# MORPHOLOGICAL VARIATION OF <u>COSTARIA</u> GREVILLE IN SOUTHWEST BRITISH COLUMBIA COASTAL WATERS

by

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# APPROVAL

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ABSTRACT

The polymorphic and polytypic genus *Costaria* of the northern Pacific has previously had uncertain taxonomic treatment. Variation has been recognized as separate species, separate forms, or ignored altogether. Comparative morphological, phenological, and ontogenetic studies of selected populations from the British Columbia coast, Canada, *in situ* and after transplanting do not support taxonomic recognition for the observed variation.

Previously two species (*C. costata* (Turn.) Saund. and *C. mertensii* J. G. Ag.), one species (*C. costata*), or *C. costata* with several variations (*C. turneri* (=*C. costata*) f. *angustifolia* and f. *latifolia*, *C. turneri* var. *pertusa*, and *C. costata* f. *cuneata* and f. *latifolia*) have been recognized.

In the present study morphological differences between selected populations of southwest British Columbia *Costaria* sporophytes were evaluated by comparing mature plants, by following their phenology and ontogeny, and by transplant studies. These studies were conducted on populations from the following four sites: Indian Arm, sheltered with low salinities and high summer temperatures; Sooke, moderately exposed to wave action; Point No Point, slightly more exposed

than Sooke; and Cape Beale, fully exposed. The latter three sites had higher salinities and more constantly low temperatures than Indian Arm.

The results demonstrated two main morphological forms of *Costaria*. The Sooke/Point No Point (wave exposed) morphological form, which is typified by *Costaria* at Sooke, Point No Point and Cape Beale, has a tough blade which does not tear readily, prominent ribs, small bullations, and sometimes the blade is perforated. The stipe is coarsely ridged. This morphological form is variable, and includes all of the taxa previously described in the literature. Most specimens of mature *Costaria* collected in the northeast Pacific and from Japan correspond to this form.

The Indian Arm (sheltered) morphological form has little in common with the first form, and is typified by *Costaria* at Indian Arm. It has a crisp blade which tears readily, flattened ribs, large bullations and no perforations. The stipe is finely ridged. This form has not been described or illustrated previously.

The Indian Arm, Sooke, Point No Point and Cape Beale populations form a discontinuous morphological series in blade shape, amount of bullation, ridges on the stipe surface and presence of perforations. Collections of *Costaria* from other sites in the northeast Pacific and Japan were found to fit into this series.

The *Costaria* transplants did not give definite results as to the plasticity of the morphological characters studied. However, wave exposure would appear to be the major factor determining morphology. Because the characters varied widely in response to variations in environment, and because distinctive habitats were not isolated, phenotypic plasticity is indicated to account for variation in the Sooke/Point No Point morphological form. Indian Arm, on the other hand, could be considered environmentaly distinct, and the *Costaria* population there could either be ecotypically divergent or else strongly phenotypically plastic.

Since variation in blade and blade base shape has been the feature most commonly used to distinguish between *Costaria costata* and *C. mertensii* and/or other taxa of *Costaria*, and since the *Costaria* described to date have been of the Sooke/Point No Point morphological form, the various names should be reduced to synonomy with *C. costata*. Although the Indian Arm morphological form has not been described or illustrated previously, it fits the sheltered extreme of the wave exposure gradient in variation. Because of wide polymorphism in the different populations and between populations, the morphological forms should not be given taxonomic status.

ACKNOWLEDGEMENTS

I would like to thank Dr. L. D. Druehl for suggesting the research topic and for his encouragement and help throughout; Dr. W. C. Austin and Dr. R. C. Brooke for guidance and constructive criticism of the manuscript; Dr. F. J. Fisher for useful discussions; Ian Britt and Neil Stainton for SCUBA diving and, with Enid Britt, for much help in the field; Stephen Hsiao for many stimulating discussions and assistance; Mr. R. Long for the photographic figures and the Audio Visual Department for the drawn figures; Miss Chris Hellwig for her careful typing of the final draft, and lastly Julian Reynolds for much help with the final stages of the manuscript.

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# INTRODUCTION

*Costaria* is a brown algal genus of the order Laminariales, family Laminariaceae. It is known in the northeast Pacific from central California to the eastern extreme of the Aleutian Islands (Druehl, 1970) (Fig. 1). It has been found in the Bering Sea (Setchell, 1893) and in the northwest Pacific on the northern end of Honshu Island, Hokkaido, the Kurile Islands, Saghalien, Kamtschatka, and the Japan Sea coast of Siberia and Korea (Miyabe and Nagai, 1933; Tokida, 1954).

The sporophyte of *Costaria* is clearly differentiated into an undivided blade, stipe and holdfast (Fig. 2). The intercalary meristem is located between the blade and the stipe. Mucilage ducts are absent. The blade is large with five longitudinal, percurrent ribs each projecting on one side only and alternately on the two surfaces. The blade is usually bullate and sometimes perforated. Stipe length is variable. The lower part of the stipe is terete in cross section, the upper part generally flattened and elliptical. The upper part may also have longitudinal ridges. The holdfast is made up of dichotomously branched haptera arising mainly from the base of the stipe (Setchell and Gardner, 1925; personal observations).

Fig. 1 Distribution of *Costaria* in the North Pacific Ocean. Inset showing the four study sites in southwest British Columbia.

A Indian Arm

B Sooke

C Point No Point

D Cape Beale

▲▲ indicates the distribution of *Costaria*.

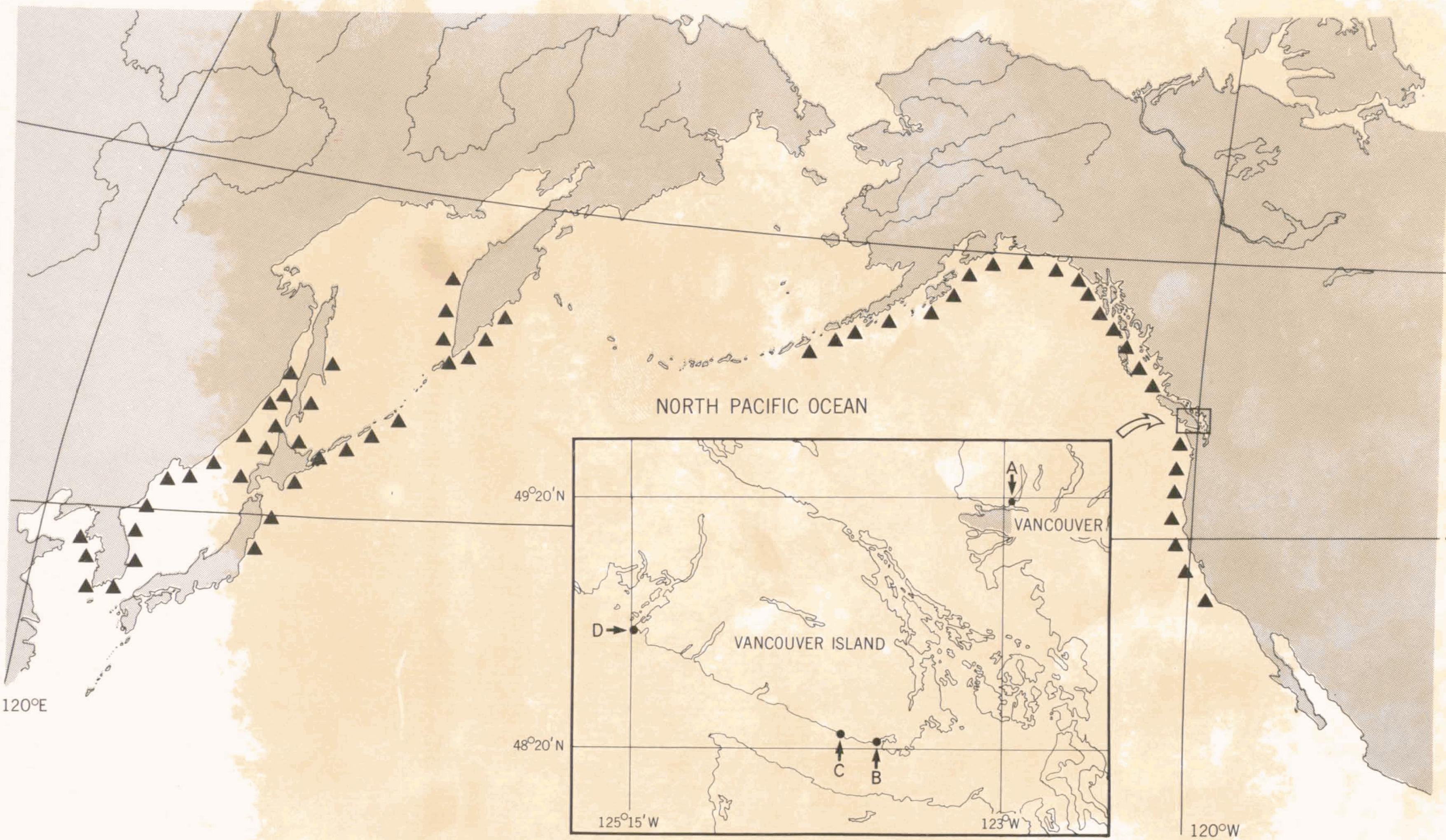

NORTH PACIFIC OCEAN
60°N
40°N
120°E
120°W
49°20'N
48°20'N
125°15'W
123°W
VANCOUVER
VANCOUVER ISLAND
A
B
C
D

Fig. 2 Diagrammatic representation of *Costaria* sporophyte showing distinctive morphological features of the genus.

