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Taxonomic and distributional notes on northeast Pacific Antithamnieae (Ceramiales, Rhodophyta)

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The number of species of antithamnioid algae recognized as occurring along the Pacific coast of North America from Alaska to Oregon is reduced from 17 to 12. *Antithamnion alternans* and *A. asymmetricum* are conspecific with *Antithamnionella pacifica,* and *Antithamnion simulans* is conspecific with *Scagelia pylaisaei. Antithamnion dendroideum* does not appear to be present in the area; the single record from southeast Alaska remains unconfirmed. *Antithamnion gardneri* and *Antithamnionella glandulifera* are conspecific with *Antithamnionella spirographidis,* which is recorded from Prince William Sound, Alaska to Baja California, Mexico in the northeast Pacific; *A. miharae* from Japan is also considered a synonym of *A. spirographidis. Antithamnionella shimamurana* comb. nov. has not been confirmed to occur east of the Aleutian Islands. New northern distribution records are established for *Hollenbergia subulata, Platythamnion reversum,* and *P. villosum.* The recognized northern distribution limit of *Antithamnion kylinii* is southern British Columbia, not southeast Alaska, and that of *Hollenbergia nigricans* is central British Columbia, not southwest Alaska.

Key Index Words: *Antithamnieae*—Antithamnion—Antithamnionella—*biogeography*—*Ceramiaceae*—*Ceramiales*—Hollenbergia—*northeast Pacific*—Platythamnion—*Rhodophyta*—Scagelia—*taxonomy.*

At present count 17 species of antithamnioid algae are recorded as occurring on the Pacific coast of North America from Alaska to Oregon (LINDSTROM 1977, PHINNEY 1977, SCAGEL *et al.* 1986). These include eight species of *Antithamnion,* four of *Platythamnion,* two of *Antithamnionella,* two of *Hollenbergia* and one *Scagelia.* Among these are the three remaining species of the 13 species of *Antithamnion,* first described by GARDNER (1927a, 1927b), that have not been investigated since their original description.

In order to ascertain the identities of these taxa and to confirm their distributions in the area from Oregon to Alaska, we have examined type specimens for most of the species and have checked records of all the species present in *UBC* (herbarium abbreviations after HOLMGREN *et al.* 1981; an exclamation mark after a specimen designation indicates that the specimen has been examined by us).

Our research indicates that only 12 species of antithamnioid algae should be recognized as occurring from Alaska to Oregon: two species of *Antithamnion* (*A. defectum* and *A. kylinii*), three *Antithamnionella* (*A. pacifica, A. shimamurana,* and *A. spirographidis*), two *Hollenbergia* (*H. nigricans* and *H. subulata*), one *Scagelia* (*S. pylaisaei*), and four *Platythamnion* (*P. heteromorphum, P. pectinatum, P. reversum,* and *P. villosum*). We follow MOE and SILVA (1980) in not recognizing the tribe Heterothamnieae; we therefore attribute these species to the Antithamnieae *sensu lato.*

Materials and Methods

Herbarium specimens were identified by direct observation, using a Zeiss dissecting microscope, or slides were prepared by cutting out a small portion of a specimen along with the mounting paper, staining with acetic acid and aniline blue (HANSEN and SCAGEL 1981), and mounting in 20–50% corn syrup. Microscope slides were examined with a Leitz Dialux compound microscope. Photographs

are of liquid preserved specimens stained as above, or of unstained material mounted on slides in corn syrup. Photographs were taken on the Zeiss dissecting microscope or on the Leitz compound microscope.

Results

ANTITHAMNION NAEGELI 1847

Following WOLLASTON (1972b), *Antithamnion* is circumscribed by these features: 1) erect or prostrate thalli lacking rhizoidal cortication and with equal and opposite whorl-branches, the basal cells of which bear no branches and are distinctly smaller (usually quadrate in shape) than the more distal whorl-branch cells, 2) gland cells on special branches, 2–5 cells in length, borne abaxially or adaxially on whorl-branches or their ramuli, 3) tetrasporangia cruciately divided and usually ovoid when mature, 4) procarps numbering 2–20 and borne on basal cells of whorl-branches or whorl-branch ramuli and 5) only one carposporophyte matures at each fertile branch apex. WOLLASTON pointed out that there appear to be two clusters of species, those from southern Australia that closely resemble the type species, *A. cruciatum,* and those from the northeast Pacific. Representatives of both of these groups occur in the northwest Pacific (Japan).

Antithamnion defectum KYLIN 1925

Antithamnion defectum is a common and widespread taxon in the local area. It is distributed from Prince William Sound, Alaska (HANSEN *et al.* 1982) to Baja California, Mexico (WOLLASTON 1976). The species has a thallus consisting of erect branches from a prostrate base. It is readily identified by its opposite whorl-branches that are pectinately branched adaxially and by the absence of a whorl-branch opposite each indeterminate branch (Fig. 1). Basal cells of whorl-branches are conspicuously smaller than more distal cells (Fig. 1) and gland cells are present on reduced whorl-branch ramuli. Other distinguishing features are listed in Table 1.

WOLLASTON (1972a) apparently did not see the type specimen of *Antithamnion defectum* when she reviewed the species of *Antithamnion* and related genera on the Pacific coast of North America. For this and other species for which she did not see the type specimen, she queried the herbarium (*LD*? for *A. defectum* and *Antithamnionella glandulifera* and *TCD*? for *Antithamnionella pacifica*). Moreover, WOLLASTON appears to have selected one of the localities from the original protologue of each species and designated it as the type locality. By indicating type locality and herbarium, WOLLASTON has effectively lectotypified those species with a single specimen from that locality in the designated herbarium. For *Antithamnion defectum,* however, the indication of Friday Harbor does not clearly select a single specimen as there are three in *LD*! with this locale written on them in KYLIN's hand. Although WOLLASTON included "growing on piles on the dock" as part of the type locality description, none of the *LD* specimens indicates where it was growing. Because one of the specimens already has been designated "Typus" by an unknown person (PER LASSEN, pers. comm.), we recognize this specimen as the lectotype. This specimen is labeled "Canoe Island, Friday Harbor, 24 June 1924", by H. KYLIN. Two other specimens on the same sheet, labeled "Friday Harbor, 30 June 1924", and "Canoe Island, Friday Harbor, 22 July 1924", would be paralectotypes.

