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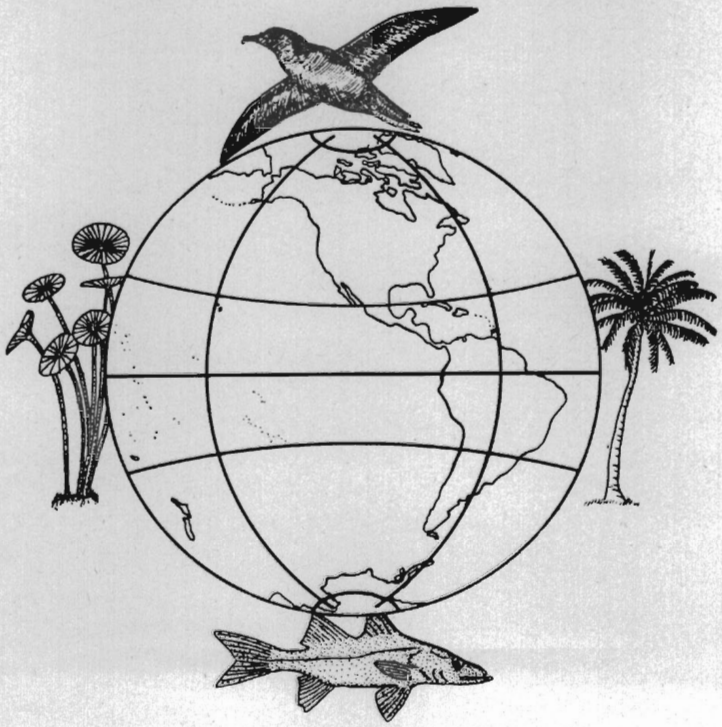

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FOREWORD

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SMITHORA, AN INTERESTING NEW ALGAL GENUS IN THE ERYTHROPELTIDACEAE

By G. J. HOLLENBERG[1]

A remarkable marine alga, which has been known as *Porphyra naiadum* since it was first described by C. L. Anderson in 1892, is common and often very abundant along the west coast of North America from British Columbia to the southern part of Baja California. It occurs exclusively as an epiphyte on *Phyllospadix* and *Zostera*. As a result of certain observations concerning this plant, which will be related below, the writer finds it necessary to conclude that it is neither a member of the Genus *Porphyra* nor of the suborder Bangieae, but should be considered as an undescribed genus in the suborder Erythrotrichieae. It is described as follows:

Smithora gen. nov. Plantae epiphyticae, laminas multas obovatas ad cuneatas ac monostromaticas, enascentes e basi prostrata pulvinata multistratosa, habentes; cellulae chromatophoro stellato singulo praeditae, cellulis laminae inferioribus sine processibus rhizoideis; carposporis in soris irregularibus, maxima ex parte terminalibus; spermatangia in soris irregularibus plurimum versus partem laminarum mediam aut inferiorem enascentia ut cellulae parvae e cellulis coloratis partium laminae localiter distromaticarum externe separatae; plantae cum soris gelatinosis irregularibus, maxima ex parte terminalibus ut monas liberatis.

Plants epiphytic, with numerous obovate to cuneate and monostromatic blades arising from a prostrate cushion-like perennial multistratose base; cells with a single stellate chromatophore; plants with no rhizoidal processes arising from the lower cells of the blades; carpospores formed in irregular, mostly terminal, sori, in packets of eight; spermatangia arising in irregular sori toward the middle portions of the blades as small cells cut off externally from colored cells of the locally distromatic portions of the blades; plants reproducing asexually by means of irregular, terminal, monostromatic gelatinous sori which are released as a unit.

This genus is named in honor of the writer's former teacher and companion on many collecting trips, Dr. Gilbert M. Smith, whose numerous and valued phycological contributions are so well known.

TYPE: **Smithora naiadum** (C. L. Anderson) comb. nov.; *Porphyra naiadum* C. L. Anderson (apud Blankinship and Keeler, 1892).

VEGETATIVE FEATURES

Setchell and Hus (see Hus, 1902) early recognized that this plant has certain features not known in other species of *Porphyra*, namely the perennial cushion-like base from which a number of erect blades arise, and in the attachment organ, the lack of rhizoidal processes, so characteris-

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tic of *Porphyra* and closely related genera. More recently, Haxo and Blinks (1950) and Airth and Blinks (1956, 1957) have shown that pigments found in this species are different from those found in other species of *Porphyra*, thus raising further question concerning the position of the species in that genus.