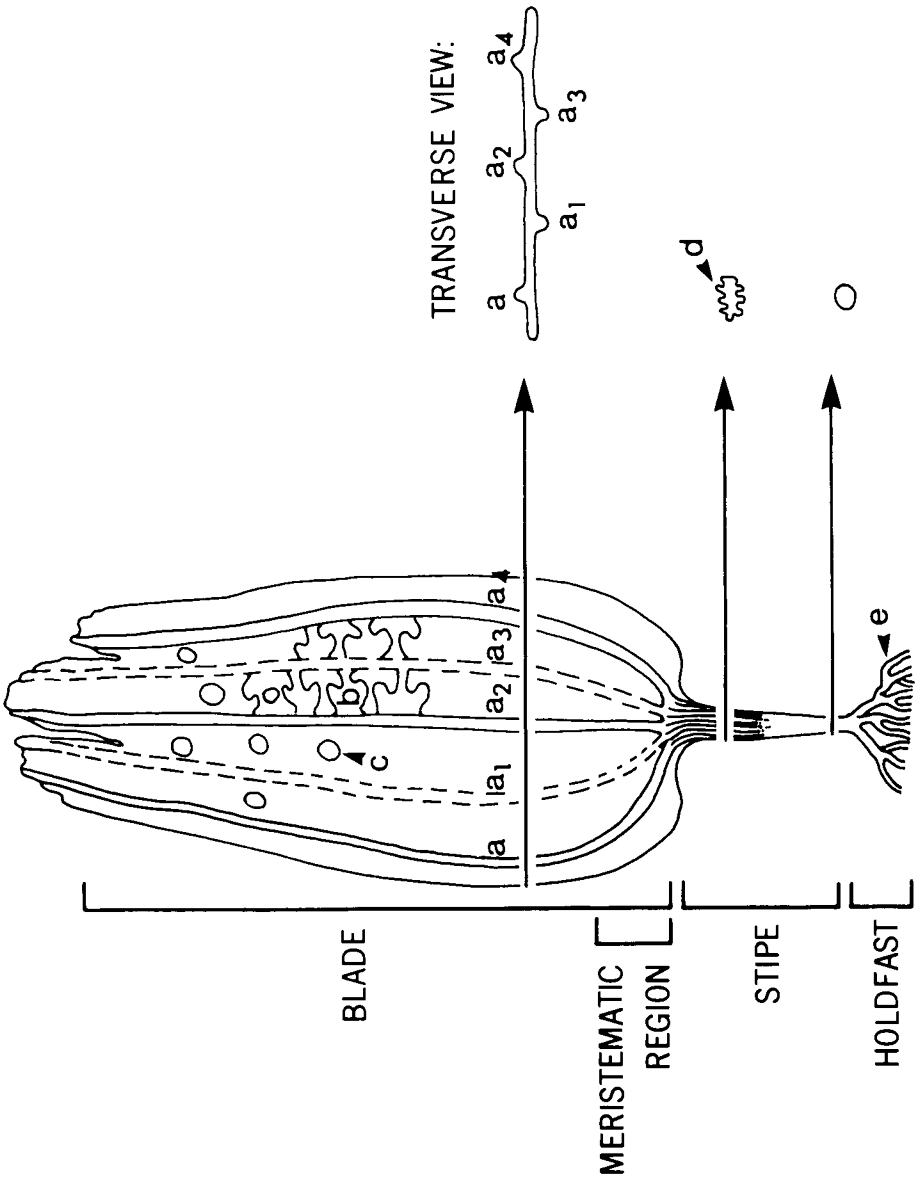
$a - a_4$ Ribs projecting on alternate sides of the blade.

b Bullations

c Perforations

d Ridges on stipe surface

e Branching haptera


BLADE
MERISTEMATIC REGION
STIPE
HOLDFAST
TRANSVERSE VIEW:
a
a1
a2
a3
a4
b
c
d
e

The blade has a single-layered epidermis, a cortex and a central medulla. The transition zone between the stipe and blade and the stipe itself differ anatomically from the blade in that they have an epidermal meristem several layers thick (Smith, 1939).

The conspicuous diploid sporophyte, which may reach 3 m in length, alternates with a microscopic haploid gametophyte. On the mature sporophyte sori develop in late spring and summer. These consist of unilocular meiosporangia and sterile paraphyses grouped on the surface of the blade. Mature meiosporangia contain 32 flagellated meiospores (Nishibayashi and Inoh, 1957), which are released in the summer and autumn (Yendo, 1911; Angst, 1927; Kanda, 1936; Sanbonsuga and Hasegawa, 1967, 1969).

Gametophytes of *Costaria* have only been studied in the laboratory (Angst, 1927; Kanda, 1936; Sanbonsuga and Hasegawa, 1967). The motile meiospores round up before germinating into microscopic, dioecious, filamentous, branched gametophytes. Usually a single flagellated antherozoid is released from each antheridium (Kanda, 1936). The egg remains attached to the neck of the oogonium (Angst, 1927), and the young sporophyte begins to develop *in situ*. Sporophytes of *Costaria* are first recognizable in the field in January and February (Yendo, 1911; Sanbonsuga and Hasegawa, 1967, 1969).

*Costaria* sporophytes are generally considered to be annual both in the northwest and northeast Pacific (Setchell and Gardner, 1925; Kanda, 1936; Sanbonsuga and Hasegawa, 1967, 1969); after the release of meiospores, sporophytes become detached and are washed away. However, Smith (1944) states that sporophytes on the Monterey Peninsula, California, are perennial. It is not known how *Costaria* found in intertidal regions overwinter, whether as meiospores, gametophytes or microscopic sporophytes.

*Costaria* was first described by Turner in 1819 (pp. 72-73; Pl. 226). He took most of his description from an unpublished written account by Menzies who collected one specimen at Port Trinidad, California, around 1788-9. This specimen is now in the British Museum (Fig. 3). Turner (1819) illustrated a plant with a narrow blade and cuneate blade base and called it *Fucus costatus*. C. A. Agardh (1823, pp. 109-110) virtually copied Turner's description but called the plant *Laminaria costata*. Bory de Saint-Vincent (1826, p. 193) knew *Costaria* only from Turner's illustration and renamed it *Agarum quinquecostatum*. Mertens (1829, pp. 45-46) described a plant, which he called *Fucus costatus*, having a blade much broader than the one illustrated by Turner. He also described sori

Fig. 3 Type of Turner's _Fucus_ _costatus_ (1819), collected at Port Trinidad, California, around 1788-9. This specimen is the type for the genus _Costaria_. Photograph provided by Dr. R. F. Scagel, University of British Columbia.

for the first time. In 1830 Greville (p. 39) changed the generic name to Costaria and provided a brief description recognizing one species, C. turneri, and as synonyms giving L. costata C. A. Ag. and F. costatus Turn. Postels and Ruprecht (1840, p. 12; Pl. 24) described Costaria turneri and a broad form which they named C. turneri f. latifolia.

J. G. Agardh (1848, pp. 139-140) was the first to describe two distinct species: C. turneri, a narrow form with a cuneate blade base, and C. mertensii, a broad form with a cordate blade base. He gave F. costatus Turn. and L. costata C. A. Ag. as synonyms for C. turneri, and gave F. costatus Mertens and C. turneri f. latifolia illustrated by Postels and Ruprecht as synonyms for C. mertensii. Saunders (1895, p. 57) changed the specific name of the narrow blade form from C. turneri to C. costata, as costata was the specific epithet first applied by Turner.

Since the designation of two species by J. G. Agardh in 1848, some authors have continued to recognize these taxa on the basis of differences in overall blade shape and blade base shape (Kjellman, 1893; Saunders, 1895; De Toni, 1895). Others have recognized only one very variable species (Harvey, 1852, 1862; Ruprecht, 1852; Setchell and Gardner, 1903, 1925;

Okamura, 1928, 1936; Miyabe and Nagai, 1933; Tilden, 1935; Smith, 1944). Different forms of Costaria have also been described: C. turneri f. angustifolia and f. latifolia by Kutzing (1849), C. turneri var. pertusa by Harvey (1859) and C. costata f. cuneata and f. latifolia by Nagai (1940).

Ruprecht (1852) described C. quadrinervia from a single specimen collected at Unalaska. De Toni (1895) repeated his description but this particular form has not been found subsequently and it has been included in C. costata (Setchell and Gardner, 1925).

Doty (1947) considered characters other than the shape of the blade base in his description of C. costata and C. mertensii in Oregon. C. costata was found "in tidepools and below LLLW[1] or higher in protected localities". The narrow, almost linear blade was never cordate and was comparatively smooth. The top of the stipe tended to be wide and flattened with prominent ridges. The haptera were delicate and almost entirely from the base of the stipe. Turner's (1819) and Smith's (1944) illustrations are supposed to support this description, though Doty said that Smith's plant was of an unusually broad and bullate form. C. mertensii was found in exposed situations particularly in the low intertidal. The

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[1] Lowest lower low water.

blade was broad, much more cordate basally than *C. costata*, and was bullate. The short, more cylindrical stipe was less prominently ridged. Accessory haptera often developed from above the first-formed haptera. Doty gave Postels and Ruprecht's (1840) and Setchell and Gardner's (1925, Pl. 56b) illustrations as examples of this species saying that Setchell and Gardner's illustrated form was rather narrow at the base. The only difference I could see between Smith's (1944) and Setchell and Gardner's (1925, Pl. 56b) illustrations was that the blade base was obtuse in the former and cordate in the latter. However, Doty claimed that, with very few exceptions, he was able to distinguish *C. costata* from *C. mertensii* in Oregon.