Antithamnion dendroideum SMITH *et* HOLLENBERG 1943

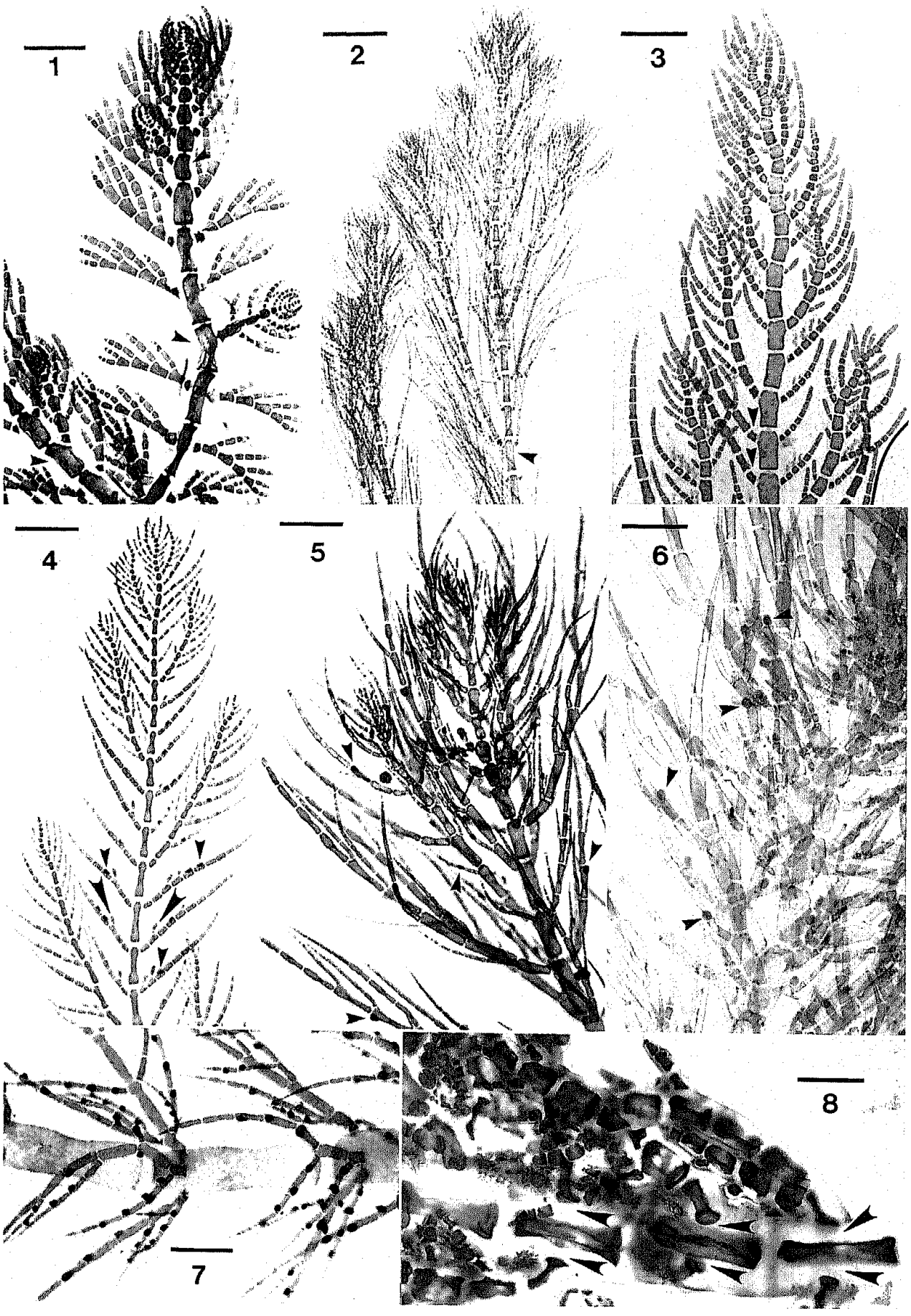
Antithamnion dendroideum (type locality: near Monterey, California) has been recorded by ROSENTHAL and BARILOTTI (1974) from Khaz Bay in southeast Alaska. We have not been able to locate any specimens from their collections, and we have found no other material referable to this taxon in the study area. We therefore reinterpret the distribution of *A. dendroideum* as central California to Baja California, Mexico (WOLLASTON 1972a, 1976).

Antithamnion kylinii GARDNER 1972b

Antithamnion kylinii (type locality: Victoria,

Table 1. Comparison of features of species of *Antithamnion, Hollenbergia, Scagelia,* and *Antithamnionella* occurring in British Columbia and adjacent waters.

	Antithamnion		*Hollenbergia*		*Scagelia*	*Antithamnionella*	
	defectum	*kylinii*	*nigricans*	*subulata*	*pylaisaei*	*pacifica*	*spirographidis*
Usual number of whorl-branches	2	2	2(3)	3	3	2	2(3)
Placement of whorl-branches on axial cell	Distal	Distal	Medial	Distal	Distal	Distal	Distal
Branching of whorl-branches	Adaxial	Adaxial	Distichous	Distichous to pseudodichotomous to 3 orders	Distichous to pseudodichotomous to 3 orders	Unbranched	Unbranched
Size of basal cell of whorl-branch relative to more distal cells	Smaller	Smaller	Same size	Same size	Same size	Smaller	Same size
Ramulus on basal cell of whorl-branch	No	No	No	Yes/no	Yes/no	No	No
Maximum diameter of axial cells	120 μm	120 μm	300 μm	300 μm	400 μm	100 μm	50 μm
Position of gland cells	Short, small-celled ramuli	Short, small-celled ramuli	Lateral	Terminal	Lateral, near base of branch	None	Lateral, near base of branch
Position of tetrasporangia	Mostly one-celled pedicels, adaxial on proximal cells of whorl-branches	One-celled pedicels	1-several celled pedicels	On adaxial ramuli	Sessile, adaxial on proximal cells of whorl-branches	Pedicellate, adaxial on whorl-branches or in place of whorl-branches	Sessile, adaxial on proximal cells of whorl-branches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British Columbia) is distinguished from *A. defectum* by its totally erect habit and by the presence of a whorl-branch opposite each indeterminate lateral branch (Fig. 2). Other features are listed in Table 1. This taxon has been reported north of southern British Columbia only once (ROSENTHAL and BARILOTTI 1974). Since no voucher specimens could be located for this record from Khaz Bay, southeast Alaska, and since there are no other reports of this taxon from northern British Columbia or southeast Alaska (SCAGEL *et al.* 1986), the distribution of this taxon is emended to southern British Columbia to Baja California, Mexico (WOLLASTON, 1976). In British Columbia this taxon is very uncommon, there being only four collections in *UBC* in addition to an isolectotype specimen (*UBC A2246*!). These records are from Ladysmith Harbour, Vancouver I. (*UBC A64975*!), from Grappler and Bamfield Inlets, Bamfield, Vancouver I. (*UBC A41880*! *A47739*!) and from Tribune Bay, Hornby I., Strait of Georgia (*UBC A68732*!).

