each, separated by a fairly thick cross wall.

Type

Krishnamurthy no. 11-00154 from Cattle Point, San Juan Island, 26 May 1968, deposited in the herbarium, Department of Botany, University of Washington, Seattle.

Distribution

Southern and western coasts of San Juan Island.

Discussion

This species comes closest to *P. thuretii* in the distribution of sporocarps and spermatangia and also in the fact that the spermatia occur in two overlying groups. However, the shape and color of the frond are very different from the characteristic shape and color of *P. thuretii*. Moreover, the base of the frond in *P. abbottae* is not stipitate. Another difference is that the frond of *P. abbottae* is 52 to 56 μ in thickness

in the vegetative portions, while it is thicker, 56 to 65 μ , in the fertile portions. These features are so constant that I have no hesitation in describing the present form as a new species. I have great pleasure in naming the alga after Dr. Isabella A. Abbott, with whom I had valuable discussions about the taxonomy of *Porphyra*.

Porphyra abyssicola Kjellman

In Kjellman, 1883, p. 240, pl. 17, fig. 4; pl. 18, figs. 10–11. Hus, 1902, p. 223.

Plants epiphytic on *Zostera*, sessile or with a small disc, frond broadly lanceolate to obovate with undulate margin and cuneate base; color a livid cerise; distromatic, but frequently monostromatic, 25 μ thick; cells of the middle of the thallus square or nearly twice as long as broad, with rounded angles; fronds monoecious or dioecious; when monoecious spermatangia and sporocarps intermixed in a marginal zone, sporocarp with two–four spores in a single tier; spermatangium with eight spermatia in two tiers.

Type

Type has not been traced.

Type Locality

Norwegian Sea.

Distribution

Species is found on Pacific coast of North America: southern British Columbia to northern Washington; Victoria, British Columbia; Whidbey Island; Friday Harbor, San Juan Island.

General Distribution

Norwegian Sea; Barents Sea; White Sea; Baffin's Bay; Pacific coast of Canada and northern United States.

Discussion

I have not been able to collect this species, although Scagel (1957) records it from Victoria, Whidbey Island, and Friday Harbor. Kylin (1925) states that he could not collect this alga either. The specimen cited by Hus (1902) was collected by N. L. Gardner from Whidbey Island and is lodged in the her-

barium of the University of California at Berkeley under no. NLG 273. I made a detailed examination of this specimen and found that the frond is distromatic to a large extent and bears only sporocarps. But I could not connect this form with *P. miniata* f. *cuneiformis* as suggested by Kylin (1925).

The type of this species is not available either at Uppsala or at Stockholm where I could find the types of all species described by Kjellman from Japan. Rosenvinge (1893) considered this to be only a form of *P. miniata*. I have examined *Ulva miniata* Lyngbye which is the type of *Porphyra miniata*, at Copenhagen and also the specimen used by C. Agardh at Lund. The spore number and arrangement in these specimens are very different from those in the specimen at Berkeley. In *P. miniata*, there are eight spores arranged in two tiers and 32 spermatia in four tiers, whereas in *P. abyssicola*, there are only four spores in a single tier. According to Hus (1902) there are eight spermatia in a spermatangium, arranged in two tiers, formed by one cruciate division followed by a transverse division in each spermatangium.

Porphyra amplissima (Kjellm.) Setchell & Hus

In Hus, 1900, p. 67; 1902, p. 215, pl. 20, fig. 13 a-b.

Diploderma amplissimum Kjellman, 1883, p. 236, pl. 17, figs. 1-3; pl. 18, figs. 1-8.

Plants attached to stones, completely submerged at a depth of 4 to 6 feet; frond membranous 20-60 cm long, 10-15 cm broad, broadly elliptical to ovate lanceolate, with undulate and deeply folded margins; color, a deep red to reddish purple; base slightly cuneate or sometimes cordate, sessile, with a small disc; distromatic, 50-80 μ thick; cells in cross section square or higher than broad, with rounded angles; sheath 5-10 μ thick; monoecious, spermatangia and sporocarps intermixed in a marginal zone; sporocarp with four to eight spores; spermatangium with 16 spermatia in four tiers, later becoming a spherical mass.

Type

Kjellman's specimen should be the type. This specimen could not be traced, however.

Distribution on Pacific Coast of North America

Amaknak Island, Alaska, down to Neah Bay in northern Washington.

General Distribution

Arctic Sea, North Sea, Greenland, northern Pacific Ocean: Japan, Alaska, Canada, and northern Washington.

Discussion

Besides examining all the specimens cited by Hus (1902) I had the opportunity of collecting for myself a number of excellent specimens of this species on the shores of San Juan Island. The specimens range from 15 to 70 cm in length and up to 60 cm in breadth. They all have a distinctly cordate base and a minute disc by which the plant is attached. No instance of a cuneate base was seen. Sporocarps and spermatangia are intermingled in a narrow marginal zone, sometimes including a few vegetative cells also. Frequently a sporocarp and a spermatangium are found overlying each other in a cross section of the frond. In the fertile region of the frond are sometimes found "carpogonia" which arise by a modification in the shape of a cell of the frond. The cell destined to form a "carpogonium" becomes rounded and produces a stout conical prolongation on the side facing the surface of the frond, the "trichogyne." In all the specimens examined the sporocarp had only four spores in a single tier, whereas the spermatangium produced 16 spermatia in four tiers. As the spermatangium ripened, the arrangement in tiers became obscure and the spermatia then formed a roughly spherical mass inside the spermatangium.

Porphyra cuneiformis comb. nov.

In Hus, 1900, p. 68; 1902, p. 218.

P. miniata (Lyngb.) Ag. f. *cuneiformis* Setchell & Hus.

Plants attached by a small disc to shells in the lower intertidal region, often found floating, up to 70 cm long, 15 cm broad, with a frequently cuneate, sometimes cordate, base and crenulate margin. Color of the frond bright red. Thallus distromatic, up to 75 μ thick. Vegetative cells in surface view square to polygonal,

up to 14 μ in greatest dimension, in section square or rectangular, up to 14 μ in height and 7 to 14 μ in width. Sheath up to 12 μ thick. Thallus monoecious, sporocarps and spermatangia intermingled in a continuous marginal zone, uniform in color. Sporocarps with four spores in one tier. Spermatangia with eight spermatia in two tiers.

Type

N. L. Gardner no. 199 *a*, from Coupeville, Whidbey Island, Washington, deposited in the herbarium, Department of Botany, University of California at Berkeley.

Distribution

Pacific coast of North America, from Alaska to Monterey Bay, California.

Discussion

Hus (1900, 1902) described this alga as a form of *P. miniata*, differentiating it from the typical species by the cuneate base and the finely crenulate margin of the frond. As stated earlier, I have examined both Lyngbye's type of *Ulva miniata* and the specimen of the same before C. Agardh and, in the light of this, I define the characters of *P. miniata* thus: frond distromatic, broadly ovate-lanceolate to obovate, deep cerise in color, monoecious; sporocarps with eight spores arranged in two tiers and spermatangia with 32 spermatia in four tiers. From this it is clear that the form described by Hus is not *P. miniata* and should be placed in a new combination, *P. cuneiformis*.

The affinities of this species are with *P. amplissima* from which it differs in the cuneate basal portion and the crenulate margin. One should also recall the remark of Kylin (1925) that *P. abyssicola* from Whidbey Island looks similar to *P. miniata* f. *cuneiformis*.

Porphyra fucicola sp. nov.

Figs. 3, 4

Plantae in *Fuco epiphyticae*, sessiles irregulariter expansae, saepe lacineatae, lamina a basi plicata, margine levi. Plantae monoeciae, usque ad 10 cm long. et lat. Frons brunneo-rubra. Thallus monostromaticus, 50–60 μ crass. Cellulae vegetativae a superficie visae polygonales,

usque ad 14 μ dimensione maxima, in sectione 21–27 μ alt., et 10–14 μ lat. Chromatophorus singulus, paucissima brachia lata quae usque ad periferiam cytoplasmatis extendunt et hic replicantur habens. Sporocarpi in zona marginali continua, quae a regione thalli vegetativa satis inperspicue differentiatur effecti. Sporae plerumque 8 in duobus ordinibus. Spermatangia in maculas marginales parvas formata. Spermatia plerumque 64, matura in duobus aggregationibus superiacentibus hemisphericis disposita, dissepimento satis crasso seiunctis.

Planta typica a Krishnamurthy (no. 11-00121) a loco Makah Bay, Olympic Peninsula dicto, m. Mai, d. 13, 1968 lecta; in Herbario Departmenti Botanici Universitatis, Washingtonensis, Seattle deposita.