Herbarium specimens of *Costaria* from British Columbia and Northern Washington were also examined, but little difference was found between specimens listed as *C. costata* and *C. mertensii* by Scagel (1957). In conclusion, my preliminary observations of herbarium specimens of *Costaria* from the northeast Pacific showed that the plants could not easily be referred to either of the two species as described by Doty (1947), or to the two species originally described by J. G. Agardh (1848) which were distinguished on the basis of blade shape.

The purpose of my study was to define morphological variation in populations of northeast Pacific *Costaria* and explain interrelations between the presently recognized taxa of this genus. Natural and transplanted populations were studied in the field at four sites in southwest British Columbia. Collections were made at other sites in this area, and herbarium specimens, including historically important specimens, were examined from the herbaria of the University of British Columbia (Vancouver), National Museum of Canada (Ottawa), University of Washington (Seattle), University of California (Berkeley), Dudley Herbarium (deposited at the University of California, Berkeley), and the British Museum (London).

# METHODS

## I. Comparative morphology and anatomy of mature Costaria.

In order to compare the morphology and anatomy of mature Costaria (i.e. with sori) the largest plants available were collected from the north side of Boulder I., Indian Arm (49° 18'47"N, 122°56'06"W) on June 18, the south side of Whiffin Spit, Sooke (48°21'30"N, 123°42'54"W) and the southwest facing rocky point at Point No Point (48°23'45"N, 123°59'05"W) on June 17, and the southwest side of Cape Beale (48°47'15"N, 125°12'45"W) on July 19, 1970 (Fig. 1). These sites will be referred to as Indian Arm, Sooke, Point No Point and Cape Beale. Since nearly all Costaria were growing subtidally, plants were collected by SCUBA. The plants were preserved in 5% formalin in seawater (v/v) and were brought back to the laboratory for study. Physical and biological aspects of the sites were described from published information and personal observations.

General observations were made of overall blade shape, colour, texture, condition of the blade end, bullations, perforations, rib arrangement, presence or absence of ridges on the stipe, stipe flexibility, amount of branching of the main haptera, and distribution of sori. In the field it had been noted how the haptera were attached to the substrate. Measurements were made of blade length, maximum blade width, width and thickness of the middle rib 15 cm above the junction of the blade and stipe, length and thickness of the stipe, and the diameter of the thickest hapteron originating from the stipe. The number of main haptera were counted. A centimetre ruler was used for large measurements and calipers for small ones.

The shape of the blade base was described as an angle which was measured to the nearest $10^\circ$ with a plexiglass protractor. The apex of the angle was approximately at the junction of the blade and stipe. Independent angle determinations and verbal descriptions were made of about 300 herbarium specimens, and a close correlation was found between the following terms and range of angles: cuneate, $40^\circ$-100; obtuse, $110^\circ$-$180^\circ$; cordate, $190^\circ$-$240^\circ$; and auriculate, $250+^\circ$.

To study the internal anatomy of Costaria, sections 20-30μ thick were cut with a freeze microtome. Observations were made on cross sections of blades, stipes and haptera. Measurements of blade and rib thickness 15 cm from the blade base (including thickness of the cortex and medulla) were made with a Filar micrometer eyepiece. The number of cell layers in the cortex was also counted.

Meiospore suspensions were made from plants collected at Indian Arm on July 15 and September 17, at Sooke on August 2 and September 6, and at Point No Point on August 3 and September 6, 1969, after the method of Druehl and Hsaio (1969). The volume of the meiospores was measured with a Coulter Counter (Model B Coulter Counter, with a Model M volume converter attachment) using a 50μ aperture tube.

Means and standard deviations were determined for data where appropriate.

II. Phenology and ontogeny.

Phenology:

In the field the first appearance of young sporophytes, the first appearance of sori, and the disappearance of the majority of the sporophyte population were noted.

Ontogeny:

During 1968 and 1969 *Costaria* plants were collected at Indian Arm, Sooke and Point No Point once a month and were preserved as herbarium specimens. Voucher specimens of these plants are deposited in the University of British Columbia Phycology Herbarium. The development of *Costaria* was studied by measuring and describing certain characters of the specimens which had been grouped into several size and developmental categories. Blade length, maximum blade width, angle of the blade base and stipe length were measured, the number of ribs were counted, and bullations, ridges on the stipe, and the development of sori were characterized.

III. Transplants and controls.

Transplant studies were undertaken in an attempt to determine the stability or plasticity of certain morphological characters of *Costaria* in different environments. *Costaria* was transplanted from Indian Arm to Sooke and Point No Point, from Sooke to Indian Arm, and from Point No Point to Indian Arm and Sooke using the methods of Sundene (1962a, 1962b, 1964) and Druehl (1967b). See Appendix for dates and numbers of transplants.

Small *Costaria* plants usually with a blade length of less than 20 cm were attached to concrete bricks with rubber bands (as in Figs. 18-23). At Indian Arm and Sooke bricks 20 X 9 X 6 cm were used, but at Point No Point larger bricks, 40 X 19 X 9 cm, were used because of increased wave exposure.

*Costaria* to be moved to other sites were wrapped in paper towelling moistened with seawater, put in plastic bags and iced. Plants were sometimes held for a few days in an aquarium with a capacity of 350 litres at approximately 10 C, salinity 26-29‰ before being transplanted.

Transplants are defined as those plants which were moved to a different site, put on bricks and placed adjacent to naturally growing Costaria there. Control plants were put on bricks and returned to the original site. Usually controls were removed from and returned to the water on the same day. In one experiment controls were kept in an aquarium for seven days before being returned to their original site (Table VII). These plants grew as well as controls which had been returned the same day (Tables VI, VIII). All the tables are in the Appendix, pp. 90-118.

Measurements and observations of the transplants and controls were made approximately once a month. Plants were usually left on the bricks until they disappeared naturally. Blade length, blade width, angle of the blade base and stipe length were measured. Observations were made of bullations, ridges on the stipe, presence of sori and the general condition of the plants. A photograph or tracing was used to record the shape of the plants.

## IV. Morphology of Costaria in the northeast Pacific, and a study of historically important specimens.

Study of Costaria in the northeast Pacific from herbarium specimens:

Bullations, perforations, ribs and stipe surfaces of mature *Costaria* were examined and the angle of the blade base was measured. Most of the specimens were from the University of British Columbia herbarium and were collected from the west and north coasts of Vancouver I., Queen Charlotte Strait, Prince Rupert area, southern Alaska, the Gulf of Alaska, and the Aleutians as far as Unalaska I.

Collections of Costaria at San Juan I., Washington, and in southwest British Columbia:

Small collections of *Costaria* were made at San Juan I., Washington (48°30'N, 123°05'W), Second Narrows (49°17'30"N, 123°01'W) and Stanley Park (49°18'N, 123°07'30"W) in Burrard Inlet, Thormanby I. (49°29'N, 123°59'W) off the Sechelt Peninsula, Hammond Bay (49°14'N, 123°,57'W) on the east coast of Vancouver I., and at Port Renfrew (48°32'N, 124°27'30"W), in the vicinity of Bamfield (48°50'N, 125°09'W), and Amphitrite Point (48°55'30"N, 125°32'30"W) on the west coast of Vancouver I.

Study of historically important specimens:

Herbarium specimens of *Costaria costata* and *C. mertensii* as listed by Scagel (1957) and specimens collected and determined by Doty were examined. These were from the University of British Columbia, National Museum of Canada, University of Washington, University of California (Berkeley) and the Dudley Herbarium. Two specimens of _Fucus costatus_ collected by Menzies were studied from photographs, the type specimen being at the British Museum, London, and the other at the Royal Botanic Garden, Edinburgh.

V. _Study of Japanese specimens_.

A few specimens of _Costaria_ from Tsugaru Strait and Muroran, Hokkaido, were examined.

## Characterization of the Sites

The descriptions of the study sites (Fig. 1) include oceanographic data taken from the literature and biotic data from personal observation.

Indian Arm is a sheltered fjord northeast of Vancouver on the British Columbia mainland. It receives freshwater from the Indian River at its north end, and opens into Burrard Inlet at its south end. The study site near the mouth of Indian Arm was on the north side of Boulder I.

There is seasonal variation in temperature and salinity (Gilmartin, 1962). The temperature profile is two layered: a thin surface layer fluctuating between 5 and 21 C, and a deeper layer constant at 6-8 C. Highest surface temperatures occurred around July, and were lowest around December (Gilmartin, 1962).

Salinity structure is also two-layered: a thin, brackish surface layer and a relatively stable deeper layer (Gilmartin, 1964). At the mouth of Indian Arm the salinity may vary from 13 to 24‰ in the surface layer, and from 25 to 27‰ in the deeper water (Gilmartin, 1962, 1964).

*Costaria* grows subtidally on a substrate of boulders, mud and broken shells below the brackish layer. *Laminaria saccharina* (Linnaeus) Lamouroux is found throughout and above the *Costaria* bed and *Agarum cribrosum* Bory is located below.