ANTITHAMNIONELLA LYLE 1922

WOLLASTON (1968, 1972b) supported recognition of *Antithamnionella* as distinct from *Antithamnion* and circumscribed the genus as follows: 1) distinct form of apical development of branches (i.e. a sinusoidal apex with one of a pair of whorl-branch initials cut off in a series from successive axial cells, first on one side of the axis, then on the other, with the apex flexing away from the side where the most recent series of initials has been produced), 2) inconsistency in number and branching of whorl-branches, 3) gland cells adaxial on whorl-branch cells, 4) tetrasporangia often tetrahedrally divided and nearly spherical in shape, 5) spermatangia (as "spermatangial mother cells") cut off laterally rather than terminally and 6) only 1–3 procarps produced per branch apex, each borne on a reduced whorl-branch. MOE and SILVA (1980) pointed out that only in certain species of *Antithamnionella* [i.e. *A. floccosa* (O.F. MUELLER) WHITTICK (as *Antithamnion floccosum*), *Antithamnionella spirographidis* (SCHIFFNER) WOLLASTON, *A. glandulifera* (KYLIN) WOLLASTON and *A. pacifica* (HARVEY) WOLLASTON, and we would add *A. miharae* (TOKIDA) ITONO and *A. shimamurana* (NAGAI) comb. nov.] does whorl-branch initiation proceed as described above and illustrated by WOLLASTON (1972b and Table 2 therein). This pattern does not appear to occur in *A. sarniensis* LYLE, the lectotype species of *Antithamnionella* (L'HARDY-HALOS 1986, Figs. 9, 10). SUNDENE (1964) suggested that *A. sarniensis* and *A. spirographidis* are conspecific, but L'HARDY-HALOS (1986) demonstrated that the two species do not hybridize and that there are several characters by which they can be distinguished. In light of L'HARDY-HALOS' results, MOE and SILVA's (1980) sug-

Fig. 1. Habit of *Antithamnion defectum* showing absence of whorl-branches on axial cells that bear indeterminate branches (arrows). *Lindstrom 5620*, Cape Suspiro, Alaska. Scale bar = 135 μm.

Fig. 2. Habit of *Antithamnion kylinii* showing whorl-branches present on axial cells that bear indeterminate branches (arrow). *UBC A64975*, Ladysmith, Vancouver I., B.C. Scale bar = 385 μm.

Fig. 3. Sinusoidal apex of male plant of *Antithamnionella pacifica* showing unequal development of opposite pairs of whorl-branches and basal cells (arrow) of mature whorl-branches that are smaller than more distal cells. *Gabrielson 364*, Whiskey Pt., Quadra I., B.C. Scale bar = 90 μm.

Fig. 4. Habit of *Antithamnionella spirographidis*. Note sinusoidal apices of indeterminate branches, lateral gland cells on whorl-branches (small arrows) and oblong, immature tetrasporangia (large arrows) also borne on whorl-branches. *Gabrielson 242*, Deep Cove, B.C. Scale bar = 135 μm.

Fig. 5. Apex of female plant of *Scagelia pylaisaei* with lateral gland cells (arrows). *Gabrielson 300*, Pt. Atkinson, B.C. Scale bar = 135 μm.

Fig. 6. *Hollenbergia subulata* apex showing subterminal gland cells (arrows) on whorl-branches. *UBC A54962*, Lasqueti I., B.C. Scale bar = 135 μm.

Fig. 7. Unequal development of three whorl-branches per mature axial cell of *Scagelia pylaisaei*. Note conspicuous dark-staining gland cells on whorl-branches. *Gabrielson 300*, Pt. Atkinson, B.C. Scale bar = 135 μm.

Fig. 8. Portion of rehydrated isotype specimen (No. *944*) of *Hollenbergia nigricans* from *UBC* copy of *Phycotheca Boreali-Americana*. Note pairs of whorl-branches (arrows) borne mid-way along axial cells. Scale bar = 135 μm.

gestion, that species of *Antithamnionella* with sinusoidal indeterminate apices should be placed in a segregate genus, merits consideration.

Antithamnionella pacifica (HARVEY) WOLLASTON 1972a

Antithamnionella pacifica originally was described by HARVEY (1862) as *Callithamnion floccosum* var. *pacificum,* a variety of an Atlantic species. KYLIN (1925) raised the variety to specific status. WOLLASTON (1972a) made the combination *Antithamnionella pacifica,* and she included *Antithamnion uncinatum* GARDNER 1927b as a variety, making the new combination *A. pacifica* var. *uncinata.* The distinctness of this northeast Pacific species has made it an easily identifiable taxon in the local flora (Table 1; Fig. 4). It is common and widely distributed, from Baja California (WOLLASTON 1976) to the Aleutian Is. (HANSEN *et al.* 1982).