Plants epiphytic on *Fucus*, sessile, irregularly expanded and often lacinate, blade folded from the base, margin smooth. Plants monoecious, up to 10 cm long, as much wide. Color of the frond, brownish red. Thallus monostromatic, 50 to 60 μ thick. Vegetative cells in surface view polygonal, up to 14 μ in greatest dimension; in section, 21 to 27 μ in height and 10 to 14 μ in width. Chromatophore single, with very few broad arms extending up to and folded at the periphery of the cytoplasm. Sporocarps formed in a continuous marginal zone rather indistinctly marked off from the vegetative region of the thallus. Spores usually eight in two tiers. Spermatangia in small marginal spots. Spermatia usually 64, when ripe arranged in two overlying groups separated by a fairly thick cross wall.

Type

Krishnamurthy no. 11-00121 from Makah Bay, Olympic Peninsula, 13 May 1968, deposited in the herbarium, Department of Botany, University of Washington, Seattle.

Distribution

Northern Washington, San Juan Island, Olympic Peninsula.

Discussion

This species is similar in appearance to *P. segregata* (described later in this paper) but it can be distinguished from the latter by its

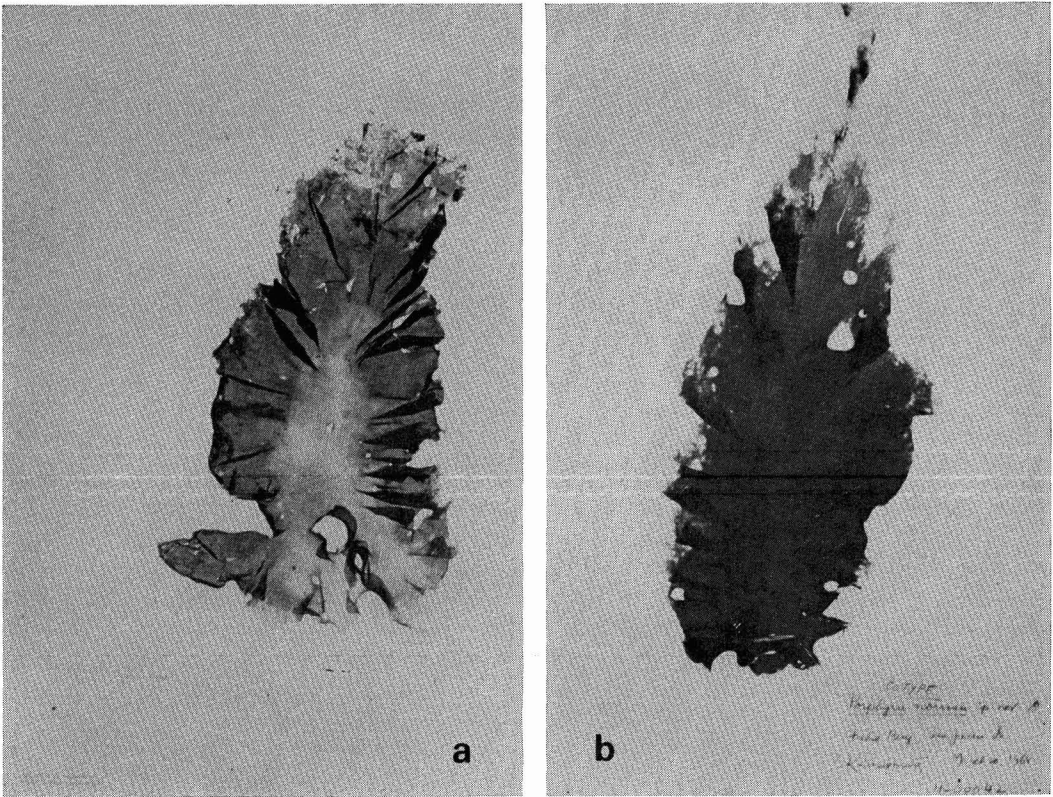


FIG. 3. *a*, *Porphyra norrisii*, sporocarpic plant; *b*, spermatangial plant.

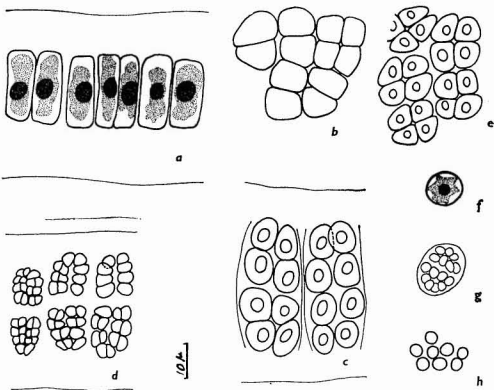


FIG. 4. *a-b*, *Porphyra fucicola* sp. nov. *a*, Section of vegetative frond; *b*, surface view of vegetative cells; *c*, section through sporocarps; *d*, section through spermatangia; *e*, surface view of sporocarps; *f*, a single spore; *g*, surface view of a ripe spermatangium; *h*, spermata.

constant appearance on *Fucus*, the occurrence of only eight spores in two tiers in each sporo-

carp, and the occurrence of spermatangia in small marginal spots. The fronds are delicate and not coriaceous as in *P. segregata*.

Porphyra hollenbergii Dawson

In Dawson, 1952, pp. 14–15, pl. 13, fig. 1.

Plants saxicolous, membranous, 6–15 cm high, consisting of several much ruffled lanceolate or linear lanceolate blades from a common basal area, attached by a small disc; blades 1.0 to 3.5 cm wide, monostromatic, 45–55 μ thick; cells in surface view polygonal up to 20 μ across, up to 23 μ in cross section; plants dioecious; sporocarps with eight spores in two tiers, spermatangia with 64 spermata in eight tiers, forming continuous marginal zones.

Type

Dawson 539–40, 12 February 1940, from upper littoral rocks, Bahia Agua Verde, Baja California (Gulf Coast), Mexico.

Distribution

Pacific Ocean off Mexico.

Discussion

I have examined isotype material both at the herbarium of the University of California at Berkeley and in U.S. National Museum, Smithsonian Institution, Washington, D.C. The alga is a distinctive species.

Porphyra lanceolata (Setchell & Hus) G. M. Smith

In Smith and Hollenberg, 1943, p. 213, figs. 8–10.

P. perforata f. *lanceolata* Setchell & Hus, in Hus, 1900, p. 69.

Plants saxicolous, membranous, 10–35 cm long, sometimes much longer, 1–10 cm broad, linear to lanceolate, with wavy margins, base cuneate to cordate, attached by a small disc, monostromatic, 75 to 150 μ thick, cells in cross section two to three times as long as broad, with two chromatophores in each cell; plants dioecious; sporocarps with 32 spores in four tiers; spermatangia with 128 spermatia in eight tiers.

Type

W. A. Setchell no. 3210 from Carmel Bay, Monterey, California, deposited in the herbarium of the University of California at Berkeley under no. 95720. This is one of the specimens used by Hus (1902).

Distribution

Species is found from northern Washington south to Carmel Bay, California. I collected this species once from Whidbey Island, in September 1967. Kylin (1925) recorded it from Kanaka Bay on San Juan Island as *P. perforata* f. *lanceolata* and it was he who first indicated that this form is a distinct species. However, he refrained from naming it and, eventually, it was described under its present name by G. M. Smith (Smith and Hollenberg, 1943). Hus (1902) mentioned having examined a large number of plants, but he apparently did not notice the presence of two chromato-

phores in each cell. Although the collections cited by Hus (1902) are all from California, there have been some records of this species north of this region (Kylin, 1925; Doty, 1947; Scagel, 1957).

Porphyra linearis Grev.

Greville, 1830, p. 170, t. 18.

Plants saxicolous, linear to linear lanceolate, base slightly cordate, stipitate, attached by a minute disc, up to 10 cm long, about 1 cm broad; monostromatic, about 50 μ thick; dioecious, sporocarps and spermatangia in continuous marginal zone; sporocarps with 16 to 32 spores in four tiers and spermatangia with 128 spermatia in eight tiers.

Type

From Peak Head near Sidmouth, England.

Specimens of this species, collected from Amchitka Island, were passed on to me for examination by Dr. R. E. Norris. These show features identical with those of *P. linearis* from the English coasts and I have no hesitation in identifying the Amchitka specimens with the English species.

Distribution

Alaska, Northern Atlantic, east coast of Canada, coasts of England.

Porphyra nereocystis Anderson

In Anderson, 1892, p. 148.

Plants epiphytic on the stipes of *Nereocystis luteana*, up to 250 cm long, up to 40 cm broad, linear to oblong, sometimes with lacinate margins, base cucullate, attached by a small disc; color red to purple; thallus monostromatic, 25 to 60 μ thick; monoecious; spermatangia in pale, sharply defined streaks among the dark, extensive patches of sporocarps; spores 32 in two tiers and spermatia about 128, in eight tiers.