The three other sites, Sooke, Point No Point and Cape Beale, are more exposed and oceanic. At Sooke, on the south-west coast of Vancouver I., *Costaria* was studied on the south side of Whiffen Spit. Point No Point is also on the south-west coast of Vancouver I. just north and west of Sooke, and *Costaria* was studied on a rocky point facing southwest. At Cape Beale, on the west coast of Vancouver I., *Costaria* was collected from a southwest facing rocky shore.

Sooke and Point No Point are on the Strait of Juan de Fuca where in open waters the annual range of surface temperature is small, 7-11 C (Pickard and McLeod, 1953), and the temperature of deeper water is approximately 7 C the year round (Herlinveaux and Tully, 1961). The surface salinity varies little from 32‰ (Pickard and McLeod, 1953; Herlinveaux and Tully, 1961). Below the surface the salinity is about 33.5‰ (Herlinveaux and Tully, 1961). Widdowson (1965a) made some measurements along the northern shore of the Strait of Juan de Fuca and found that there may be more seasonal variation in temperature and salinity than in the open water of the Strait.

The study site on Whiffen Spit, Sooke, is moderately exposed being protected by a headland to the south of the Spit. Point No Point is more exposed being further northwest along the coast (Widdowson, 1965a) and thus there may be less variation in onshore temperature and salinity patterns than at Sooke because of more wave mixing.

Cape Beale is fully exposed to open ocean swell. In this area there is reported to be more seasonal variation in surface temperature and salinity than in the Strait of Juan de Fuca (Pickard and McLeod, 1953). Surface temperatures range from 7 to 13 C and surface salinities from 28 to 31‰ (Pickard and McLeod, 1953).

At Sooke *Costaria* grows mainly subtidally. The substrate consists of boulders and sandy mud and the shore slopes gently westwards. There is a great abundance of algae and the number of species is considerably greater than at Indian Arm. Costaria is codominant in the kelp bed with many other Laminariales: Cymathere triplicata (Postels and Ruprecht) J. Agardh, Hedophyllum sessile (C. Agardh) Setchell, Laminaria groenlandica Rosenvinge, Pleurophycus gardneri Setchell and Saunders, Nereocystis luetkeana (Mertens) Postels and Ruprecht, Alaria marginata Postels and Ruprecht, Egregia menziesii (Turner) Areschoug, and Pterygophora californica Ruprecht.

At Point No Point the shore is rocky intertidally with sand beyond the rocks subtidally. Costaria grows mainly subtidally in rock crevices and on boulders in the sand. As at Sooke there is an abundance of algae and a richness of species but with much less Costaria. Other Laminariales present are Cymathere triplicata, Hedophyllum sessile, Laminaria groenlandica and L. setchellii Silva, Pleurophycus gardneri, Lessoniopsis littoralis (Farlow and Setchell) Reinke, Nereocystis luetkeana, Alaria marginata, Egregia menziesii and Pterygophora californica.

At Cape Beale Costaria was collected from the low intertidal where it was growing in rock crevices. Postelsia palmaeformis Ruprecht, an alga found only in very wave exposed areas, is found in this region along with *Cymathere triplicata*, *Hedophyllum sessile*, *Laminaria groenlandica* and *L. setchellii*, *Pleurophycus gardneri*, *Lessoniopsis littoralis*, *Nereocystis luetkeana*, *Alaria marginata* and *A. nana* Schrader, and *Egregia menziesii*.

# RESULTS

## I. Comparative morphology and anatomy of mature *Costaria*.

The following is a description of the morphology and anatomy of some of the largest *Costaria* with sori collected June, 1970, at Indian Arm, Sooke and Point No Point, and July, 1970, at Cape Beale. Standard deviations and absolute ranges are given for measurements in Tables I and II to indicate plant variability.

### Blade morphology:

All blades displayed distal erosion. The ends of Indian Arm blades tended to be eroded at right angles to the longitudinal axes of the plants whereas blade ends at Sooke, Point No Point and Cape Beale were usually eroded longitudinally (Figs. 4-7). Point No Point blades were shorter than plants from the other three places (Table I). Blades decreased in width relative to length from Indian Arm to Sooke, to Point No Point, to Cape Beale (Table I). Blade bases were mostly obtuse or cordate at Indian Arm, mostly cordate at Sooke, mostly obtuse at Point No Point, and were cuneate at Cape Beale (Figs. 4-7; Table I).

The ratio of blade length to maximum blade width and the angle of the blade base determined overall blade shape.

Fig. 4 Mature *Costaria* from Indian Arm collected on June 18, 1970, showing blade and blade base shape and large bullations. Blade end tends to be eroded at right angles to the longitudinal axis. (Compare with Figs. 5-7).

Fig. 5 Mature <u>Costaria</u> from Sooke collected on June 17, 1970, showing blade and blade base shape and small bullations. Blade end tends to be eroded longitudinally.

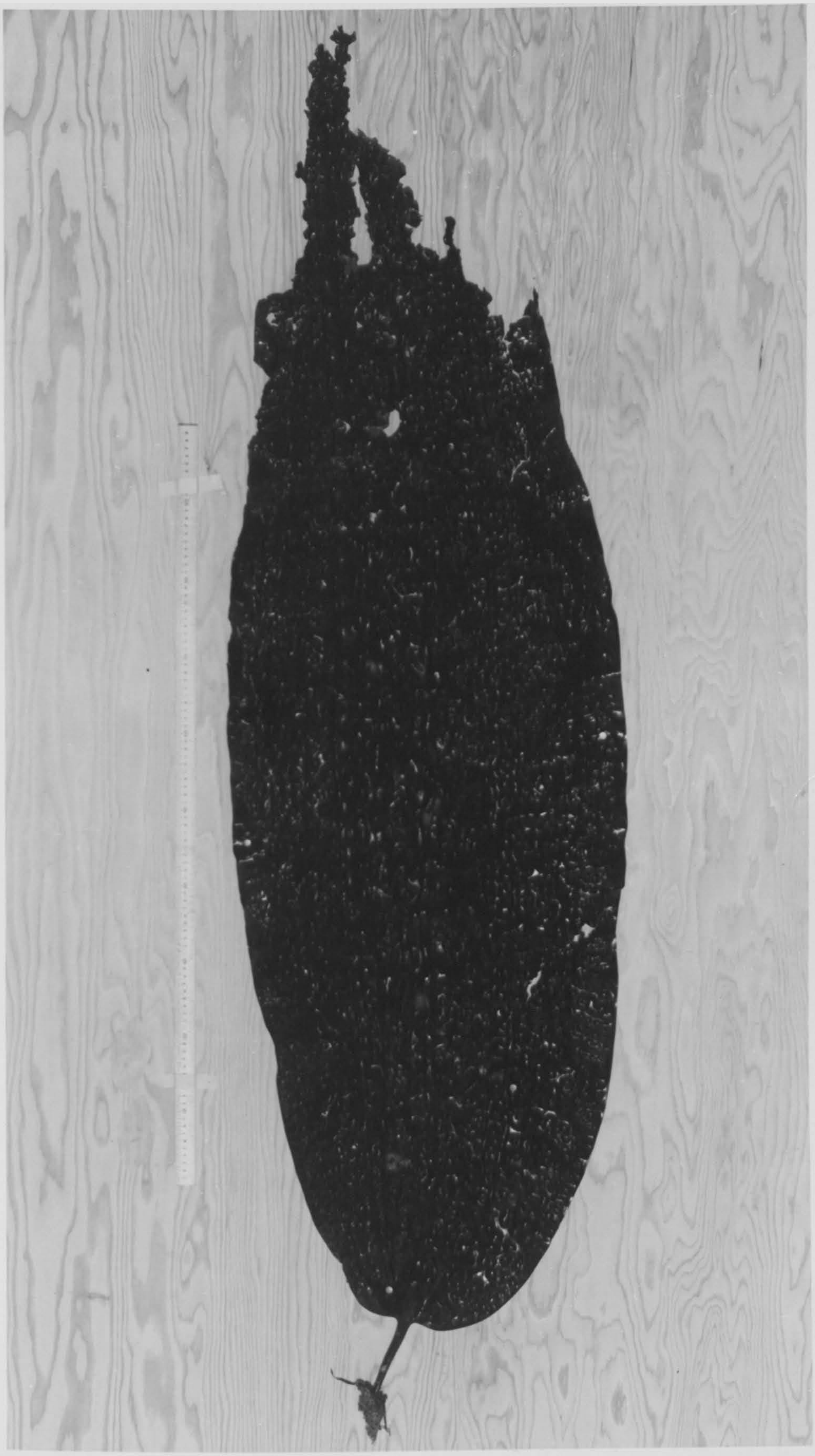
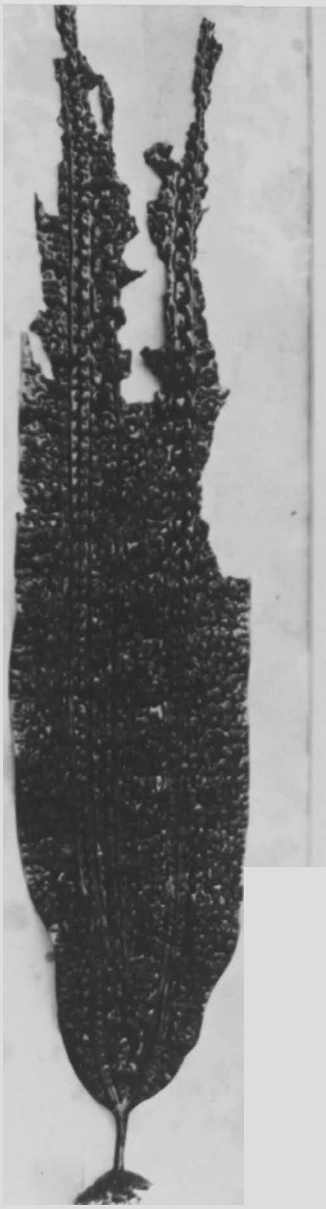


Fig. 6 Mature *Costaria* from Point No Point, collected on June 17, 1970, showing blade and blade base shape, small bullations and prominent ribs. Blade end tends to be eroded longitudinally.