WOLLASTON (1972a) indicated Esquimalt to be the type locality of *Antithamnionella pacifica* and included "on stems of larger algae" as part of the type locality description. However, she queried the location of the type in *TCD.* HARVEY (1862) originally had referred to specimens from both Orcas I. [Washington] and Esquimalt, and KYLIN (1925) followed HARVEY in mentioning type specimens from both localities. Only specimens from Orcas I. can be found in *TCD*!. All were collected in April 1858 by DAVID LYALL. One of the specimens also has "found covering the stem of larger algae" in HARVEY's hand; it is the only specimen to have "var. ß. pacificum" in HARVEY's hand. It is this specimen that should be considered the lectotype. In addition to the specimens in *TCD,* three HARVEY specimens are in *K-BM*! Two of these are also from Orcas I. and were found on stems of larger algae. The third, collected by DAVID LYALL, Feb. 1859, at Esquimalt, does not include information on where it was growing.

During our examination of some of GARDNER's species of *Antithamnion,* we came across two that clearly belong to this species. *Antithamnion alternans* GARDNER (1927a, type locality: Cook Inlet, Alaska) is represented by *UC 296622*! (*G.B. RIGG & R.J. GRIGGS* No. *61*). The basal cells of the simple, usually opposite whorl-branches are smaller than more distal cells and nearly quadrate; branch tips are acute, and "tetrahedral" tetrasporangia (55–60 × 68–75 μm) are pedicellate, branched or unbranched, and adaxial on whorl-branches. An unusual feature of this specimen is the occurrence of tetrasporangial branches in place of whorl-branches along the main axis or abaxially on the basal cell of a whorl-branch rather than adaxially on the basal or suprabasal cells. Such a disposition of tetrasporangia has been observed on several relatively coarse *Antithamnionella pacifica* specimens from Alaska (*UBC A23065*!, Lituja Bay, and *A20853*!, Coronation I.). Gland cells are absent. *Antithamnion alternans* has the habit of a robust *Antithamnionella pacifica,* and we consider the former to be a synonym of the latter.

Antithamnion asymmetricum GARDNER 1927b (type locality: Sitka, Alaska) is represented by *UC 296633*! (*NLG* No. *3937*). It also has the habit of *Antithamnionella pacifica,* with slightly recurved, simple, opposite whorl-branches whose basal cells are slightly to distinctly smaller than more distal cells. Gland cells are absent, and branch tips may or may not be acute. Near the apex, branches are arranged in alternate secund series of three's. Tetrasporangia are pedicellate. Based on the features listed above, we consider *Antithamnion asymmetricum* a synonym of *Antithamnionella pacifica.* In summary, then, we list below the synonyms of this species:

Antithamnionella pacifica (HARVEY) WOLLASTON 1972a, p. 87

BASIONYM: *Callithamnion floccosum* var. *pacificum* HARVEY 1862, p. 176

=*Antithamnion floccosum* var. *pacificum* (HARVEY) SETCHELL *et* GARDNER 1903, p. 341

=*Antithamnion pacificum* (HARVEY) KYLIN 1925, p. 47, Figs. 28a-d?, 29a-f, 30f?

=*Antithamnion alternans* GARDNER 1927a, p. 377, Pl. 78 (Figs. 1, 2)

=*Antithamnion asymmetricum* GARDNER 1927b, p. 411
=*Antithamnion uncinatum* GARDNER 1927b, p. 408 Pl. 89 (Fig. 2), Pl. 90

We would like to reiterate (LINDSTROM 1987) the need for experimental work to determine just how closely related Pacific *Antithamnionella pacifica* is to Atlantic *A. floccosa*. Morphologically, these two species have failed to diverge in any significant features. Whorl-branches are paired, simple, subequal, subulate, and taper to an acute tip; they are arranged distichously. Indeterminate branches replace whorl-branches usually every third axial cell and alternate from one side of the rachis to the other. Gland cells are rare if not entirely absent (never seen by us in *A. pacifica*; reported not to occur in *A. floccosa* by WHITTICK 1980). Tetrasporangial, male, and female reproductive structures and post-fertilization development also are identical.

Antithamnionella spirographidis (SCHIFFNER) WOLLASTON 1968

SCHIFFNER (1916, p. 137) described *Antithamnion spirographidis* based on specimens that he collected from the harbor at Trieste on August 12 and 14, 1914 growing in 0.5–3 m on the tube worm *Spirographidis*. He provided a detailed description and figures of the habit (erect axes to 10 mm from creeping filaments with rhizoids formed from the basal cells of opposite whorl-branches), branch initiation (in unilateral alternating series from the high side of subapical cells such that the major axis has a sinusoidal appearance), gland cells (sparsely present and not well-developed to abundant and well-developed on the second and third cells of whorl-branches), tetrasporangia (adaxial and sessile on basal and second cells of whorl-branches to 50 μm diameter and tetrahedrally, although appearing cruciately, divided) and spermatangia (adaxial in series on whorl-branches). WESTBROOK (1934) first described cystocarpic plants collected at the Davenport Dockyard and Plymouth Sound in England. Her observations on the habit, gland cells, tetrasporangia and spermatangia corroborated those of SCHIFFNER, as did FELDMANN-MAZOYER's (1941, pp. 265-267) based on Mediterranean Sea collections and WOLLASTON's (1968, pp. 345-347) based on Australian collections. WOLLASTON (1968) transferred *A. spirographidis* to *Antithamnionella* LYLE (1922).

GARDNER (1927a) described *Antithamnion tenuissimum* based on material collected in the drift from La Jolla, California and grown in an aquarium (WOLLASTON 1972a). *Antithamnion tenuissimum* GARDNER is antedated by *A. tenuissimum* (HAUCK) SCHIFFNER (1916) based on type material from the Adriatic Sea, and therefore DE TONI (1936) proposed the substitute name *A. gardneri* for GARDNER's specimen. GARDNER described his plant as erect to 30–60 mm with opposite whorl-branches that produce rhizoids from their basal cells, gland cells sparse and tetrasporangia adaxial in series of 3–6 on whorl-branches, sessile and nearly tetrahedrally divided. DAWSON (1962) stated that *Antithamnion gardneri* was equivalent to *Antithamnion spirographidis*, but he gave no reason for his opinion. UMEZAKI (1963) reported *A. gardneri* from Osaka, Japan and for the first time described and illustrated spermatangia in this species. His illustrations of habit, rhizoid formation and tetrasporangial position agree with those of GARDNER, but axial cell diameters are smaller than those reported by GARDNER, and tetrasporangia are larger (Table 2).