Type

The original description was based on specimens from the Farallon Islands off San Francisco.

Distribution

From Alaska south to California on the Pacific coast of North America.

Porphyra norrisii sp. nov.

Figs. 5, 6

Plantae saxicolae per discum bene evolutum c. 1 mm lat., ovali-oblongum aut late lanceolatum, margine valde undulata, basi valde cucullata affixae. Plantae dioeciae, usque ad 40 cm long., et usque ad 12 cm lat. Frons olivacea ad brunneo-purpuream, margine plantae femineae roseo, masculae subflavo. Thallus distromaticus, 110–120 μ crass. Cellulae vegetativae, a superficie visae polygonales, angulis rotundatis, usque ad 18 μ dimensione maxima, in sectione 26–30 μ alt., 11–18 μ lat. Vagina 12–14 μ crass., matrix gelatinosa inter duo strata cellularum 22–24 μ crass., lineam disjunctionis mediam perspicuam praebens. Chromatophorus singulus, stellate lobatus, lobis ad periferiam cytoplasmatis admodum attingentibus, et pyrenoidem perspicuam ovalem praebens. Sporocarpium

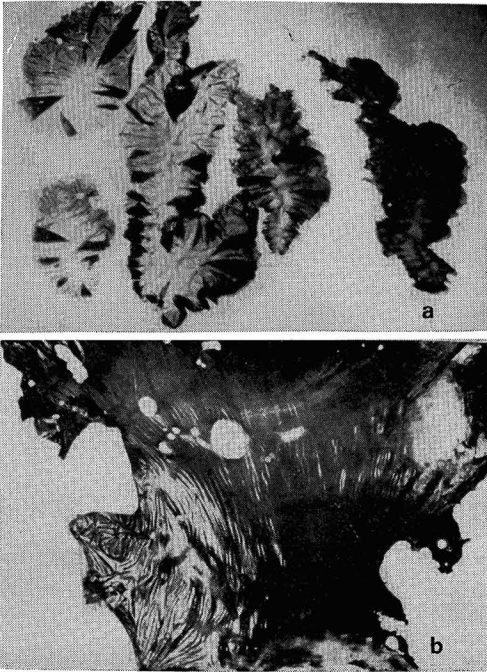


FIG. 5. *a*, *Porphyra perforata* J. Ag. f. *patens*; *b*, *Porphyra papenfussii*.

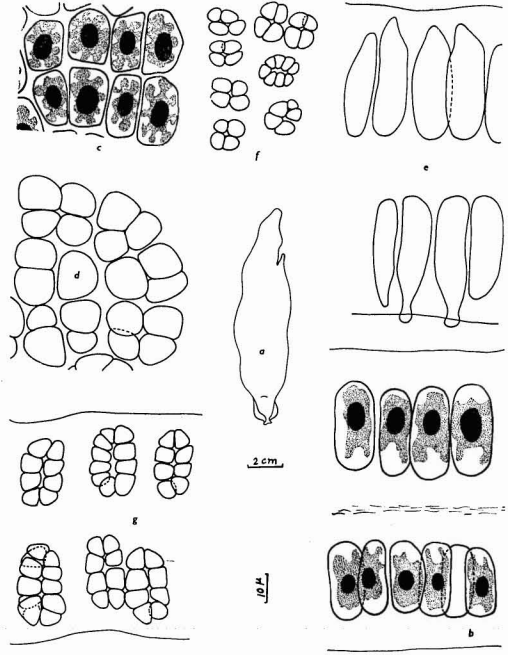


FIG. 6. *a-g*, *Porphyra norrisii* sp. nov. *a*, Habit of a young plant showing the cucullate base; *b*, section of vegetative frond; *c*, surface view of frond showing the elongated cells; *d*, surface view of sporocarpic region; *e*, section through frond showing "carpogonia" with "trichogynes"; *f*, surface view of spermatangia; *g*, spermatangia in section.

in zona marginali 5–10 mm lat. Sporae in duo ordinibus. Spermatangia in zona marginali ab apice deorsum per marginem atque introrsus versus partem thalli mediam extendentia. Spermatangia 32 in 8 ordinibus disposita.

Planta typica a Krishnamurthy (no. 11-00041) e loco Deadman's Bay, San Juan Island dicto, m. Mai, d. 20, 1968 lecta; in Herbario Departmenti Universitatis Washingtonensis deposita.

Plants saxicolous, attached by a well-formed disc about 1 mm across, oval oblong or broadly lanceolate, with strongly undulate margin and a strongly cucullate base. Plants dioecious, up to 40 cm long and up to 12 cm broad. Color of the frond, olive green to brownish purple, the female with rosy red and the male with yellowish margin. Thallus distromatic, 110 to 120 μ thick. Vegetative cells in surface view polygonal with rounded angles, up to 18 μ in the greatest

dimension, in section, 26 to 30 μ in height and 11 to 16 μ in width. Sheath 12 to 14 μ in thickness and the gelatinous matrix between the two layers of cells 22 to 24 μ in thickness with a prominent median line of separation. Chromatophore single, stellately lobed with the lobes just reaching the periphery of the cytoplasm and with a prominent oval pyrenoid. Sporocarps in marginal zone, 5 to 10 mm wide. Spores eight in two tiers. Spermatangia in marginal zone, starting at the apex and extending downward along the margin and inward toward the median portion of the thallus. Spermatia 32 in eight tiers.

Type

Krishnamurthy no. 11-00041 from Deadman's Bay, San Juan Island, 20 March 1968, deposited in the herbarium, Department of Botany, University of Washington, Seattle.

Discussion

My first collection of this species was in Deadman's Bay in San Juan Island. Subsequently I was able to collect the same at high-water level all over the west side of San Juan Island. The species can be recognized readily in the field by its characteristic base which is cucullate, markedly expanding upward into the frond. The frond itself is leathery and can withstand considerable desiccation; it revives rapidly when the rising tide moistens it.

This species resembles *P. bulbopes* (Yendo) Okamura in the shape of the basal portion, but the similarity ends there. *P. norrisii* differs from *P. bulbopes* in being dioecious and in the number and arrangement of spores and spermatia.

I am naming this species after my friend Dr. R. E. Norris, who first suggested to me that I should study the species of *Porphyra* on the Pacific coast.

Porphyra occidentalis Setchell & Hus

In Hus, 1900, p. 69; 1902, p. 228.

Plants saxicolous or epiphytic, subtidal extending from 15 to 100 feet below the surface, lanceolate, with broadly rounded base, sessile, attached by means of a small disc; apex rounded

or pointed, margin slightly undulate; frond distromatic, 50 to 100 μ thick; cells in cross section slightly longer than broad, 12–15 μ across; cell wall gelatinous, not laminate; plants apparently dioecious, only spermatangial plants being recorded; spermatangia forming a continuous yellowish margin in upper part of the plant; spermatia in four tiers.

Type

I have examined one herbarium sheet, no. 95678 of the herbarium of the University of California at Berkeley, on which three specimens are mounted and labelled in Setchell's hand. One of the specimens is marked "type as to habit" and another "type as to structure." All the specimens were collected by Mrs. J. M. Weeks at Carmel Bay, Monterey County, California, and dated 23 April 1897. These specimens should be considered as the type of *P. occidentalis*. There is no sporocarpic specimen on this sheet.

Distribution

Southern part of British Columbia, Canada south to central California.

Discussion

Setchell and Gardner (1903) were the first to point out that *P. occidentalis* Setchell & Hus and *P. variegata* (Kjellman) Kjellman in Hus (1900) were the same species, but opined that *P. occidentalis* should be considered the antheridial plant of *P. variegata*. Tanaka (1952) considered *P. occidentalis* as the antheridial plant of *P. amplissima* which, according to him, was dioecious. However, the description by Hus (1902) of *P. amplissima* leaves no doubt whatever that that species is monoecious. More recently, Hollenberg and Abbott (1966) have concluded that *P. variegata* (Kjellm.) Kjellman in Hus (1900) is the sporocarpic plant of *P. occidentalis*. They based this conclusion on an examination of plants of *P. variegata* occurring in the northwestern Pacific Ocean off Hokkaido and the Kurile Islands. These plants were earlier referred to *P. variegata* by Tanaka (1952). The latter states that the Japanese specimens agree with the descriptions given by Kjellman (1889) and by Hus (1902) for *P.*

variegata. It is not clear whether Tanaka examined the type of Kjellman (*Diploderma variegatum*) from the Bering Sea.