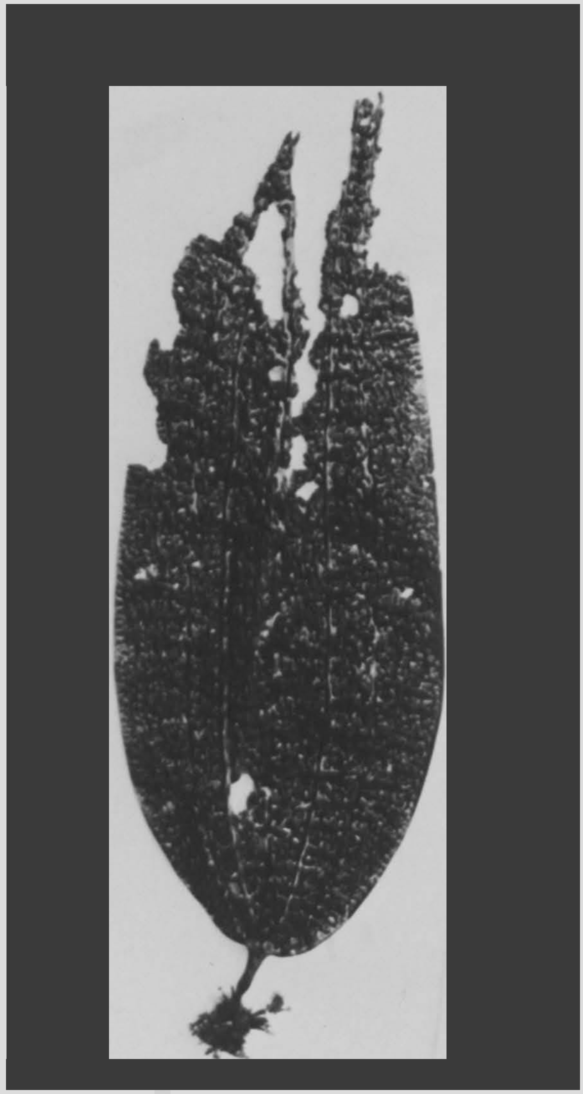
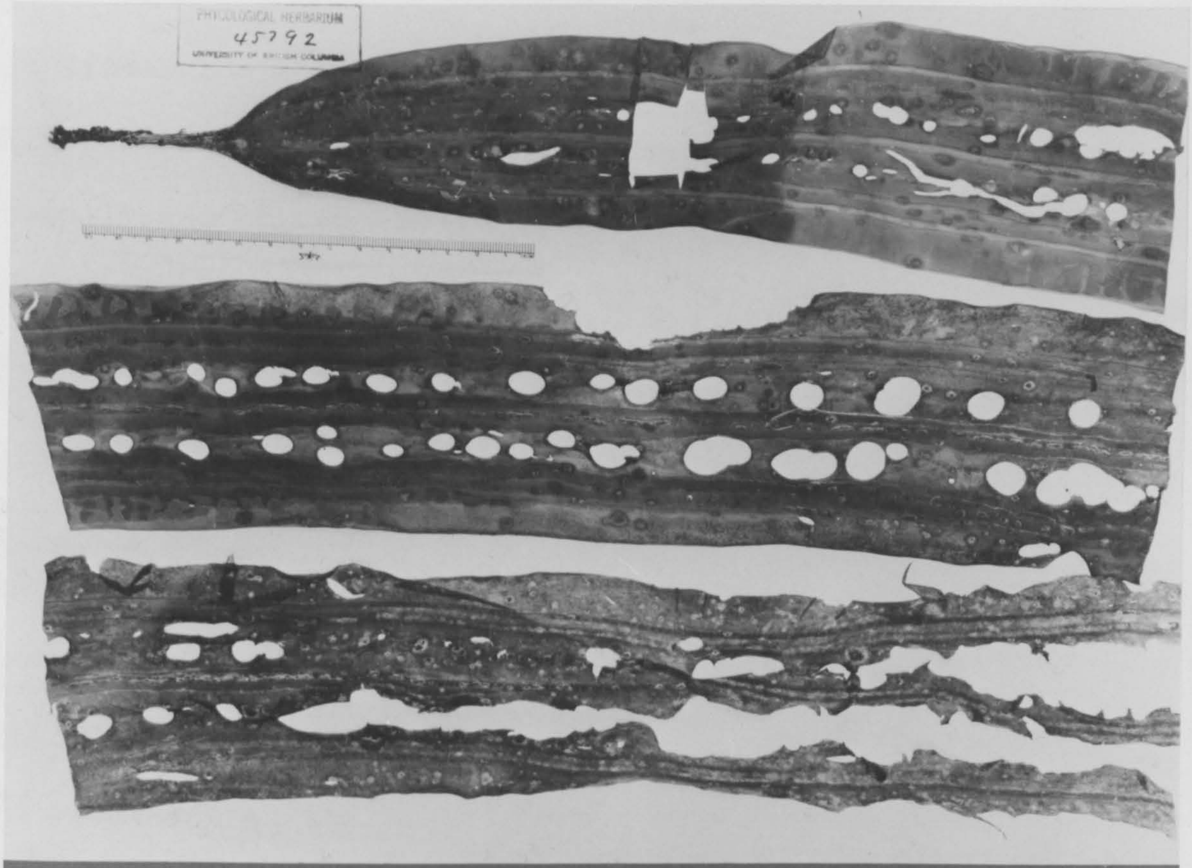


Fig. 7 Mature *Costaria* from Cape Beale collected on July 19, 1970, showing blade and blade base shape, bullations along the edges of the blade, prominent ribs and perforations. Blade end tends to be eroded longitudinally.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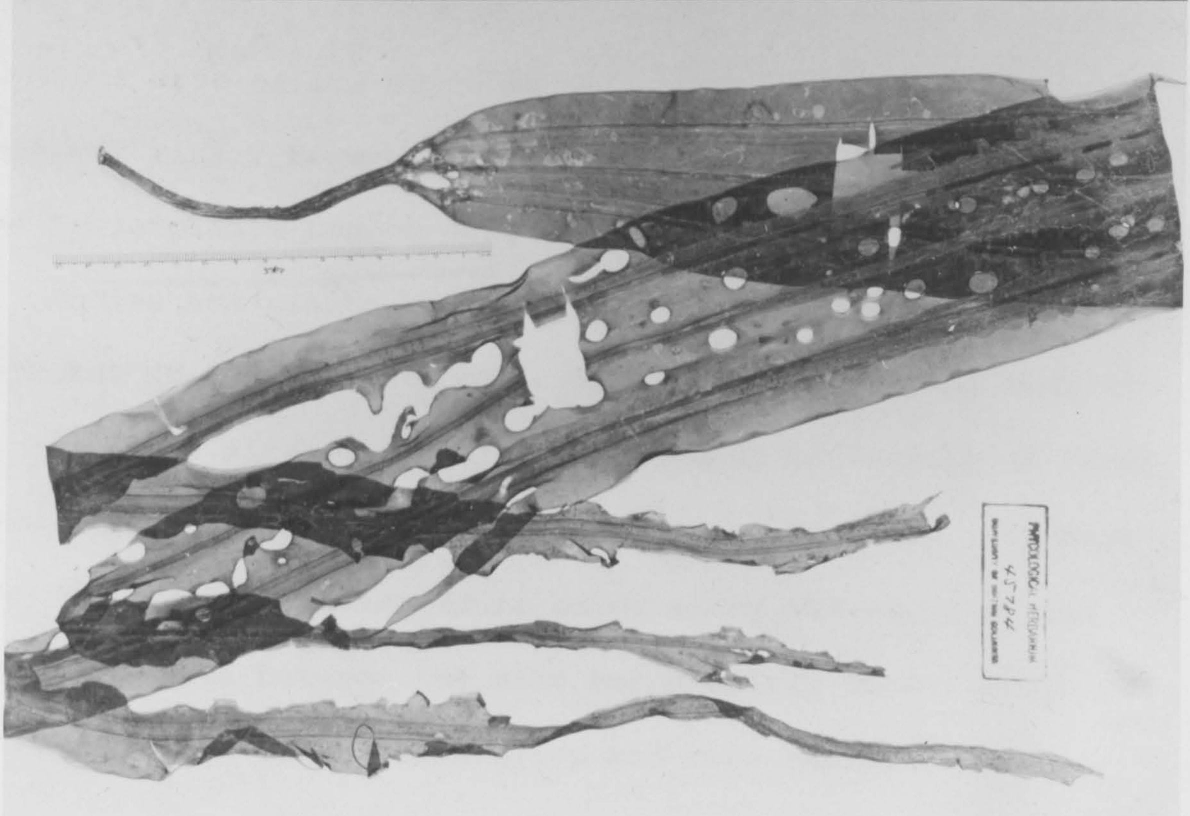
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In a linear blade, the sides were almost parallel. Cape Beale plants had narrow linear blades, Point No Point plants generally had narrow linear blades but some had ovate blades, Sooke blades were broad linear and ovate, and Indian Arm blades were mostly ovate (Figs. 4-7).