WOLLASTON (1972a) included *A. gardneri* under "doubtful species or records". Although she agreed with DAWSON's suggestion regarding the identity of GARDNER's specimen, she did not propose *A. gardneri* as a synonym of *Antithamnionella spirographidis*. We have re-examined GARDNER's original glycerine slides of *Antithamnion tenuissimum* (=*A. gardneri*) (*UC 296692*!=GARDNER *5085a*, the holotype), and although in poor condition, they clearly represent a species of *Antithamnionella* based on vegetative features, including a sinusoidally curved apex with whorl-branch initials developing in a series first on one side of the main axis and then on

Table 2. Comparison of features of *Antithamnion gardneri*, *Antithamnionella glandulifera*, *Antithamnionella miharae*, *Antithamnionella spirographidis*, and *Antithamnion tenuissimum* GARDNER non SCHIFFNER.

	A. gardneri	*A. glandulifera*			*A. miharae*	*A. spirographidis*				*A. tenuissimum*
Source	UMEZAKI (1963)	KYLIN* (1925)	DAWSON* (1962)	WOLLASTON (1971)	TOKIDA* (1942)	SCHIFFNER* (1916)	WESTBROOK* (1934)	FELDMANN-MAZOYER* (1940)	WOLLASTON (1968)	GARDNER (1927a)
Axial cell diameter	32–50 μm	60–100 μm	30–40 μm	30–35 μm	70–112 μm	60 μm	20–45 μm	30–40 μm	30–50 μm	60–75 μm
Axial cell length/width ratio	5–8	3–5	1.5–2	8	3–6	1.5–3	3–7	8–10	3–6	n.g.
Pattern of whorl-branch initiation at apex	unilateral in alternating series	n.g.	n.g.	unilateral in alternating series	unilateral in alternating series	unilateral in alternating series	unilateral in alternating series	unilateral in alternating series	unilateral in alternating series	unilateral in alternating series
Number of whorl-branches	2	2	2(3)	2(3–4)	2(3)	2	2	2	2	2
Origin of rhizoids	Basal cells of whorl-branches	n.g.	n.g.	n.g.	Basal cells of whorl-branches	Axial cells at base	Basal cells of whorl-branches	Basal cells of whorl-branches	Basal and occas. 2nd cell of whorl-branch	Basal cells of whorl-branches
Presence of gland cells	Present	Abundant	Absent, occasional, or abundant	Present	Sparse	Sparse to abundant	Sparse	Absent to sparse	Sparse	Sparse
Position of gland cells	Adaxial	Adaxial on inner cells of whorl-branches	Inner & central cells of whorl-branches	Adaxial on inner to central cells of whorl-branches	Adaxial on 2nd cell of whorl-branches	Adaxial on inner cells of whorl-branches	Adaxial on inner cells of whorl-branches	Adaxial on inner cells of whorl-branches, esp. 2nd cell	Adaxial on 2nd or 3rd cell of whorl-branches	On cells of whorl-branches
Position of tetrasporangia	Adaxial on whorl-branches	Sessile on 2nd and more distal cells of whorl-branches	Sessile on lower 2 cells of whorl-branches	Sessile, adaxial on inner to central cells of whorl-braches	Sessile, adaxial on inner 2–3 cells of whorl-branches	Adaxial on inner cells of whorl-branches	Sessile, adaxial on inner one or two cells of whorl-branches	Sessile, esp. 1st cell	Sessile, basal and occas. 2nd cell of whorl-branches	Adaxial on cells of whorl-branches
Size and shape of tetrasporangia	24–45 μm × 40–75 μm, orbicular-ovate	n.g., ovoid	35–50 μm, ellipsoidal, ovoid	>60 μm long ovoid-subspherical	32–48 μm × 48–66 μm, ellipsoid-ovoid	50 μm long, ovate	30 × 50 μm, ellipsoidal	35 × 60 μm, ovoid	30–35 μm × 40–48 μm, ovoid	18–22 μm × 34–38 μm, broadly ellipsoidal
Division pattern of tetrasporangia	Most cruciate, some tetrahedral	Cruciate	Tetrahedral	Cruciate or tetrahedral	Tetrahedral	Tetrahedral	Tetrahedral toward cruciate	Cruciate or tetrahedral	Tetrahedral	Almost tetrahedral

* As *Antithamnion*

n.g. = not given

the other. Tetrasporangia are sessile, a feature characteristic of *A. spirographidis,* and gland cells are sparse. GARDNER's tetrasporangia have smaller dimensions than any others reported for *A. gardneri* or *Antithamnionella spirographidis,* but in all other vegetative and reproductive features that have been observed, there is close agreement (Table 2). Thus, we consider *Antithamnion gardneri* DE TONI a synonym of *Antithamnionella spirographidis* (SCHIFFNER) WOLLASTON.

In the area from northern Washington to southeast Alaska, there are only two reported collections of *Antithamnion gardneri,* both from northern Puget Sound (PHILLIPS and VADAS 1967, PHILLIPS and FLEENOR 1970). We were able to examine only one of PHILLIPS and VADAS' collections, that from Smith I. (48°19′30″N, 122°50′33″W). The specimens (*UBC WS1487*!), including both tetrasporic and male thalli, are typical of *Antithamnionella* in their vegetative structure, and the pedicellate tetrasporangia are characteristic of *A. pacifica.* No other locally recorded species of *Antithamnionella,* including *A. spirographidis,* bears pedicellate tetrasporangia. We therefore suspect that all records of *Antithamnion gardneri* reported by PHILLIPS and VADAS (1967) and PHILLIPS and FLEENOR (1970) are *Antithamnionella pacifica.*

The only other report of *Antithamnion gardneri (as A. tenuissimum sensu* GARDNER) in the northeast Pacific is that of DOTY (1947), based on a specimen collected on floating timber in Coos Bay near Marshfield, Oregon. We have examined DOTY's original collection (*MD 2359* in *UC*!). It also belongs in *Antithamnionella* and is *A. spirographidis.* As noted by DOTY on the herbarium sheet and observed by us, branching is opposite; a branch occurs opposite each indeterminate axis; apices of cells are blunt to broadly rounded; gland cells are absent, and tetrasporangia are sessile. In his description, DOTY noted that "branching, cells and general proportions are quite like GARDNER's description and figures; however no gland cells were found and the largest tetrasporangia were about 50 × 70 μm." In a notation on the herbarium sheet, however, DOTY stated that most tetrasporangia are smaller.