I tried to get at the type of *Diploderma variegatum* both at Uppsala and at Stockholm, but could not see it. The location of the type is apparently not known. In the absence of Kjellman's specimen, we should turn to the specimens used by Hus. Hus (1900, 1902) cited a number of specimens of which the first specimen cited was no. 177 of N. L. Gardner's collection, a specimen collected from the west coast of Whidbey Island, in Puget Sound, Washington. This specimen is located in the herbarium of the University of California at Berkeley. This specimen agrees very well with the description given by Hus (1902).

My own examination of the specimens collected by me indicate two main differences between *P. occidentalis* and *P. variegata*: (1) The frond of *P. variegata* is thicker than that of *P. occidentalis* and is a darker purple. The thickness of the frond in *P. variegata* is 110 to 220 μ , whereas in *P. occidentalis* the thickness is 50–100 μ only. (2) The cell wall in *P. variegata* is distinctly lamellate, whereas in *P. occidentalis* the gelatinous wall, as far as I could make out, is homogeneous in structure. Against this, it may be argued that both these forms have been collected repeatedly from the same regions and apparently no record is available of the sporocarpic plants of *P. occidentalis* or of spermatangial plants of *P. variegata*.

If we contend that *P. occidentalis* and *P. variegata* are one and the same species, we still must determine which is the valid name. This can be settled only when Kjellman's type specimen of *Diploderma variegata* is examined. Until then I think it best to consider the two species as distinct. However, the probability of the two species being identical appeals to one's judgment.

Porphyra papenfussi sp. nov.

Figs. 7, 8

Plantae saxicolae sessiles, late expansae, 35 cm long., 50 cm lat. Frons subbrunea, margine in regionibus carpogonialibus rosea, in regionibus spermatangialibus subflava. Thallus distro-

maticus, 116–170 μ crass. Cellulae vegetativae a superficie visae polygonales, usque ad 14 μ dimensione maxima, in sectione 28–34 μ alt., 10–14 μ lat. Vagina 23–27 μ crass., matrice gelatinosa inter duo strata cellularum 52–60 μ , lineam perspicuam disjunctionis inter duo strata praebente. Thallus monoecious. Carpogonia in maculis marginalibus magnitudine formaque irregularibus. Sporae non visae. Trichogyna carpogoniae 15–16 μ long., 2 μ lat., e vagina eminent. Spermatangia in maculis marginalibus amplis. Spermatia 128 vel plus in 16 ordinibus disposita.

Planta typica a G. J. Hollenberg (no. 3836) e loco Deadman's Bay, San Juan Island dicto, in saxis in regione littorali-media, m. Jun. c. 24, 1968 lecta; in Herbario Departementi Botanici Universitatis Washingtonensis Seattle deposita.

Plants saxicolous sessile, broadly expanded, 35 cm long and 50 cm broad. Color of the frond, brownish with the margin rosy red in carpogonial regions and yellowish in spermatangial regions. Thallus distromatic, 116–170 μ thick. Vegetative cells in surface view polygonal, up to 14 μ in the greatest dimension, in section, 28–34 μ in height and 10–14 μ in width. Sheath 23–27 μ in thickness and the gelatinous matrix between the two layers of cells 52–60 μ with a clear line of separation between the two layers. Thallus monoecious. Carpogonia in marginal patches of irregular size and shape. Spores not seen. Carpogonia with trichogyne projecting out of sheath, 15–16 μ long and 2 μ wide. Spermatangia in extensive marginal patches. Spermatia 128 or more arranged in 16 tiers.

Type

G. J. Hollenberg no. 3836 from Deadman's Bay, on rocks in midlittoral, San Juan Island, 24 June 1968, deposited in the herbarium, Department of Botany, University of Washington, Seattle.

Distribution

This species has been collected so far only from San Juan Island, Puget Sound, Washington.

Discussion

Porphyra papenfussi is very readily distinguished from all other species of *Porphyra* by

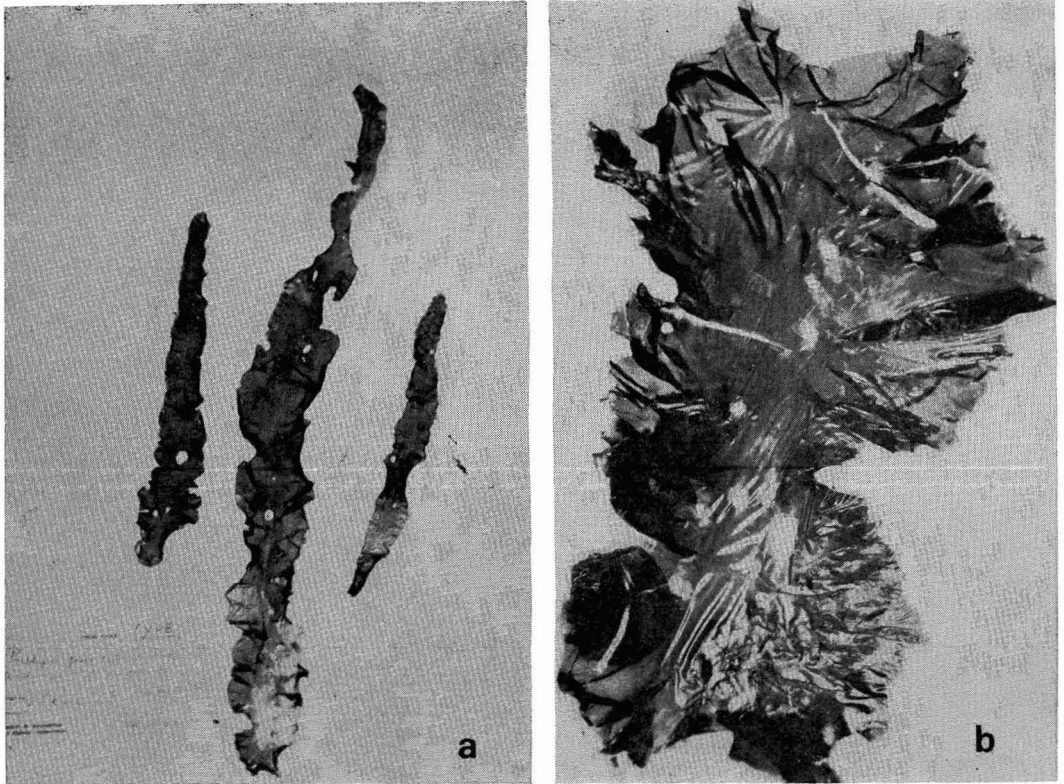


FIG. 7. *a*, *Porphyra pseudolanceolata*; *b*, *Porphyra sanjuanensis*.

its distromatic, monoecious thalli, which are leathery in texture. The most characteristic feature, however, is the spermatangium which contains spermatia arranged in 16 tiers as seen in a cross section. The species was collected by Dr. G. J. Hollenberg, who also pointed out to me that it is probably a new species. I am grateful to him for both the specimen and for his valued opinion.

I name this after Professor G. F. Papenfuss in grateful remembrance of his kind suggestions and advice during my stay at Berkeley.

Porphyra pendula Dawson

In Dawson, 1952, p. 16, pl. 13, fig. 2.

Plants saxicolous, membranous, pale to bright rose red in color; frond simple, occasionally divided near the base into two or more segments, linear, attached by a very small disc; up to 25 cm long and 3–12 mm wide; margins

prominently ruffled; frond monostromatic, 45–50 μ thick, with cells irregular in shape, 7–11 μ across and 22–25 μ in height; plants dioecious; sporocarps forming a continuous marginal zone, bright rose in color, containing eight spores in two tiers; spermatangia forming a continuous yellowish zone on either margin, with spermatia in eight tiers and up to 128 in number.

Type

Dawson, 982 *a*, collected on shaded cliff rocks in spray zone, at Isla Partida, Gulf of California, 22 February 1946, no. 4117 in herbarium of Allan Hancock Foundation.

Discussion

I have examined isotype material both at Berkeley and at the Smithsonian Institution, Washington, D.C. It is a good species and differs from both *P. linearis* Grev. and *P. pseudolinearis* Ueda in the strongly ruffled margin and the small number of spores, viz., eight.