Five ribs project alternately from the two faces of the blade (Fig. 2). Blades with fewer or more ribs were rarely found, but such anomalies could generally be explained by rib fusion or splitting. The ribs were often very flattened particularly near the blade base at Indian Arm, but were much more prominent at the other three places. At Indian Arm and Sooke, the middle rib was usually wider and flatter than those on either side of it, which in turn were wider than the outermost ribs. However, all five ribs of Point No point and Cape Beale plants tended to have similar widths.

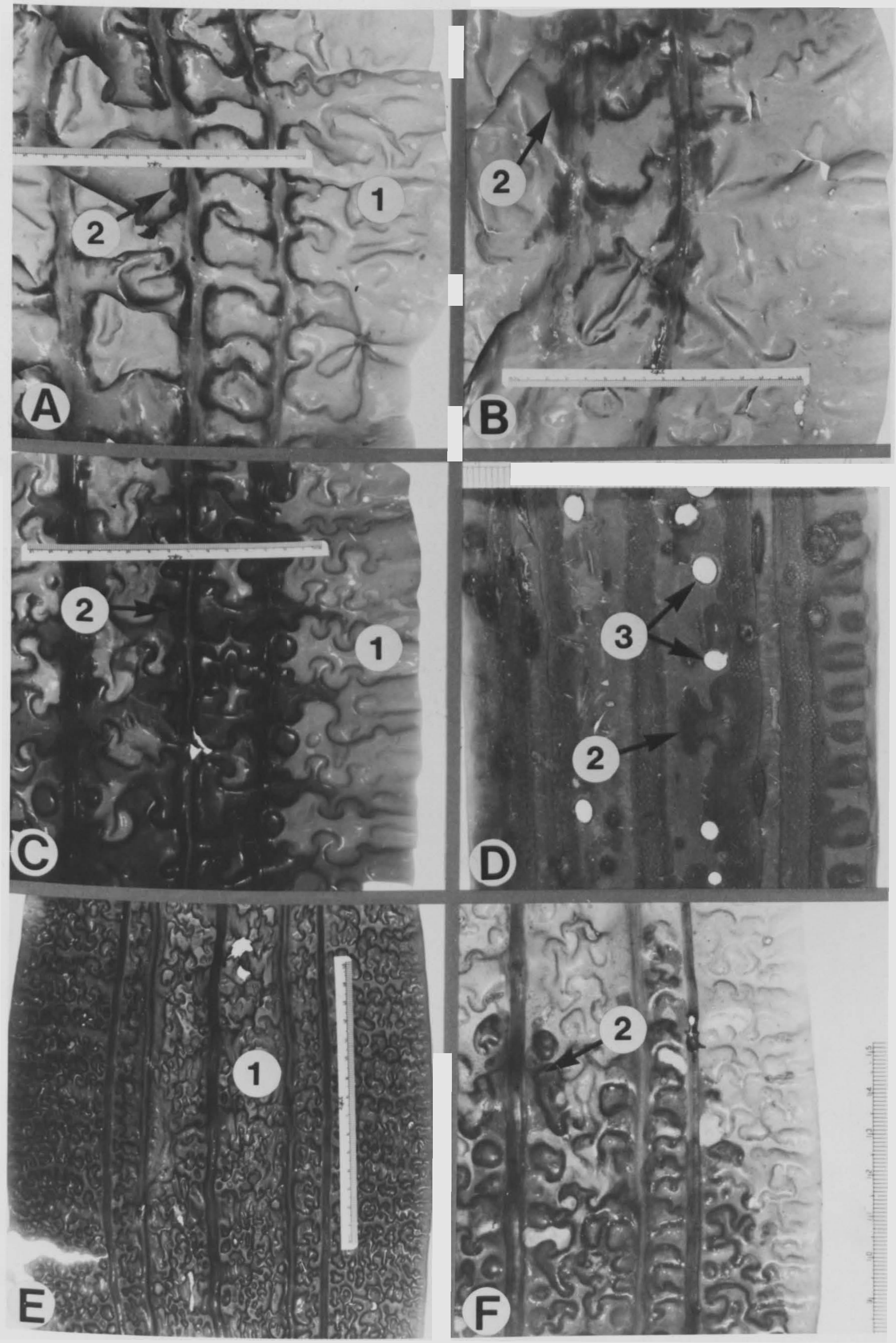
Indian Arm plants had larger bullations than Sooke plants, and Point No Point plants had much smaller bullations than at the other two sites (Fig. 8). The size of bullations on Cape Beale plants was similar to those at Point No Point. At Cape Beale the bullations tended to occur along the edges of the blade, the area between the ribs being nearly smooth (Fig. 8D).

Indian Arm blades were crisp and tore easily when they

Fig. 8 Part of *Costaria* blades from Indian Arm, Sooke, Point No Point and Cape Beale showing bullations, perforations and sori along ribs.

| | |
|---|---|
| A and B | Indian Arm, June 18, 1970 |
| C | Sooke, June 17, 1970 |
| D | Cape Beale, July 19, 1970 |
| E and F | Point No Point, June 17, 1970 |

1. Bullations
2. Sori
3. Perforations


A
B
C
D
E
F
1
2
3

were handled, whereas plants from the other three places were tougher and tore much less readily. All blades were a golden brown colour, and the thicker or more bullate a blade, the darker the colour. The blades were more opaque where sori were present.

Perforations, nearly round, smooth-edged holes, 2-10 mm in diameter, were found in some blades. Indian Arm blades were not perforated. Some blades at Sooke and Point No Point had a few scattered perforations. However, there were many perforations in Cape Beale blades, regularly arranged in two rows on either side of the middle rib (Fig. 7). Blades in all areas often had irregular-edged holes, the result of grazing and abrasion.

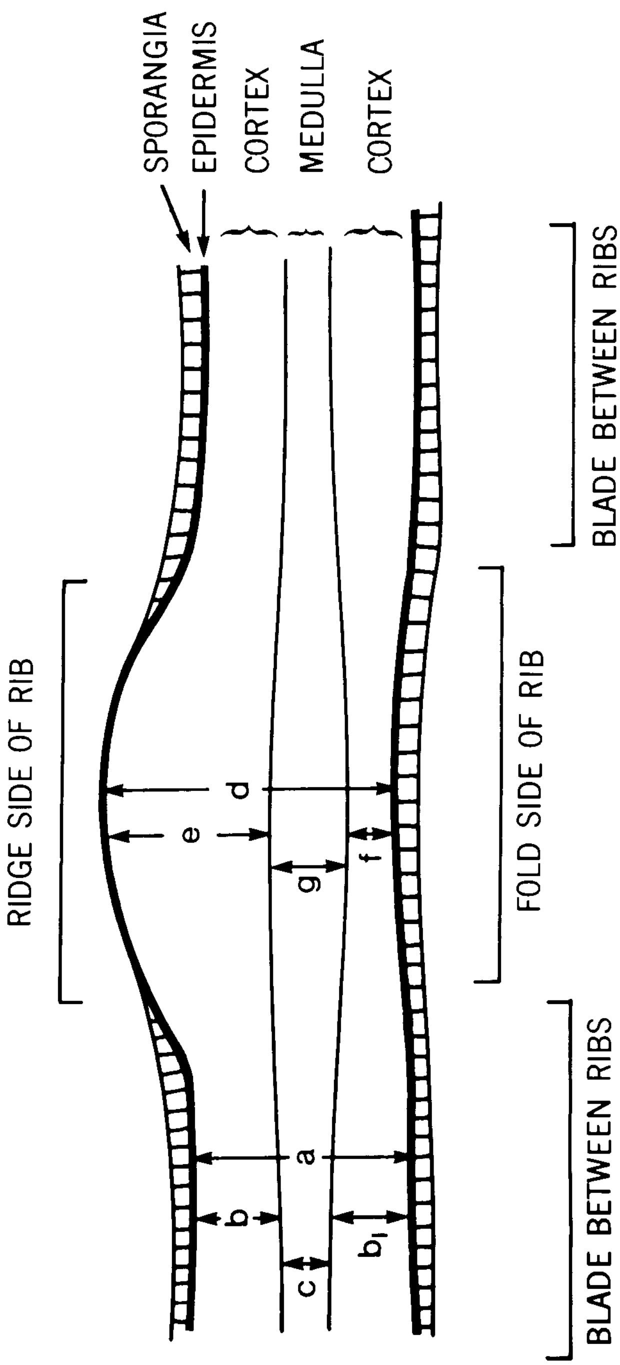
Blade anatomy:

The locations of blade and rib measurements are given in Fig. 9. Blade thickness between the ribs, 15 cm from the blade base, was similar at all four study sites. (Table II).