While comparing the local species of *Antithamnionella* to *Antithamnion gardneri,* we discovered that *Antithamnionella glandulifera* (KYLIN) WOLLASTON, based on *Antithamnion glanduliferum* KYLIN (1925), also strongly resembles *Antithamnionella spirographidis.* KYLIN provided only a brief description of *Antithamnion gladuliferum,* citing only general habit features such as height, branching, presence of gland cells, size of axial cells and occurrence of sessile tetrasporangia (Table 2).

We have examined the only specimen of KYLIN's *Antithamnion glanduliferum* in *LD*! This specimen, epiphytic on a kelp, was collected at Friday Harbor, Washington, 18 July 1924. It conforms to KYLIN's original protologue and should be considered the lectotype.

During our investigations, we recognized that another North Pacific *Antithamnion, A. miharae* (TOKIDA 1942, type locality: Tomari Bay, Kunashiri I., Kurile Is.), also bore a striking resemblance to *Antithamnionella spirographidis.* When TOKIDA described *A. miharae,* he noted its similarity to both *A. glanduliferum* and *A. gardneri* (as *A. tenuissimum*), separating it from the former in having tetrahedrally divided tetrasporangia, fewer gland cells and the occasional presence of branched whorl-branches, and from the latter in less sparse branching more markedly tapered whorl-branches, shorter rhizoidal filaments without gland cells and somewhat larger axial cells and sessile tetrasporangia.

DAWSON (1962) stated that *Antithamnion miharae* "···is apparently exceedingly like, if not identical with *A. glanduliferum.*" He noted that SMITH (1944) had pointed out that tetrasporangia of *A. glanduliferum* are cruciate, but often appear as if tetrahedrally divided. DAWSON, in his key to North Pacific species of *Antithamnion,* segregated *A. gardneri,* which he believed to be conspecific with *A. spirographidis,* from *A. miharae* and *A. glanduliferum* based upon the common supression of one member of a pair of whorl-branches in the former, whereas whorl-

branch supression was said to occur only rarely in the latter two species. Our observations of numerous specimens of *Antithamnionella glandulifera* in *UBC* indicate, however, that one whorl-branch of a pair commonly is supressed (Fig. 3), as in *A. spirographidis.*

WOLLASTON (1972a) repeated DAWSON's and TOKIDA's observations that *Antithamnionella glandulifera* closely resembles *Antithamnion miharae.* She stated, however, that *A. glandulifera* most closely resembles *A. pacifica,* but was distinguished by having conspicuous gland cells and sessile tetrasporangia. She made no comparison between *A. glandulifera* and *A. spirographidis.*

YOSHIDA (1981), in observing the vegetative and reproductive morphology of *A. miharae,* also noted the similarity of this species to *A. glandulifera.*

Antithamnion scrippsiana (DAWSON 1949), a minute species with unbranched whorl-branches, no gland cells, and sessile, adaxial tetrasporangia has been synonymized with *A. glandulifera* DAWSON (1962).

Table 2 compares vegetative and reproductive features of *Antithamnion gardneri, Antithamnionella glandulifera, A. miharae* and *A. spirographidis* discussed above. It is evident that there are no consistent discontinuities that can be used to segregate these taxa. Size of thalli depends upon age of the plant, with reported sizes ranging from 3–5 mm to 80 mm. Likewise, diameter of axial cells and length to width ratios depend upon the location of the axial cells measured. Consistent among all the taxa is the pattern of whorl-branch initiation at the apex, number of whorl-branches per whorl, branching of whorl-branches, origin of rhizoids from the basal or second cell of whorl-branches, and the position of tetrasporangia, gland cells and spermatangia on whorl-branches. Gland cells range from abundant to rare to absent. The pattern of division of tetrasporangia varies from cruciate to tetrahedral, with both patterns being observed by some workers. Reports of sizes of tetrasporangia vary because sporangia continue to increase in size following cleavage into four spores. Based on the foregoing observations we propose the following synonymies:

Antithamnionella spirographidis (SCHIFFNER) WOLLASTON 1968, p. 345.

BASIONYM: *Antithamnion spirographidis* SCHIFFNER 1916, p. 137, Figs. 19–27.

=*Antithamnion gardneri* G. DE TONI 1936, p. 1

=*Antithamnion glanduliferum* KYLIN 1925, p. 47, Figs. 28e-g

=*Antithamnionella glandulifera* (KYLIN) WOLLASTON 1972a, p. 86

=*Antithamnion miharae* TOKIDA 1942, p. 90, Figs. 5, 6

=*Antithamnionella miharae* (TOKIDA) ITONO 1977, p. 24

=*Antithamnion scrippsiana* DAWSON 1949, p. 15, Figs. 26, 27, 58

=*Antithamnion tenuissimum* GARDNER 1927a, p. 377, Pl. 77 *non Antithamnion tenuissimum* (HAUCK) SCHIFFNER 1916

Most reports of *Antithamnionella spirographidis* (SCHIFFER 1916, WESTBROOK 1934, WOLLASTON 1968) have been from harbors or dockyards, except in the north Pacific, where, based on the above synonymies, the taxon is widespread, occurring from Prince William Sound, Alaska (HANSEN *et al.* 1982) to Baja California, Mexico (WOLLASTON 1976), in the southern Kurile Is. (TOKIDA 1942), and in eastern Hokkaido (YOSHIDA 1981). *Antithamnionella spirographidis* may have been introduced to localities outside the north Pacific by man.

Antithamnionella spirographidis is compared to other antithamnioid algae in the local area in Table 1.