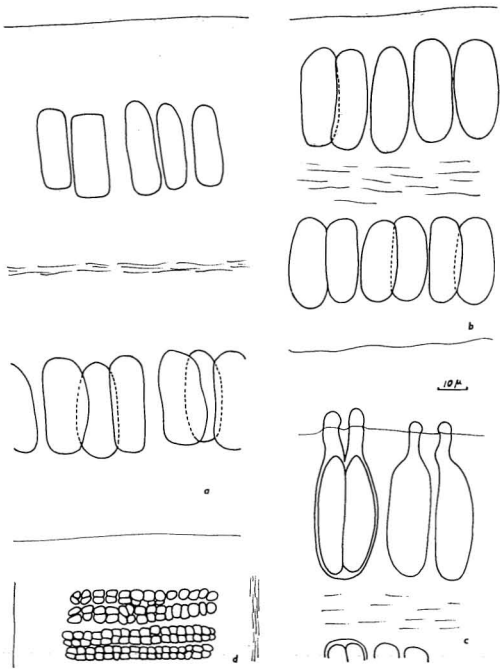


FIG. 8. *a-d*, *Porphyra papenfussii* sp. nov. *a*, *b*, Section of vegetative frond; *c*, section showing one-half of frond with "carpogonia" showing "trichogynes"; *d*, section through the spermatangia showing 16 tiers of spermatia.

Porphyra perforata J. Ag.

In J. Agardh, 1882, p. 69, pl. 2, figs. 62–64.

Plants saxicolous, up to 70 cm long, up to 20 cm broad, lanceolate to oblong, often much expanded and lobate to lacinate; base cordate; attached by means of a small, well-defined disc; color grey to brownish purple; frond monostromatic, 45–140 μ thick, with thick gelatinous sheath; cells in cross section rectangular, about 30 μ broad, up to 100 μ long; thallus monoecious, sporocarps and spermatangia in irregular patches; vegetative cells intermixed with sporocarps but not with spermatangia; spores up to 32 in two tiers and spermatia up to 128 in eight tiers.

Type

The type has not been designated, but Dawson (1952) stated that syntypes of Lyall, Berggren, and Bingham are in the Agardh Herbarium Botanical Museum, University of Lund, Sweden.

I examined the specimens of all the above collectors in the Agardh Herbarium. One sheet bearing no. 12746 bears a specimen collected by Berggren near the Golden Gate, San Francisco, and is labelled "*Porphyra pacifica*." Figures pertaining to this specimen are found on sheet no. 12747 and are labelled *Porphyra perforata*. There is also another specimen no. 13037 marked "Lectotypus" collected by Berggren from the same locality. On examination, I found these specimens to tally with the description given by me above. Lyall's specimens in the Agardh Herbarium are of the same species. However, a specimen from Santa Barbara, California, collected by Mrs. Bingham, under no. 13032, should be placed under *Porphyra segregata*. This will be discussed under that species. In my opinion, the chief character of *P. perforata* consists in the distribution pattern of the sporocarps and spermatangia, with vegetative cells intermingled with the sporocarps, a feature which this species shares with *Porphyra columbina* Mont. In view of these data, I consider no. 12746 of the Agardh Herbarium, from Golden Gate, San Francisco, California, as the type of *Porphyra perforata* J. Ag.

Number 13037 is marked "Lecto-type" but the published figures are those of no. 12746.

Distribution

Porphyra is found on the Pacific coast of North America.

Discussion

Hus (1902) described two distinct forms of this species: f. *lanceolata* and f. *segregata*. Of these, f. *lanceolata* has already been transferred to a new species by G. M. Smith (Smith and Hollenberg, 1943). I consider f. *segregata* also to be a distinct species as this form does not share with *P. perforata* the main character—the distribution pattern of sporocarps and spermatangia with vegetative cells intermingled with the sporocarps. When these two forms are recognized as distinct species, all the confusion in delimitation of *P. perforata* is dispelled. However, there is considerable variability in form in the species as it occurs all over the intertidal and sometimes also extends into the subtidal. One form is very distinctive in its habit and

is found at the highest part of the intertidal. This form is here described as a new form, *P. perforata* f. *patens*. I have already given a complete account of the morphology and ecology of this form (Krishnamurthy, 1969). I have not given a description and a Latin diagnosis. I give these here.

Porphyra perforata J. Ag. f. *patens* f. nov.

Fig. 9

Plantae saxicolae, usque ad 25 cm alt., in loco per aestum tantummodo supremum attacto crescentes, plerumque simplices, ovatae ad lanceolatas, margine undulato ad plicatum vetere crispissimo facto, per discum minutum affixae. Frondis in parte media vegetativa vivide coeruleo-viridis, per marginem rosea, in partibus quae sporas efficiunt rubra intensior. Thallus monostromaticus monoecious, 60 ad 72 μ crass.; cellulae vegetativae a superficie visae 13–16 μ diam., a sectione visae 2 plo longiores quam

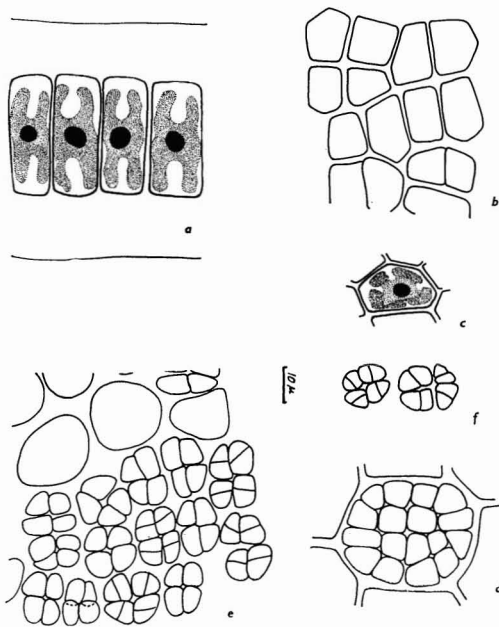


FIG. 9. a-f, *Porphyra perforata* J. Ag. f. *patens* f. nov. a, Section of vegetative frond; b, surface view of vegetative frond; c, a single cell in surface view; d, a sporocarp in surface view; e, spermatangial sorus in surface view; f, spermatangia showing final division before differentiation of spermata.

latae; vagina usque ad 20 μ crass. Sporocarpia spermatangiaque eis in *P. perforata* similia. Spores 8 ad 14 μ diam., spermata 4 ad 5 μ diam.

Planta typica in Herbario Krishnamurthy No. 11-00012, e loco Deadman's Bay, San Juan Is. dicto, m. Jan. d. 22, 1968 lecta, in Departamento Botanico Universitatis Washingtonensis Seattle, deposita.

Plants saxicolous, up to 25 cm tall, growing at high-water mark, generally simple, ovate to lanceolate with undulate to plicate margin becoming much ruffled when old, attached by a minute disc. Color vivid blue-green in median vegetative part of the frond, rosy red along the margin, darker red in spore-producing parts. Thallus monostromatic, monoecious, 60–72 μ in thickness, vegetative cells in surface view 13–16 μ across, in section twice as long as broad, sheath up to 20 μ in thickness. Sporocarps and spermatangia similar to those in *P. perforata*. Spores 8 to 14 μ in diameter, spermata 4 to 5 μ in diameter.

Type in Herbarium

Krishnamurthy, no. 11-00012 from Deadman's Bay, San Juan Island, 22 January 1968, deposited in the Department of Botany, University of Washington, Seattle.

Porphyra pseudolanceolata sp. nov.

Fig. 10

Plantae saxicolae, per discum minutum ad basim affixae, lineares ad lanceolatas, simplices, marginibus undulatis aut paululum corrugatis. Plantae dioeciae, masculae usque ad 25 cm long., 3 cm lat., femineae usque ad 40 cm long., 5 cm lat. Frons cinerascens-viridis, margine frondis iuvenis roseo. Thallus monostromaticus, cellulae vegetivae a vertice visae polygonales usque ad 25 μ dimensione maxima, thallus in sectione 30–35 μ alt., 18–25 μ lat., vagina gelatinosa 17–20 μ crass. praeditus. Chromatophorus singulus, pyrenoidem mediam magnam, et brachia tenuia, quae usque ad periferiam cytoplasmatis extendunt atque hic replicantur, habens. Sporocarpia in lineas sanguineas e marginibus introrsus extendentes, et

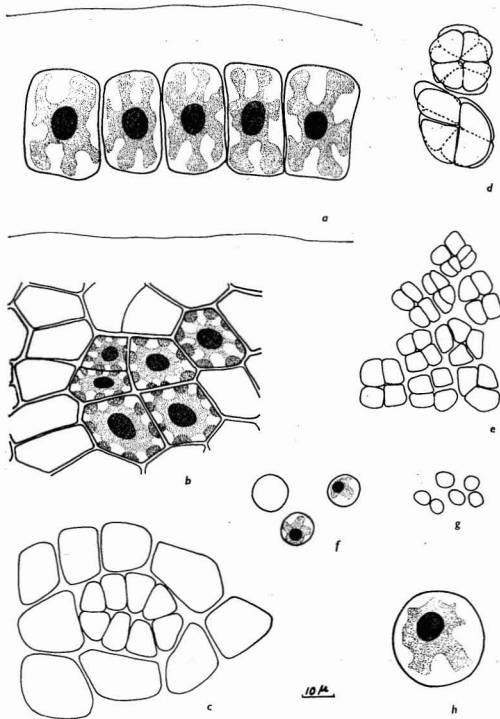


FIG. 10. *a-b*, *Porphyra pseudolanceolata* sp. nov. *a*, Section of vegetative frond; *b*, surface view of vegetative cells; *c*, *d*, sporocarps, showing division into eight; *e*, a group of spermatangia in surface view; *f*, spores; *g*, spermatia; *h*, a monospore(?) formed by the rounding up of the contents of a vegetative cell.

areis cellularum vegetativarum a se disiunctae. Sporae 8 in duobus ordinibus, rarissime 16. Spermatangia in zona marginali, 2–3 mm lat., ab apice deorsum per marginem extendentia, 128 in 8 ordinibus.