As a result of this doubt concerning the relationships of *Porphyra naiadum* the writer began a study of this plant during the summer of 1953 at the Hopkins Marine Station at Pacific Grove, California. As Hus (1902) had observed, no rhizoidal processes could be found in connection with the attachment of the erect blades to the prostrate portion nor in the prostrate base itself. However, Hus describes rudimentary rhizoidal processes arising from the lower cells of the basal cushions and these are referred to by Knox (1926). The writer was unable to find any such rudimentary structures which he could consider comparable with those characteristic of *Porphyra*.

The origin of the numerous blades from the cushion-like base is accurately described by Hus (1902). In the vicinity of Pacific Grove the erect blades are commonly lost during the winter, but new blades arise from the persistent base the following spring as described by Hus (1902) and by Smith (1944). Hus states that the plant may disappear entirely in local areas to reappear the following spring in prothalloid form. The writer observed that in a similar manner these plants seemed to be totally absent during June of one year in an area near Pacific Grove where they are usually very abundant. A month later an abundance of cushion-like bases and young blades were present in this area. Dr. E. Yale Dawson, in a private communication, reports that in the southern portion of its range these plants tend to decline in spring and summer rather than in winter. From these observations it seems evident that local conditions are very important in determining the occurrence and persistenec of this plant.

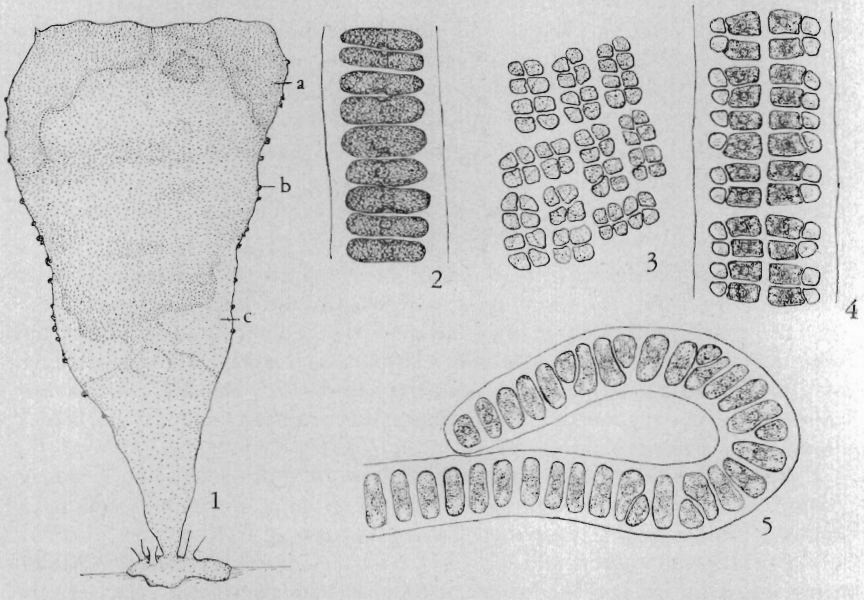
Sexual Reproduction

CARPOSPORES:—Hus (1902) found only one type of reproductive structure, the "sporocarps" (carpospores), and Smith (1944) mentions only carpospores specifically. Both of these investigators describe the carpospores as arising in packets of eight as a result of two divisions at right angles to each other and to the plane of the blade, followed, according to Hus, by a division in the plane of the blade, and forming a group of four cells on either side of the blade (see Hus, 1902, Pl. 21, figs. 21a, 21b; Pl. 22, fig. 24). The writer has found instances of cells dividing much in the manner indicated by Hus, but in most such instances he was unable to be certain whether these were carpogonia or stages in the development of spermatangia. Examination of a plant collected by Maxwell S. Doty from Coos Bay, Oregon (Herb. A. Hancock Found., 15338) revealed the presence of cells dividing in the manner described by Hus. In this particular collection the writer found a number of fairly convincing

instances of carpospores. These occurred toward the tip of the blades rather than in the median portion of the blades as described later in this paper for spermatangia. The experience of the writer indicates that it is practically impossible to distingush such reproductve areas from spermatangial areas except in a sectional view perpendicular to the plane of the blade.