The blade has an epidermis, cortex and medulla. The epidermis consists of one cell layer of pigmented cells. The cortex is several cells thick; the outer cells are smaller and pigmented, and the inner ones are larger and unpigmented. The thickness of the cortex and number of cell layers were

Fig. 9 A diagrammatic transverse section of a <u>Costaria</u> blade showing internal structure and positions of measurements taken for Table II.

| | |
|---|---|
| a | Blade thickness including epidermis but not sporangia. |
| $b, b_1$ | Thickness of blade cortex. |
| c | Thickness of blade medulla. |
| d | Rib thickness including epidermis but not sporangia. |
| e | Thickness of rib cortex, ridge side. |
| f | Thickness of rib cortex, fold side. |
| g | Thickness of rib medulla. |


SPORANGIA
EPIDERMIS
CORTEX
MEDULLA
CORTEX
RIDGE SIDE OF RIB
FOLD SIDE OF RIB
BLADE BETWEEN RIBS
BLADE BETWEEN RIBS
a
b
$b_1$
c
d
e
f
g

similar at all four places (Fig. 10; Table II). The medulla is made up of loosely intertwining filaments (Fig. 10). Although the thickness of the medulla was similar at all four places (Table II), the measurements may not be very accurate as the medulla tended to get squashed during sectioning.

The edge of blades at all four places had the same thickness or was only a little thicker than the rest of the blade at the same distance from the blade base (Figs. 11A-E). The edges of perforations have similar anatomy to blade edges (Fig. 11F).

The width of the middle rib 15 cm from the blade base became progressively narrower from Indian Arm to Sooke, to Point No Point, to Cape Beale (Table I). Rib thickness of Indian Arm plants was significantly thinner than rib thickness of plants from the other three places (Table II).

In describing rib anatomy 'ridge side' refers to the side of the rib which projects from the blade surface and 'fold side' to the opposite side (Fig. 9). In all plants cortical cells on the ridge side tended to be smaller than those on the fold side, which were similar in size to cortical cells of the blade. The cortex on the ridge side of Sooke, Point No Point and Cape Beale plants was considerably thicker

Fig. 10 Transverse sections of blades of mature Costaria from Indian Arm, Sooke, Point No Point and Cape Beale, showing similar thickness and number of cell layers in the cortex of each. (Sections taken approximately 15 cm from the blade base).

A Indian Arm, June 18, 1970

B Sooke, June 17, 1970

C Point No Point, June 17, 1970

D Cape Beale, July, 19, 1970

1 Epidermis

2 Cortex

3 Medulla

4 Sorus

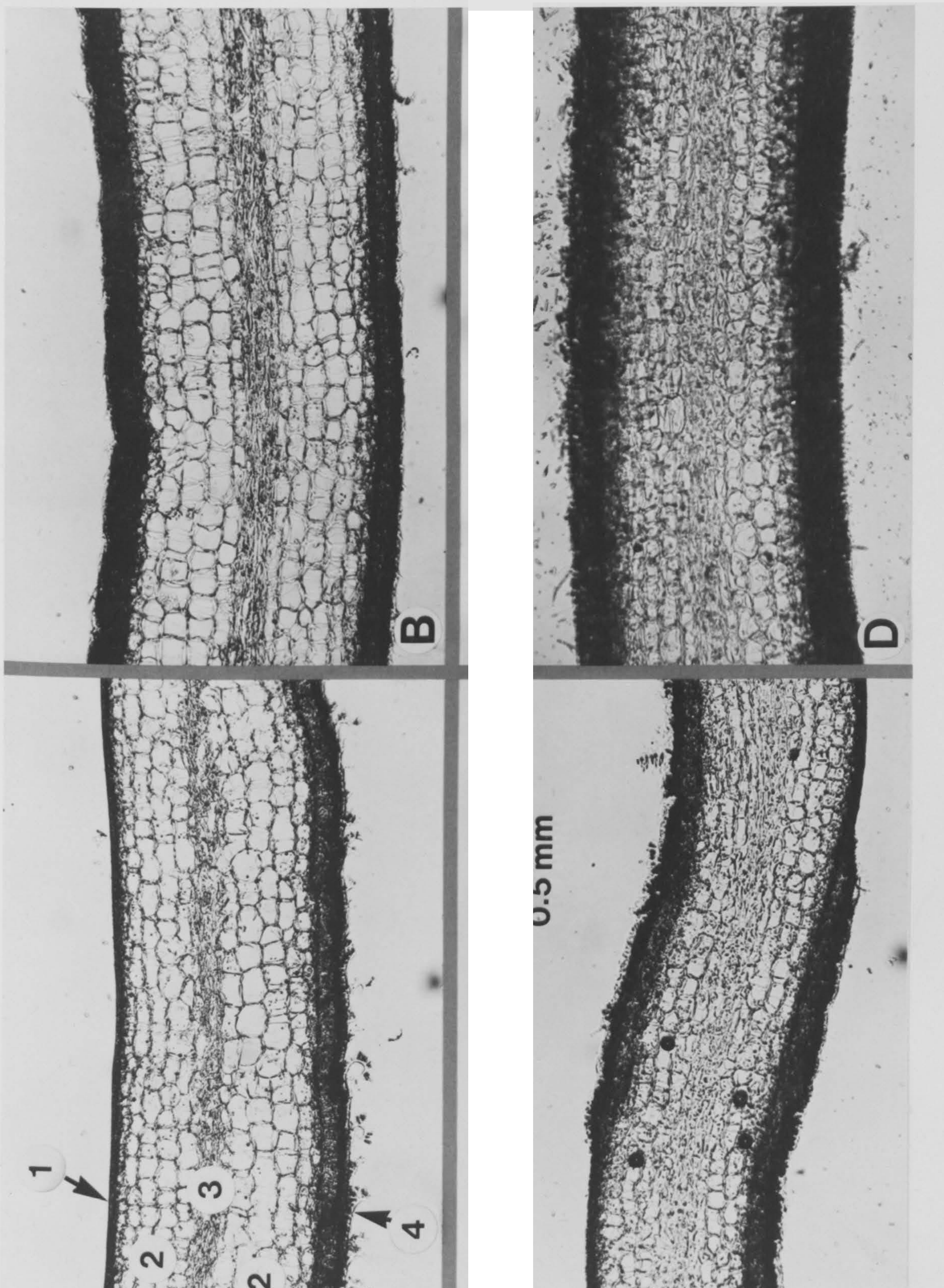
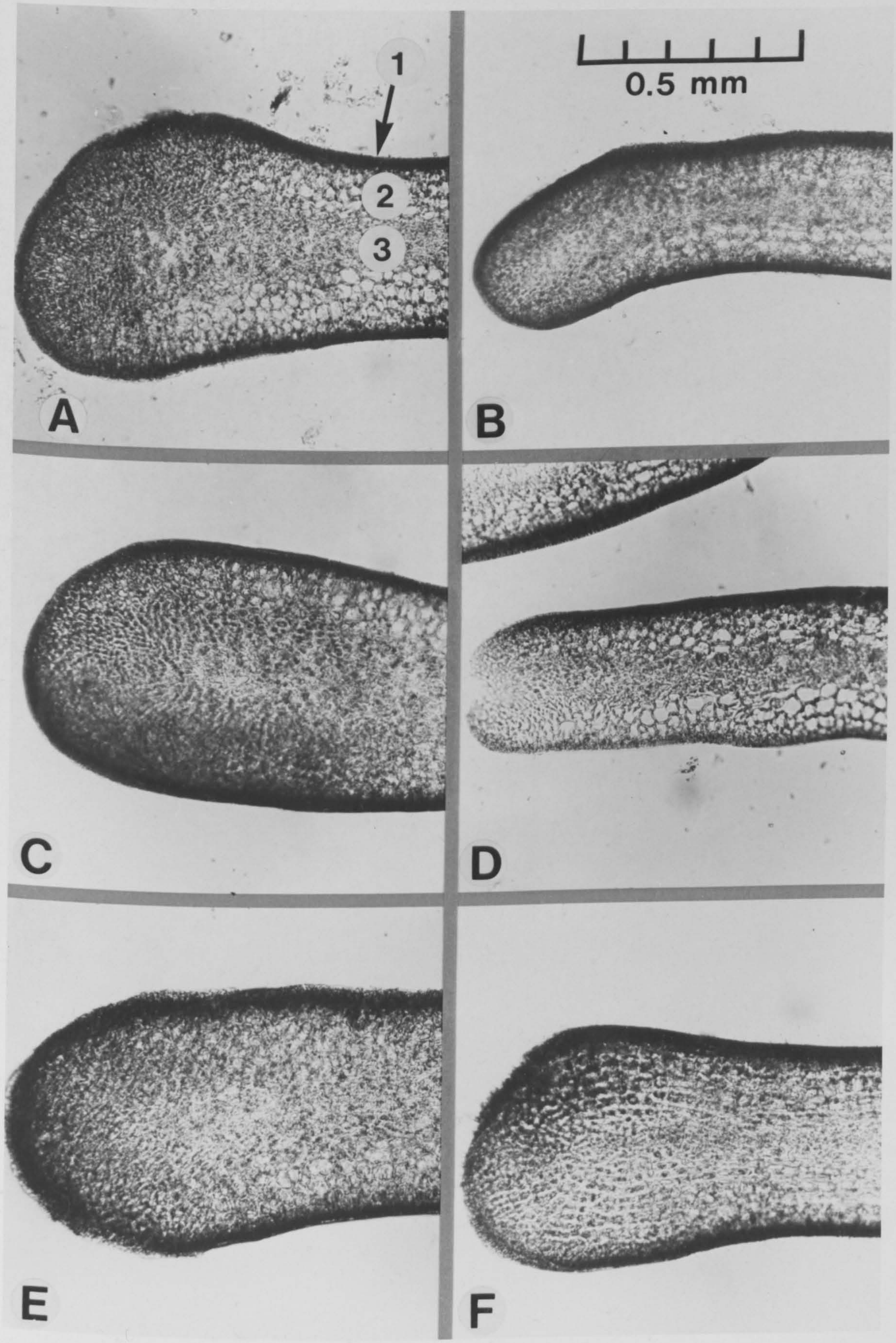