Planta typica a Krishnamurthy (no. 11-00021) e loco Deadman's Bay, San Juan Island dicto, m. Jan. d. 22, 1968 lecta; in Herbario Departmenti Botanici Universitatis Washingtonensis, Seattle deposita.

Plants saxicolous, attached by means of a minute disc at the base, linear to lanceolate, simple with undulate or slightly ruffled margins; plants dioecious, male reaching up to 25 cm in length and 3 cm in width and female up to 40 cm in length and 5 cm in width. Color of the frond greyish green with rosy red margin when young. Thallus monostromatic, vegeta-

tive cells in surface view polygonal, up to 25 μ in the greatest dimension, in section, 30–35 μ in height and 18–22 μ in width, with a gelatinous sheath 17–20 μ in thickness. Chromatophore single, with large median pyrenoid and slender arms extending up to and folded at the periphery of the cytoplasm. Sporocarps in blood-red streaks extending from margin inward and separated by areas of vegetative cells. Spores eight in two tiers, very rarely 16. Spermatangia in marginal zone, 2–3 mm wide, starting from apex and extending downward along the margin. Spermatia 128 in eight tiers.

Type

Krishnamurthy no. 11-00021 from Deadman's Bay, San Juan Island, 22 January 1968, deposited in the herbarium, Department of Botany, University of Washington, Seattle.

Discussion

When I first collected this species, I believed it to be *P. lanceolata*; after examining it more closely, however, I realized that it was distinct. *P. pseudolanceolata* differs from *P. lanceolata* in possessing a single chromatophore in each cell and in producing only eight spores in a sporocarp. The appearance of *P. pseudolanceolata* is quite striking, the fronds always being lanceolate, greyish green in color, and the sporocarpic plant showing sporocarps in the form of dark red streaks.

Porphyra pulchra Hollenberg

In Smith and Hollenberg, 1943, p. 213, figs. 1–12.

Plants epiphytic on *Phyllospadix*, up to 15 cm broad, lanceolate, sessile or umbilicate with an indistinct attaching disc; color of frond a delicate purple; thallus monostromatic, 50 to 95 μ thick; cells in cross section 25 to 45 μ high, each with two chromatophores; sheath gelatinous, homogeneous; plants monoecious; sporocarps in marginal groups intermingled with vegetative cells, containing 16–32 spores in two tiers; spermatangia in submarginal linear or oblong sori, with spermatia in eight tiers.

Type

Hollenberg 2890, epiphytic on leaves of *Phyllospadix* at Moss Beach, near Pacific Grove, California.

Distribution

Santa Cruz and Monterey Peninsula, California.

The description given above follows the delimitation of this species by Hollenberg and Abbott (1968).

Porphyra purpureo-violacea (Roth)
comb. nov.

Ulva purpureo-violacea Roth, 1788, Tent. Fl. Germ. I, p. 524.

Ulva purpurea Roth, 1797, Cat. Bot., I, p. 209.

Plants saxicolous, occurring in the lower part of the intertidal region, linear to oblong to broadly ovate, up to 30 cm high and up to 20 cm broad, often lobed or lancinate; sessile; frond monostromatic 35 to 50 μ thick; color reddish purple; thallus dioecious; occasionally intersex plants are met with, sporocarpic and spermatangial portions of the frond delimited by a sharp line; sporocarps forming a continuous marginal zone; spores eight to 32, in two tiers; spermatangia in continuous marginal zone; spermatia in eight tiers, up to 128.

Type

No specimen is now available.

Distribution

North Sea, North Atlantic Ocean, Alaska, east coast of North America.

Discussion

This is the species described by Hus as *Porphyra laciniata* but recent opinion appears to favor the name *P. purpurea* for this species. *Ulva purpurea* Roth on which this name is based, however, was superfluous when published as Roth himself had published an earlier name, *Ulva purpureo-violacea*, for the same taxon. Some specimens from Amchitka were passed on to me for examination by Dr. R. E. Norris and I have no hesitation in identifying

them with this species. The same species is found widely on the British coasts. This species has long been described as *Porphyra laciniata* or *Porphyra umbilicalis* f. *laciniata* or *Porphyra umbilicalis* var. *laciniata*. The basionym is generally cited as *Ulva laciniata* Lightfoot. The description and, especially, the figure given by Lightfoot (1777) for *Ulva laciniata* suggest that the alga that he was describing was not a *Porphyra* but a membranous red alga with fruit bodies scattered marginally. Drew (1955) and Dixon (1959) have indicated that the Lightfoot specimen was a member of the Delesseriaceae (Ceramiales). However, C. Agardh appears to have used the name given by Lightfoot in the genuine understanding that it should be applied to a *Porphyra*. J. Agardh (1892) reduced both *P. laciniata* and *P. purpurea* as varieties under *P. umbilicalis*, based on *Ulva umbilicalis* L. C. Agardh (1824) cited *Porphyra umbilicata* under *P. laciniata*, based on *Ulva umbilicalis* and another *Porphyra umbilicata* under *P. purpurea* from the English coast. Later authors have been making various combinations of these epithets, adding considerably to the confusion. Kützing (1843) described *P. umbilicalis* from Scotland but without referring to the Linnean *Ulva umbilicalis*. Conway (1964) discussed *Porphyra umbilicalis* in the light of the Dillenian specimen of *Ulva umbilicalis* L. located at Oxford and has shown that this is a distinct species.

I have examined the Agardh specimens of *Porphyra purpurea* (Roth) C. Ag., *P. laciniata* (Lightf.) J. Ag., and *P. umbilicalis* (L.) J. Ag. In the Agardh Herbarium, Lund, no. 12750 and no. 12845 are specimens of *P. purpurea*; nos. 12846 to 12857 are further specimens, descriptions, and figures of the same species. Number 12749 bears drawings of *P. laciniata*, no. 12784 is a specimen of *P. laciniata*, and nos. 12799, 12780, and 12781 are specimens of *P. umbilicalis* from Berwick upon Tweed, collected by Batters in 1884-1885.

The specimens of *P. umbilicalis* are distinctive in structure and so this should be regarded as a good species. The specimens of *P. purpurea* and *P. laciniata* show no differences in habit and structure, so that these two may be considered conspecific and we should select the earlier

name for this taxon. If we consider the basionyms of these two names, *Ulva laciniata* is the earlier name but Lightfoot's specimen was not a *Porphyra*. On the other hand, Roth's specimen is not available although his figure suggests the possibility of the alga being a *Porphyra*.

If we consider C. Agardh as the original author of the two names in question, the first described species (C. Agardh, 1824) is *P. laciniata* and this should apply irrespective of what Lightfoot's specimen was. Undoubtedly C. Agardh (1824) was describing a *Porphyra* under this name.

This is a nomenclatural tangle which will need further consideration. But I use *P. purpureo-violacea* here as this name is the earliest to be applied to this taxon. I am indebted to Dr. P. S. Dixon and Mr. R. Ross for information on Roth's earlier publication.

Porphyra sanjuanensis sp. nov.

Fig. 11

Plantae saxicolae sessilesque, iuvenes cordatae, veteres irregulariter expansae laciniataeque factae, usque ad 50 cm long., 40 cm lat., late plicatae. Plantae brunneae ad rubro-brunneas,

submersae irridescentes; textura thalli elastica. Thallus monostromaticus, 42–50 μ crass., cellulae vegetativae a superficie visae polygonales, 14–25 μ diam., a sectione visae paululo aut duplo longiores quam latae, vagina tenui. Sporae octo ad 16, in duobus vel quattuor stratis, 14 vel 15 μ diam., interdum minores. Spermatia ignota.

Planta typica in Herbario Krishnamurthy No. 11-00061 e loco Minnesota Reef, San Juan Island dicto, m. Feb. d. 19, 1968 lecta; in Departmenti Botanici Universitatis Washingtonensis, Seattle deposita.