SPERMATANGIA:—Hus seems not to have recognized spermatangia. Judging by her figure, Knox (1926, fig. 26) may have seen spermatangia on one occasion, but her figures and description leave room for considerable doubt. The present writer was at first unable to find spermatangia and may have confused developing carpospores with stages in the development of spermatangia, as Hus may also have done. The spermatangial areas are paler than the carposporangial areas as at present interpreted by the writer, but are distinctly pigmented in surface view (Fig. 3), a feature distinct from corresponding areas in *Porphyra* and closely related genera.

The spermatangial sori occur most commonly in an irregular band across the lower middle part of the blades, and can frequently be detected



Figs. 1-5 *Smithora naiadum* (C. L. Anderson) comb. nov.
Fig. 1. Habit Sketch of *Smithora* showing one blade with terminal deciduous sori (a), numerous small marginal sori (b), and spermatangial sori (c), × 2.5.
Fig. 2. Section through mature terminal deciduous sorus, × 400.
Fig. 3. Surface view of a portion of a spermatangial sorus, × 600.
Fig. 4. Section of spermatangial sorus, × 600.
Fig. 5. Section through one of the small marginal sori showing the formation of "neutral spores", × 400.

with the naked eye. They may be marginal in position, but do not usually occur on the terminal half of the blade. Upon sectioning such areas it is immediately evident that they represent stages in the development of spermatangia. The first two cell divisions occur at right angles to the plane of the blade and the third division in the plane of the blade. Probably a still earlier division perpendicular to the plane of the blade accounts for the common surface appearance of cells in groups of eight on either side of the blade (Fig. 3). The sequence of cell division is practically identical with that described by Hus (1902) for carpospore development. However, a final very unequal division, readily detected only in sectional view (Fig. 4), cuts off the very pale spermatangia from the distinctly pigmented mother cells. Frequently the wall cutting off spermatangia is somewhat curved as described for *Erythrotrichia* by Berthold (1882), who considers the spermatangia of that genus homologous in origin with monospores. Furthermore, the spermatangia are relatively large as in *Erythrotrichia*, without evident pigment but with a relatively distinct plastid. Spermatangia are conical to spherical and measure 3-4 μ in diameter. The pigmented cells from which the spermatangia are cut off are probably capable of cutting off additional spermatangia at later fruiting periods, although no evidence was obtained on this point. Since the spermatangial mother cells are pigmented it seems obvious why Hus (1902) failed to find spermatangia and may have interpreted stages in their development as "sporocarps".

On several occasions the writer placed pieces of blades bearing seemingly mature spermatangia each in a drop of sea water on cover glasses in covered dishes. Many of such pieces released numerous spermatia within 12 hours.

When a given blade is found to bear mature spermatangial areas other blades from the same base will usually be found to bear these structures also, although many blades of the same collection or on the same leaf of the host may bear no spermatangial areas. The significance of this observation is not clear. Also, no satisfactory explanation is available for the observation that spermatangia occur most commonly on blades of medium size.

Berthold (1882) describes the formation of spermatangia in *Erythrotrichia*. He indicates that they are cut off from a pigmented cell in a manner similar to that described for *Smithora*.

FERTIZATION:—Berthold (1882) illustrates for *Erythrotrichia* structures which he interpreted to be trichogynes with spermatia attached. He states that carpogonia are very infrequent, and he concludes that fertilized carpogonia are released as single undivided cells, although he had only negative evidence for his conclusion, namely his failure to find evidence of a division of the cells which he interpreted to be carpogonia. Knox (1926) claims to have observed fertilization in *Porphyra naiadum*, but in view of the fact that she claims to have seen spermatangia but once and was

evidently not aware of the distinctive manner of their external abscission, it seems doubtful that she really observed fertilization.

Repeated efforts by the writer to obtain information concerning fertilization in *Smithora* have thus far been fruitless. Sections of the several types of sori at different stages of development were repeatedly made, but no structures were found which could be positively identified by the writer as carpogonia with trichogynes or with spermatia attached. Indeed, as Drew (1956) points out, convincing evidence concerning the details of fertilization in any of the Bangiophycidae is still lacking.