Antithamnion shimamuranum NAGAI 1941

Antithamnion shimamuranum NAGAI (type locality: Minamishima, Ushishiru I., Kurile Is.) looks like an extreme form of *Antithamnionella floccosa-A. pacifica* in habit. Like the latter, *Antithamnion shimamuranum* cuts off a series of three to six whorl-branches along one side of the apex before switching to the other side. The basal cell of a whorl-branch tends

to be quadrate, and branch tips are acute. Gland cells are lacking. In contrast to *Antithamnionella floccosa-A. pacifica, Antithamnion shimamuranum* has its "tetrahedral" tetrasporangia borne on a single-celled pedicel; we saw no evidence of a multicellular pedicel, as is typical of *Antithamnionella floccosa-A. pacifica,* in the isotype material, *SAP 021972*!, that we examined. Moreover, the whorl-branches of *Antithamnion shimamuranum* are branched whereas they are unbranched in *Antithamnionella floccosa-A. pacifica.* These differences suggest that *Antithamnion shimamuranum* is a species distinct from *Antithamnionella floccosa-A. pacifica* although, as noted by NAGAI (1941), no doubt closely related to them. We therefore propose the new combination:

Antithamnionella shimamurana (NAGAI) LINDSTROM *et* GABRIELSON
BASIONYM: *Antithamnion shimamuranum* NAGAI 1941 p. 207 Pl. VI (Figs. 8–11)

PHILLIPS and VADAS (1967) reported *Antithamnionella shimamurana* (as *Antithamnion shimamuranum*) from two localities, Deception Pass (*UBC WS1485*!) and Ebey's Landing (*UBC WS1486*!), Whidbey I., Washington. We have examined both of these collections and observed that whorl-branches are opposite and unbranched, and tetrasporangia are on one to several-celled pedicels. These features correspond to *A. pacifica* and not to *A. shimamurana.*

Antithamnionella shimamurana also has been reported from the Aleutian Is. (NAKATANI and BURGNER 1974, as *Antithamnion shimamuranum*). We have been unable to locate any material of this species from there, but we believe it is likely that the species is present in the Aleutian Is. as well as in intermediate areas between there and the middle Kurile Is., where NAGAI (1941) recorded it.

HOLLENBERGIA WOLLASTON 1972a

Hollenbergia, another segregate genus of *Antithamnion,* was established by WOLLASTON (1972a) to include *Hollenbergia subulata* (HARVEY) WOLLASTON, the type species (type locality: Esquimalt, Vancouver I.), and *H. nigricans* (GARDNER) WOLLASTON (type locality: Botanical Beach, Port Renfrew, Vancouver I.). The genus was characterized as having 1–4 whorl-branches of which the basal cell is of similar length to other branch cells. Gland cells are terminal on whorl-branch ramuli in *H. subulata* and lateral near apices of whorl-branches in *H. nigricans.* Location and development of reproductive structures are similar to *Antithamnion.*

Hollenbergia subulata (HARVEY) WOLLASTON 1972a

Although present throughout the year, *Hollenbergia subulata* is most conspicuous in the local flora during winter and spring in habitats ranging from exposed to protected. The distinctive terminal position of its gland cells (Fig. 6) prevents it from being confused with any other local taxon. Other features are listed in Table 1. *Hollenbergia subulata* has been recorded from British Columbia to Monterey, California (WOLLASTON 1972a, 1976). We have confirmed its occurrence in Alaska (SCAGEL *et al.* 1986) and extend its range northwesterly to Chugach I., Kenai Peninsula (*UBC A59909*!). Additional Alaskan records in *UBC* are *A20941*! (Kayak I.) and *A59911*! (Port Etches).

Hollenbergia nigricans (GARDNER) WOLLASTON 1972a

In contrast, *Hollenbergia nigricans* has been collected only rarely and then only from exposed habitats. In addition to the type collection from Botanical Beach (*P.B.-A. No. 944* in *UC*! and an isotype in the *UBC P.B.-A.*!), we have observed one other collection from there (*UBC A69639*!) and one from Hedley I. (50°54.5′N 127°35.2′W—*UBC A17048*!). *Hollenbergia nigricans* has been reported to occur from Vancouver I., B.C., to northern California (WOLLASTON 1972a, 1976). A specimen identified as this species from Cold Bay, Alaska (in *ALA*!; MCROY *et al.* 1971) has been identified by M.J. WYNNE as *Scagelia pylaisaei.*

As indicated by Table 1, *Hollenbergia*

nigricans also has a distinctive set of features. It is most easily identified by its relatively short, broad cells and by the placement of whorl-branches near the middle of mature axial cells (Fig. 8) rather than subapically, a characteristic of the other taxa considered here.

SCAGELIA WOLLASTON 1972a

Scagelia, a monotypic genus segregated from *Antithamnion* by WOLLASTON (1972a), is circumscribed as follows: erect thallus with 2–4 whorl-branches per cell, often unequal in length (Figs. 5, 7); branch apices curved with irregular initiation of whorl-branches [as in northeast Pacific species of *Antithamnionella* (see above)]; gland cells lateral on cells of whorl-branches (Figs. 5, 7); procarps on basal cells of whorl-branches; branch apex and fertile whorl-branch continuing to grow during carposporophyte development, so that several carposporophytes may be borne on a single fertile axis; spermatangia on short ramuli of whorl-branches; tetrasporangia sessile on whorl-branches, cruciately or occasionally appearing tetrahedrally divided.

Scagelia pylaisaei (MONTAGNE) WYNNE 1985

Along with *Antithamnionella pacifica, Scagelia pylaisaei* (type locality: Newfoundland) is the most common antithamnioid alga in the local flora. Although distinctive from all other locally occurring antithamnioid algae based on vegetative and reproductive features (see above; Table 1), the taxon is highly variable with regard to size and robustness of the thallus, as well as the abundance of its laterally disposed gland cells. Recently, WHITTICK (1988) has demonstrated that in northwest Atlantic populations the abundance of gland cells is controlled to some extent by temperature and salinity. *Scagelia pylaisaei* occurs in the Arctic Ocean, North Atlantic Ocean, Bering Sea (HANSEN and SCAGEL 1981), the northeast Pacific Ocean from the Aleutian Is. to southern California (SCAGEL *et al.* 1986), and has been reported from the Galapagos Is. in the southeast Pacific (TAYLOR 1945, as *Antithamnion occidentale* KYLIN).

Antithamnion simulans GARDNER (1927a, type locality: Sitka, Alaska) is represented by *UC 276134*! (*NLG 3938*). It has the habit, both macroscopic and microscopic, of *Scagelia pylaisaei.* Two or three whorl-branches, of different lengths, occur on each axial cell, and whorl-branches are lax and taper to an acute tip. The lateral gland cells are typical of *S. pylaisaei* and occur mostly near the base of whorl-branches and their ramuli. Basal cells of branches are of similar shape and size to more distal branch cells. We therefore consider *Antithamnion simulans* GARDNER (1927a) a synonym of *Scagelia pylaisaei* (MONTAGNE) WYNNE. [See Note added in proof.]