Plants saxicolous, sessile, cordate when young, becoming irregularly expanded and lacinate when old, up to 50 cm in length and 40 cm in breadth, broadly folded. Color brown to reddish brown, irridescent when submerged; texture of thallus rubbery. Thallus monostromatic, 42–50 μ thick, vegetative cells in surface view polygonal, 14–25 μ across, slightly longer or twice as long as broad in section, sheath thin. Spores eight to 16 in two or four tiers, 14 to 15 μ in diameter, occasionally smaller. Spermatia not known.

Type in Herbarium

Krishnamurthy, no. 11-00061 from Minnesota Reef, San Juan Island, 19 February 1968, deposited in the Department of Botany, University of Washington, Seattle.

Distribution

So far collected only in San Juan Island, Puget Sound, Washington.

Discussion

I have already given an account of this species, its life history and ecology (Krishnamurthy, 1969). I consider this to be a new species because of its apparent dioecism, spores occurring in two to four tiers, and, above all, because of its characteristic habit. The frond shows irridescence when submerged under water and has a rubbery texture which I have not come across in other species of *Porphyra*.

Recently, I had a communication from Dr. R. E. Norris (16 March 1970) stating that he had recently collected a specimen of *P. sanjuanensis* which had what he thought to be a male

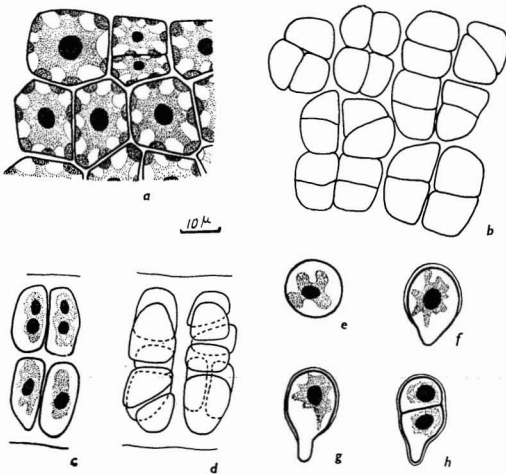


FIG. 11. *a-b*, *Porphyra sanjuanensis* sp. nov. *a*, Surface view of the vegetative frond; *b*, surface view showing divisions leading to the formation of sporocarps; *c*, section through a young sporocarp; *d*, later stage of development of a sporocarp; *e*, spore; *f-h*, stages in germination of the spore.

streak in it. He did not give further details, but more detailed investigation of this species is necessary to ascertain its life history.

Porphyra schizophylla Hollenberg

In Smith and Hollenberg, 1943, p. 213, figs. 6-7.

Plants saxicolous sessile, oblong, often lacinate with undulate plicate margins; up to about 15 cm tall, half as broad; blades distromatic, 200 to 250 μ thick; gelatinous matrix of blade with a conspicuous line of separation between the two cell layers and with stratifications close to the surface of the thallus, cells pyriform, with narrower end directed inward, 20-25 μ across; plants dioecious, sporocarps in a marginal zone, with eight spores each in two tiers; spermatangia in a narrow marginal zone with 16 to 32 spermatia in four tiers.

Type

Hollenberg, 1914, growing at high-tide level on rocks swept by heavy surf, at Pescadero Point, Monterey Peninsula, California.

I have not collected this species myself and I am including this species here on the authority of Smith and Hollenberg (1943).

Porphyra segregata comb. nov.

Porphyra perforata f. *segregata* Setchell & Hus

In Hus, 1900, p. 64; 1902, p. 207.

Plants saxicolous, attached by a small disc, irregularly expanded and lacinate, segments up to 15 cm long and up to 5 cm broad. Thallus monostromatic, 40 to 60 μ in thickness. Vegetative cells in surface view polygonal, with thick cell walls up to 14 μ in greatest dimension, in section up to 25 μ in height and up to 14 μ in width; thallus monoecious. Sporocarps in a continuous marginal zone except where interrupted by spermatangia, with no areas of vegetative cells intervening between them. Spores eight to 32 in two tiers. Spermatangia in marginal patches. Spermatia up to 128, arranged in eight tiers but in two overlying groups of four tiers each, separated by a thick crosswall.

Type

Mrs. E. Snyder in Phycotheca Boreali-Americana no. 684, from La Jolla, San Diego, California, deposited under no. 11173 in the herbarium, Department of Botany, University of California at Berkeley.

Distribution

Alga is found in Southern California only.

Discussion

This is the species which Hus (1902) described as *P. perforata* f. *segregata*. However, this differs from *P. perforata* in several important respects and, therefore, should be considered a distinct species. The most important feature is the occurrence of sporocarps in a continuous marginal zone except where interrupted by spermatangia, with no vegetative cells intermingled among them. Another feature of importance was already noticed by Hus (1902). The spermatia occur in two overlying groups, separated by a thick gelatinous layer.

I have examined the specimens cited by Hus. Of these, the Tilden specimen from Seattle shows sporocarps in small patches scattered amongst the vegetative cells, and so this specimen should be considered as *P. perforata*. The other two specimens are undoubtedly *P. segregata*.

Porphyra smithii Hollenberg & Abbott

In Hollenberg and Abbott, 1968, p. 1243, fig. 7.

Plants epiphytic, orbicular, up to 15 cm broad and up to 20 cm long, base umbilicate; blades monostromatic, 125 to 135 μ thick; cells in vegetative portions oblong, 40-60 μ high, 20-25 μ broad as seen in cross section; chromatophores two, widely separated, one at each end of the cell; plants monoecious; sporocarps forming a dark purplish red marginal zone, interrupted at intervals by relatively small, pale-to-dark-yellow, marginal or submarginal spermatangial spots; spermatangial spots often causing deep marginal indentations as spermatia are liberated; spores generally 32, sometimes more, in two or four tiers; spermatia 64 to 128, in eight tiers.

Type

H. 3701.6 (GMS), collected at Mission Point, Monterey Peninsula, California, 27 July 1965, epiphytic on *Gigartina agardhii*.

Distribution

Puget Sound, Washington, south to Southern California.

Porphyra tenuissima (Stromf.) Setchell & Hus

In Hus, 1900, p. 68; 1902, p. 220. *Diploderma tenuissimum* Stromfelt, 1886, p. 173.

Plants saxicolous growing at subtidal levels, orbicular or oblong-ovate with umbilicate base, up to 25 cm long and up to 15 cm broad; color a delicate red-purple; frond very thin and membranous, 25 μ thick, distromatic; vegetative cells in cross section of frond either square in outline or broader than long; plants monoecious, sporocarps and spermatangia occurring in marginal patches; spores eight in two tiers; spermatia 16 in four tiers.

Type

It is very difficult to pinpoint Stromfelt's specimen. However, I have seen one specimen in the Rijksmuseum, Stockholm, from Ost Ise Is. (18 June 1883). But Setchell and Hus had not seen Stromfelt's specimen but only specimens collected from Alaska during the Harriman Alaska Expedition, 1899. There are several specimens in the herbarium of the University of California at Berkeley. The specimen first cited is no. 241, collected by de Alton Saunders from Yakutat Bay, Alaska. There is no date of collection but the specimen is one of the algae of Alaska from the Harriman Alaska Expedition, 1899. Specimens have also been distributed in the Phycotheca Boreali-Americana, under no. 1239.

I have examined all the specimens at Berkeley and I have no doubt that they are identical with the one Stromfelt specimen I have seen at Stockholm.

Porphyra thuretii Setchell & Dawson

In Dawson, 1944, p. 253. *P. leucosticta* Hus (non Thuret), Hus, 1902, p. 199.

Plants saxicolous, ovate-lanceolate, sessile, a delicate red in color, membranous, up to 30 cm long and up to 10 cm broad; frond monostromatic, monoecious; sporocarps in scattered sori along the margin of frond; spores eight in two tiers; spermatangia forming narrow linear streaks, parallel to either margin; spermatia 64 in two overlying groups as seen in cross section.

Type

Lectotype has been selected by Dr. P. C. Silva. This is W. A. Setchell, no. 5161, dated 19 May 1900, on *Gracilaria sjeostedtii* Kylin, floating in Carmel Bay, Monterey County, California, deposited in the herbarium of the University of California at Berkeley under no. 791973.

Distribution

Alga is found off central California.

I have collected this species only at Pacific Grove, California, and, so far as I am aware, this species has been reported only from this region. I have seen one specimen in Scripps Institution of Oceanography, La Jolla, collected by Dr. M. Neushul from Whidbey Island, Washington, under no. 354. This specimen is more like *Porphyra abbottae* than *P. thuretii*.

Porphyra torta sp. nov.