Asexual Reproduction

DECIDUOUS SORI:—Hus (1902) and Smith (1944) seem not to have observed a relatively conspicuous type of sorus common in *Smithora*. This type of sorus is formed at the distal ends of the blades. It seems to have been first described by Knox (1926) who also observed that these sori are released as entire units. The reproductive cells formed in this type of sorus were at first interpreted by the writer as monospores or neutral spores, since each cell seems to be transformed into a single spore-like body, the blade remaining monostromatic (Fig. 2). The sori occur as irregular and mostly terminal areas on the blades. They usually form a single continuous strip (Fig. 1). When first recognizable the sorus is delimited at its inner margin by a faint clear line. The cells gradually become more rounded in surface view and slightly more deeply pigmented. At this time sections show that the cells have become more elongate in a line perpendicular to the plane of the blade, and the latter has, thus, become slightly thicker in the area of the sorus. On the outer margin of the sori one or more rows of cells remain as a vegetative strip. At no time does the sorus become distromatic, although a medial indentation occurs in each cell (Fig. 2). Slightly plasmolyzed cells indicate that this indentation is probably related to slender cytoplasmic connections between adjacent cells.

When mature these sori loosen along the clear line previously mentioned and the entire sorus is shed, as observed by Knox (1926), leaving only the tattered narrow marginal strip of sterile cells, which is likewise soon lost. Wall layers on either side of the discharged sorus often remain intact immediately following its release. These delicate layers, from between which the reproductive mass has been released, are likewise soon lost. The discharged mass of cells is very gelatinous, as decribed by Knox (1926), and readily adheres to various objects.

During the summer months a new sorus is commonly evident back of the older one before the latter is shed, its boundaries indicated by the clear line previously mentioned. There is, furthermore, considerable evidence that the formation and release of these sori is a periodic phenomenon related to periods of low tides. On the morning of June 29, 1953, almost every mature blade of this plant bore this type of sorus. Since it was a sunny day, these sori could readily be detected by holding one's hand under a clump of slightly submerged blades. On this particular

morning the sori were so ripe that, when some of the plants were taken into the laboratory for examination, the inside of the plastic bag in which they had been placed was covered with numerous shed sori, and relatively few could be found attached. July 27 and 28 were the days when the lowest tides occurred in the tidal series. Three additional periods of release of sori were observed later the same summer, and in each case the time of release of most of the sori occurred within a day or two of the time of lowest tides of the respective series. On approximately 15 other times during that summer, when plants from the same area were examined in the laboratory, only immature sori were found.

During the summers of 1954 to 1957, inclusive, a heavy release of these sori was observed five times, once on the day of the lowest tide of the series, once the day following, once one day before, once two days before, and once three days before the lowest tide of the series.

In most cases the release is very sharp, few mature sori being found the day following the day of general sorus release. Sometimes, however, intact sori could be found several days after most of the sori had been released. It was found possible in most cases to predict fairly accurately the time of release of the sori. The periodic release of these sori at first led the writer to suspect that the cells of the sori might represent fertilized or unfertilized carpogonia as reported by Berthold (1882) for *Erythrotrichia* and by Smith and Hollenberg (1943) for *Porphyrella*. Knox (1926) seems to have concluded that these gelatinous masses constitute a vegetative type of reproduction, the released sori adhering to the host and directly forming the cushion-like basal part of the plant. The writer made certain observations which seem to point in the same direction. When these gelatinous sori are placed on slides or cover glasses in the culture solutions, the cells mostly disintegrate within a few days as Knox observed. However, during the summer of 1957 several such masses were kept in a seemingly healthy state by placing them in a continuous flow of sea water in the culture dishes. Not only did the cells retain their normal color for a period of about 30 days, until overrun by diatoms, but the masses became firm, indicating that new cell walls had probably been formed. At this stage they very closely resembled the basal pads of the plants found in the ocean. In no case, however, was any indication of erect blades observed. It must be kept in mind that in their natural habitat these plants occur exclusively on *Phyllospadix* or on *Zostera*, but it is of interest that despite the frequent observation of great numbers of these gelatinous masses in the tide pools adjacent to plants recently having released these sori, no such gelatinous masses were found clinging to the host.

If these deciduous sori represent a vegetative type of reproduction functioning in the manner suggested by Knox (1926), their periodic release during series of low tides would seem to be best understood as a means of facilitating attachment to the host or to some other substrate. Culture studies indicate some interesting possibilities in this connection.

but the fact that *Smithora* is an obligate epiphyte presents serious difficulties for culture studies.

In a private communication Dr. E. Yale Dawson reports finding only these deciduous sori and no other type of reproductive structure in all of the specimens collected from the coast of Baja California, Mexico and has suggested that sexual reproduction may normally occur only in the northern part of the range of this plant. The writer's observations indicate that the plant is more vigorous for the most part in the cooler northern waters.