PLATYTHAMNION J. AGARDH 1892

The genus *Platythamnion* is distinguished by its four whorl-branches, two longer lateral ones and two shorter transverse ones, and by a pattern of indeterminate branch initiation before whorl-branches are formed and a subsequent deflection of the apex away from these alternately formed indeterminate branches (WOLLASTON 1968, 1972c). Moreover, gland cells are sessile and adaxial on central cells of whorl-branches. Of these features, only the regular occurrence of four whorl-branches distinguishes *Platythamnion* from the sometimes-recognized *Pterothamnion* NAEGELI, which also can possess whorls of four branches in robust specimens (ATHANASIADIS 1985, MOE and SILVA 1980, WOLLASTON 1979); however, these two genera have types from widely separated geographic areas [*Platythamnion heteromorphum* (J. AGARDH) J. AGARDH—Santa Cruz, California; *Pterothamnion plumula* (ELLIS) NAEGELI—Brighton, England]. No one has yet proposed synonymy although it has been hinted at. In reproductive features, *Platythamnion* resembles *Antithamnion* although the cruciate tetrasporangia of Northeast Pacific *Platythamnion* spp. are significantly smaller than those of local *Antithamnion* spp.: 36–45 μm maximum length versus 70–80 μm.

Four species of *Platythamnion* occur in the study area. They are most easily distinguished

on the pattern of branching of lateral whorl-branches: lateral whorl-branches with four ramuli (two long and two short) with the longer ramuli branched on both sides of their axes (*P. heteromorphum*); lateral whorl-branches usually with four ramuli (two long and two short) but with longer ramuli pectinately branched adaxially [*P. reversum* (SETCHELL *et* GARDNER) KYLIN; type locality: Whidbey Island (west coast), Washington]; lateral whorl-branches pectinately branched adaxially with two ramuli and sometimes with an abaxial ramulus from the basal cell of the whorl-branch (*P. pectinatum* KYLIN); whorl-branches usually with two adaxial and 0–1 abaxial ramuli (*P. villosum* KYLIN).

WOLLASTON (1972c) did not see the type specimens of *Platythamnion villosum* and *P. pectinatum,* but she quoted their type localities from part of KYLIN's (1925) original descriptions and queried the specimens as being in *LD.* A specimen of *P. villosum* in *LD*!, collected at Friday Harbor, 15 July 1924, by H. KYLIN, has been marked "Typus" by an unknown person. This specimen can be considered the lectotype based on WOLLASTON's selection of "Friday Harbor" as type locality. In the case of *P. pectinatum,* a Peavine Passage specimen in *LD*!, collected 10 July 1924 by H. KYLIN, has been designated "Typus" by an unknown person, but WOLLASTON selected "Friday Harbor" as the type locality for this species. A lectotype of this species has yet to be defined.

Among the species occurring in British Columbia, two (*P. pectinatum* and *P. villosum*) are common and widespread; one (*P. reversum*) is uncommon but widely distributed, and one (*P. heteromorphum*) is rare and narrowly distributed. Both *P. pectinatum* and *P. villosum* are known from Mexico (WOLLASTON 1972c, 1976) to Prince William Sound, Alaska (*P. pectinatum* to Bass Harbor, Alaska—HANSEN *et al.* 1982 and *UBC A60548*! *A61351*! *A61353*! *A61373*! *A61385*! and *A61386*!, and *P. villosum* to Little Smith I., Alaska—*UBC A61326*!—a northern distribution record). *Platythamnion reversum* has been recorded from southern British Columbia to Charleston, Oregon (WOLLASTON 1972c), but we have not confirmed its occurrence in Oregon. Specimens in *UBC* are from the San Juan Is. (Lopez Pass—*UBC A1142*!), the Strait of Georgia (Lasqueti I.—*UBC A56100*! and Pt. Atkinson—*UBC A56631*!), and the Queen Charlotte Is. (off Robber Inlet, Maude, I., at Haina—*UBC A64619*!), a northern range extension. *Platythamnion heteromorphum* is known locally only from Salmon Bank, off San Juan I., Washington (*UBC A69638*!), southern Vancouver I. (Edward King I.—*UBC A40982*! and between Fleming and Tzartus Is., Barkley Sound—*UBC A47726*!), and the north end of the Strait of Georgia (Waiatt Bay—*UBC A58611*!). Outside the area, it has been recorded from Oregon, California, and Baja California, Mexico (WOLLASTON 1972c, 1976).

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Sandra C. LINDSTROM・Paul W. GABRIELSON：北東太平洋岸産フタツガサネ族（紅藻イギス目）の分類と分布上の知見

アラスカからオレゴンまでの北アメリカ太平洋岸から知られているフタツガサネ族の種数は17から12に減らされた。*Antithamnion alternans* と *A. asymmetricum* は *Antithamnionella pacifica* と同種であり，*Antithamnion simulans* は *Scagelia pylaisaei* と同種である。*Antithamnion dendroideum* はこの地域には分布しないようであり，アラスカ南東部からの唯一の記録は確認されていない。*Antithamnion gardneri* と *Antithamnionella glandulifera* は，北東太平洋岸ではアラスカの Prince William Sound からメキシコの Baja California にかけて報告されている *Antithamnionella spirographidis* と同種であり，日本から報告されている *A. miharae* も *A. spirographidis* の異名と考えられる。*Antithamnionella shimamurana* comb. nov. の分布はアリューシャン列島の東ではまだ確認されていない。*Hollenbergia subulata, Platythmnion reversum* および *P. villosum* の北部での新しい分布が明らかにされた。*Antithamnion kylinii* の分布の確認された北限はアラスカ南東部ではなくブリティッシュコロンビア南部であり，*Hollenbergia nigricans* の確認された北限はアラスカ南西部ではなくブリティッシュコロンビア中部である。(Department of Botany, University of British Columbia, Vancouver, B.C., V6T 2B1 Canada)