Fig. 12

Plantae saxicolae, per discum minutum ad basim affixae, lanceolatae, simplices, interdum laciniatae, lamina per lineam mediam saepe plicata atque torta; margo valde corrugatus; plantae monoeciae; 6–22 cm long., 2–6 cm lat.; frons griseo-brunnea ad purpuream. Thallus monostromaticus, cellulae in partibus submarginalibus mediisque excrescentias rhizoideas, quae per lineam frondis mediam deorsum curvant, efficientes. Cellulae a superficie visae polygonales, angulis rotundatis, usque ad 35 μ dimensione maxima; cellulae in sectione ut videtur binae dispositae, usque ad 65 μ alt., 30–35 μ lat., vagina 24–27 μ crass. Chromatophorus singulus, unam pyrenoidem mediam atque c. 6 brachia tenuia radialiter extensa habens. Vacuola utraque in extremitate cellulae a sectione saepe visa. Sporocarpium in maculis, areis cellularum vegeta-

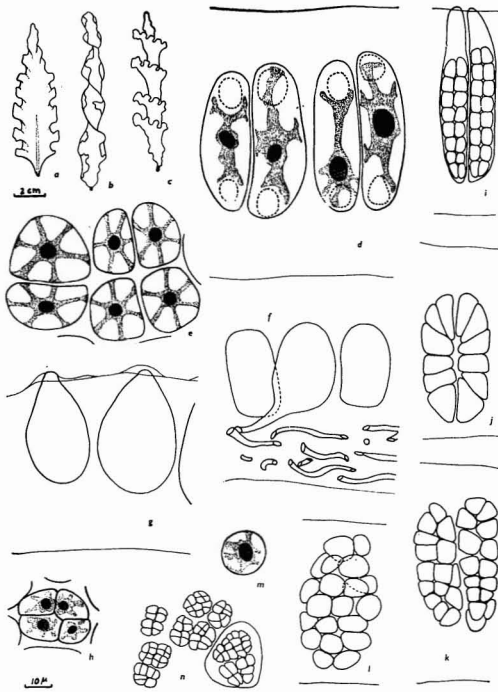


FIG. 12. *a-n*, *Porphyra torta* sp. nov. *a-c*, Habit of the plants; *d*, section of vegetative frond showing cell structure; *e*, surface view of vegetative cells; *f*, section through an older part of frond showing internal rhizoids; *g*, section showing female cells; *h*, a young sporocarp in surface view; *i*, a mature sporocarp in surface view; *j*, section through a sporocarp in course of development; *k*, later stage in development of sporocarp; *l*, a mature sporocarp showing irregular arrangement of spores; *m*, spermata in surface view; *n*, spermata in surface view.

tivarum seiuncti. Sporae multae in 8 ordinibus, ob amotionem interdum inperspicuis. Spermata in maculis sparsis disposita, omni macula multa spermata in massa habente.

Planta typica a Krishnamurthy (no. 11-00161) e promontorio prope locum False Bay, San Juan Island dicto, m. Mai d. 26, 1968 lecta; in Herbario, Departmenti Botanici Universitatis Washingtonensis, Seattle deposita.

Plants saxicolous attached by means of a minute disc at the base, lanceolate, simple, occasionally lacinate, with blade often folded along median line and twisted; margin strongly ruffled; plants monoecious, from 6–22 cm long and 2–6 cm broad; color of frond grey-brown to purple. Thallus monostromatic, cells in sub-

marginal and median portions producing rhizoidal outgrowths which curve downward along the median line of the frond. Cells in surface view polygonal with rounded angles up to 35 μ in the greatest dimension; in section appearing to be disposed in pairs, up to 65 μ in height, 30–35 μ in width, sheath 24–27 μ in thickness. Chromatophore single with a single median pyrenoid and about six slender arms extending radially. Often a vacuole is seen at either end of a cell in sectional view. Sporocarps in patches, separated by areas of vegetative cells. Spores numerous in eight tiers which may be indistinct due to displacement. Spermata in scattered patches each with numerous spermata in a mass.

Type

Krishnamurthy no. 11-00161 from point near False Bay, San Juan Island, 26 May 1968, deposited in the herbarium, Department of Botany, University of Washington, Seattle.

Discussion

This species can be readily recognized in the field by its strongly ruffled margin. Very often the plants are folded along the median line and twisted and a strong well-defined midrib can be made out. Anatomically also this species is interesting in that the submarginal and median cells of the frond send out rhizoids internally along the midrib. The vacuolated cells, the shape of the chromatophore, and the large number of spores and spermata are also distinctive features.

Porphyra umbilicalis Kütz.

In Kützing, 1843, p. 383.

P. laciniata f. *umbilicalis*, Hus, 1902, p. 199.

Plants saxicolous, orbicular to ovate-lanceolate, often cordate at the base, umbilicate, up to 15 cm long, as much broad; frond coriaceous, reddish violet in color, 40–65 μ thick, monostromatic; plants dioecious, with occasional intersex plants, with sporocarpic and spermatangial portions of the frond marked by a clear longitudinal line; sporocarps and spermata forming marginal zones toward the apex of

the plant; sporocarps with 32 spores in two or four tiers; spermatangia with spermatia in eight tiers.

Distribution

North Atlantic Ocean, shores of British Isles and Alaska.

Discussion

This species has been described from the Pacific coast of North America by Hus (1902) as *P. laciniata* f. *umbilicalis*. However, the nomenclatural problem involved is of a different nature. *P. umbilicalis* was first used by Kützing (1843) for a specimen from Scotland seen by him. His description is meager and does not mention the umbilicate base which is so characteristic. Moreover, he makes no mention of *Ulva umbilicalis* L., on which J. Agardh (1882) named his *Porphyra umbilicalis* (L.). I have no doubt whatever that both he and J. Agardh were describing the same alga, as the three specimens of *P. umbilicalis* in the Agardh Herbarium, Lund, all collected at Berwick upon Tweed, England, and Kützing's specimens, are identical.

Porphyra variegata (Kjellman) Kjellman

In Hus, 1900, p. 69. Hus, 1902, p. 225.

Diploderma variegatum Kjellman, 1889, p. 33, pl. 2, figs. 1-4.

Plants sessile with a discoid attachment, up to 100 cm long, up to 20 cm broad, brownish red in color; base rounded, apex gradually tapering, obtuse; margin of blade slightly undulate; frond distromatic, up to 220 μ in thickness; cells subspherical about 12 μ diameter; each cell surrounded by a stratified gelatinous sheath, stratification pronounced toward the surface of frond; thalli dioecious, sporocarps scattered and intermingled with vegetative cells; spermatangia not known; spores eight to 32 in two tiers.

Type

Kjellman's specimen of *P. variegata* from the Bering Sea was not available although I made an effort to see it both at Uppsala and at Stockholm.

Distribution

Northern Pacific Ocean; Bering Sea; Japan; Puget Sound, Washington.

Discussion

Setchell and Gardner (1903) first suggested that *P. occidentalis* was probably the spermatangial plant of *P. variegata*. Tanaka (1952) described a monoecious species as *P. variegata* but stated that the plant agreed with the description given by Hus (1902). More recently, Hollenberg and Abbott (1966) have considered *P. variegata* of Hus to be different from the species described by Kjellman (1889) and to be the sporocarpic plant of *P. occidentalis* Setchell & Hus. They exclude *P. variegata* from the Pacific coast of North America. They state, however, that specimens from the northwestern Pacific (northern Hokkaido and the Kurile Islands) are smaller and more delicate than the specimens from California and in their anatomy resemble the type specimen of *Porphyra variegata* (Kjellman) Kjellman in Hus. This statement gives the impression that the specimens described by Hus and those before these authors are not the same. Although the plants from California may not be identical to *P. variegata*, there appears to be reason to consider the specimens from Whidbey Island as belonging to this species. I consider *P. variegata* (Kjellman) Kjellman in Hus to be distinct from *P. occidentalis* mainly because of the distinctive anatomy. The plants are very thick, up to 220 μ , and the vegetative cells have a prominently stratified gelatinous sheath.

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and enlightenment: Professor G. F. Papenfuss, Dr. P. C. Silva, Dr. G. J. Hollenberg, Dr. Ralph A. Lewin, Dr. P. S. Dixon, Dr. Maxwell Doty, and Dr. Isabella A. Abbott. My stay in the United States was rendered happy and enjoyable owing to the constant help and friendliness of Dr. R. E. Norris. There were many collection trips and discussions with Dr. Joseph Powell and Dr. Michael Wynne, both of whom were good companions on field trips and whose discussions were stimulating. The diagnoses of the new species were rendered into Latin by Dr. Hannah Croasdale to whom I am greatly indebted.

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