NEUTRAL SPORES:—No previous workers have mentioned the occurrence of another type of sorus, which is usually abundant on the blades of *Smithora* in the Monterey region during the summer. These smaller but more numerous sori occur almost exclusively at the margins of the blades and consist of very small and relatively deeply pigmented swellings or seemingly local malformations of the margins of the blades (Figs. 1, 5). They are of variable sizes and shapes and are mostly about 100 μ in diameter. Sections show that the larger ones are hollow and that this form results from a local bulging and buckling of the blade, due it seems, to the activity of the cells in forming the spores. The latter are cut off unilaterally from the sorus.

In the Monterey region these small non-deciduous sori usually do not appear as early in the summer as the terminal deciduous sori. For example, very few of the small marginal sori were observed during the summer of 1954, although an abundance of the deciduous terminal sori were found. During June of 1957 not a single instance of the former was seen while examining a number of collections, but by the latter part of July of the same year this type of sorus was abundant in the same collecting area. It should also be noted that none of these non-deciduous sori has yet been found on the larger form of *Smithora* growing on *Zostera*, even when these structures were very abundant on the smaller form of the plant growing on *Phyllospadix*.

On numerous occasions bits of the marginal tissue of blades bearing one or more of these marginal sori were detached and placed on cover glasses in culture solution. Almost invariably numerous spores were found to have been discharged within 24 hours. For example, on August 10, 1953, ten such sori were placed in culture solution. The next morning all but one had discharged spores. In some cases 50-100 spores had been discharged. These spores are formed singly, and surface and sectional views show that the wall cutting off the spores is somewhat curved (Fig. 5). Culture studies of the development of these spores, to be described in a later paper, indicate that they are probably neutral spores. The release of these spores seems to be more or less continuous and unrelated to stages in the tidal series.

Bits of seemingly sterile portions of the blades and also basal pads detached from the *Phyllospadix* were similarly placed in culture solution

on several occasions in an effort to determine whether some type of spore might be formed by seemingly sterile portions of the plant. Results of these experiments were always negative.

If the deciduous terminal sori are, indeed, exclusively a sort of vegetative means of propagation as suggested by Knox (1926), and if the smaller marginal sori constitute another type of asexual reproduction, as the writer believes, it seems likely that these asexual means of reproduction are so highly successful that sexual reproduction has become a less prominent feature in the life cycle. This might account for the seeming difficulty of finding carposporangial sori. The writer has observed that sexual reproduction is rare in certain red algae which have developed special vegetative means of propagation.

Relationships

The observations reported herewith make it clear that the plant which has for so long been known as *Porphyra naiadum* C. L. Anderson can no longer be considered a member of that genus. The newly proposed genus *Smithora* must be placed in the suborder Erythrotrichieae rather than in the Bangieae. This is indicated by the lack of rhizoidal processes from the lower cells of the blades, but more definitely by the manner in which the spermatangia are cut off externally from the pigmented cells of the blades. That the plant belongs in the Erythropeltidaceae is indicated by the formation of several blades from the cushion-like base. *Smithora* differs from *Erythrotrichia* and from *Erythropeltis* in the very distinctive, deciduous, terminal sori which seem to be released periodically in relation to periods of low tides, and which seem to constitute an unusual type of asexual reproduction not as yet fully understood.

Culture studies, the fuller results of which will be presented in a later paper, are still in progress. These have yielded some interesting, but so far inconclusive, information concerning the life cycle and the nature of the several types of reproductive structures.

Summary

Smithora must be considered as a new genus in the Erythropeltidaceae. From *Porphyra* and closely related genera it differs in the origin of several blades from a common base, in the lack of rhizoidal processes in connection with the attachment organ, and especially in the manner in which spermatangia are cut off singly from pigmented cells. Carpospores are infrequent, arising in packets of eight as described by previous workers. Two distinctive types of asexual sori are formed. Large terminal sori are released as entire units. Their release seems to be periodic, occurring during series of low tides. They seem to represent an unusual type of asexual reproduction. Another type of sorus is described for the form of the plant growing on *Phyllospadix*. These smaller and more numerous sori occur on the margins of the blades and produce what seem to be neutral spores.

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PACIFIC NATURALIST, VOL. 1

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