A
B
C
D
1
2
3
4
0.5 mm

Fig. 11 Transverse sections of blade margins of mature <u>Costaria</u> from Indian Arm, Sooke and Point No Point, and of the edge of a perforation of mature <u>Costaria</u> from Cape Beale. (Sections taken approximately 15 cm from the blade base).

| | |
|---|---|
| A and B | Indian Arm, June 18, 1970 |
| C and D | Sooke, June 17, 1970 |
| E | Point No Point, June 17, 1970 |
| F | Cape Beale, July 19, 1970 |

| | |
|---|---|
| 1 | Epidermis |
| 2 | Cortex |
| 3 | Medulla |


1
2
3
0.5 mm
A
B
C
D
E
F

and had more cell layers than that of Indian Arm plants. The former plants had approximately 30 cell layers in the ridge side cortex compared to approximately 15 cell layers in Indian Arm plants. The cortex of the fold side was also thinnest at Indian Arm, but there was a similar number of cell layers at all four places. The thickness of the medulla was similar for all plants but most variable at Cape Beale. The rib medulla was slightly thicker than the medulla of the blade between the ribs (Fig. 12; Table II).

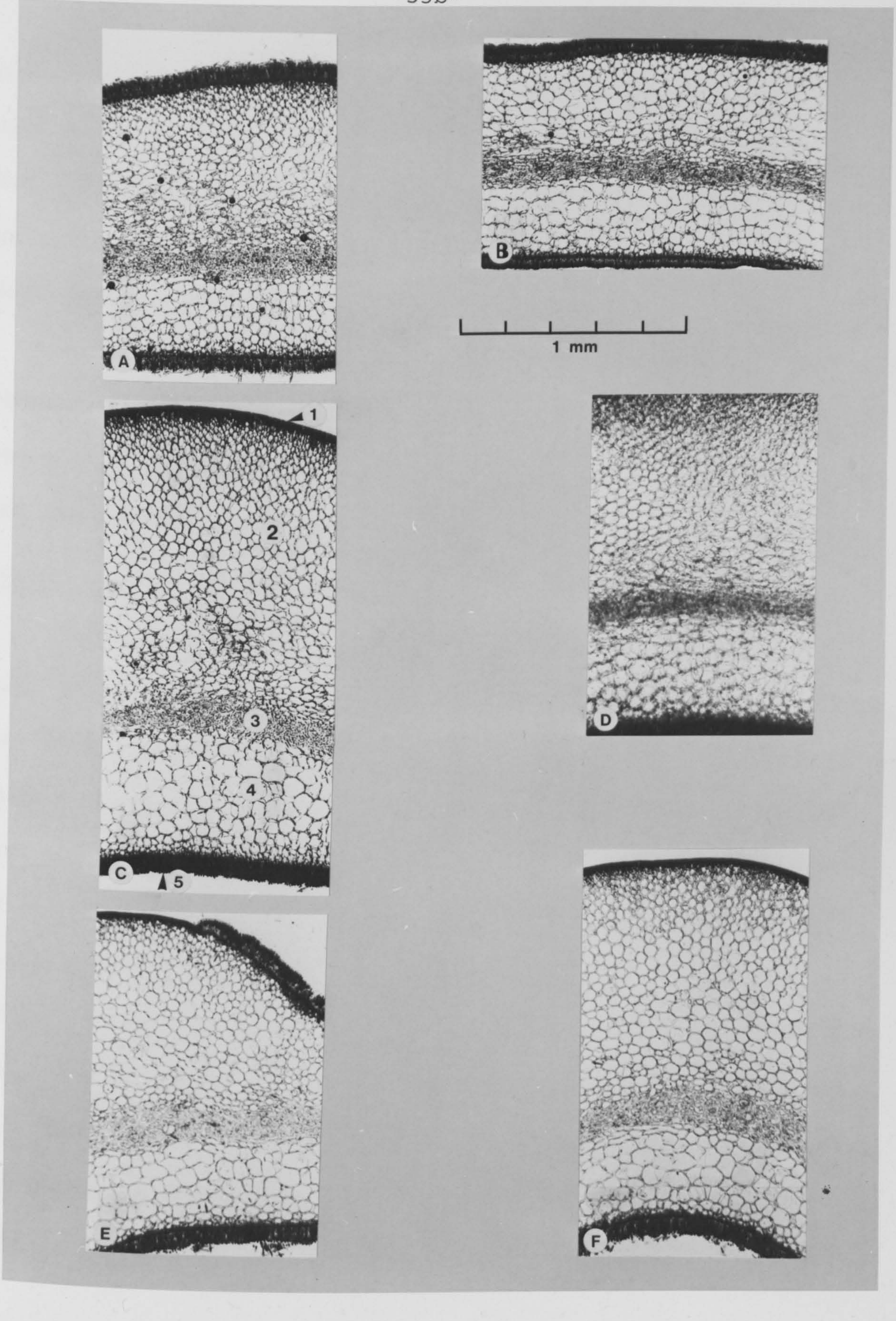
Sori:

Soral cover varied on the blades of *Costaria* at the different locations. On the basis of a few plants, the following trends were seen. Sori covered most of the basal third of mature blades; were found along and on the fold side of ribs of the middle third, and occurred occasionally along ribs of the top third. At Indian Arm, since the ribs were flattened, sori were found on the ridge side as well as the fold side of ribs on the basal third of blades (Figs. 12A, B) and since the bullations were large, the soral cover was nearly continuous. Sori were only very rarely found on the ridge side of the prominent ribs at the other three places (Figs. 12C-F). On Sooke, Point No Point and Cape Beale

Fig. 12 Transverse sections of ribs of mature <u>Costaria</u> from Indian Arm, Sooke, Point No Point and Cape Beale. Meiosporangia are absent on the ridge side of ribs at Sooke, Point No Point, and Cape Beale (C-F). (Sections taken approximately 15 cm from the blade base).

| | |
|---|---|
| A and B | Indian Arm, June 18, 1970 |
| C | Sooke, June 17, 1970 |
| D | Cape Beale, July 19, 1970 |
| E and F | Point No Point, June 17, 1970 |

| | |
|---|---|
| 1 | Epidermis |
| 2 | Cortex on ridge side of rib |
| 3 | Medulla |
| 4 | Cortex on fold side of rib |
| 5 | Sorus |


A
B
1 mm
1
2
3
4
C
5
D
E
F

plants which had smaller bullations than Indian Arm plants, sori were found in the hollows of bullations (Fig. 10C). Sori can be seen along the ribs of Indian Arm, Sooke, Point No Point and Cape Beale blades in Figs. 7A, B, C, D and F. Sori did not extend to the edge of blades.

Mature meiosporangia were approximately 70μ long. The volume of a meiospore was approximately $47\mu^3$ at Indian Arm, Sooke and Point No Point. Meiospores from Cape Beale were not measured.

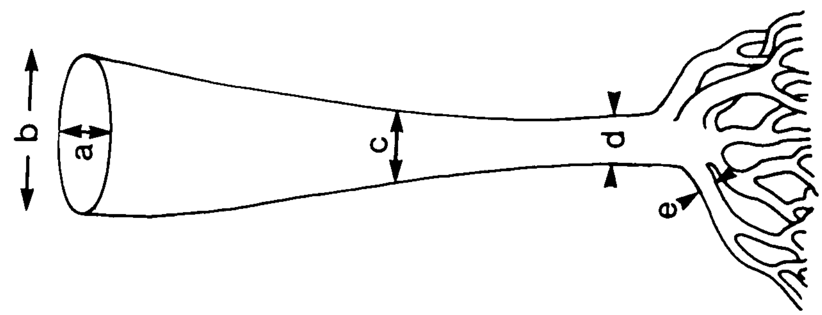
Stipe morphology:

Stipe length was variable at all four places (Table I). Some of the longest stipes were found at Point No Point, though not in the June 1970 collection. The top of the stipe for all plants was elliptical in cross section and the bottom terete. The greatest diameter (Fig. 13b) of the stipe top and diameters of the stipe middle and bottom (Fig. 13c, d) were variable but similar at Indian Arm, Sooke, Point No Point and Cape Beale. The least diameter of the stipe top (Fig. 13a) was smallest at Indian Arm (Table I).

The top half of stipes, or more if the stipes were long, was almost always ridged. Sooke, Point No Point and Cape Beal stipes were coarsely ridged, whereas stipes from Indian

Fig. 13 Diagram showing positions of stipe and hapteron measurements for Table I.

| | |
|---|---|
| a | Least diameter of stipe top |
| b | Greatest diameter of stipe top |
| c | Diameter of stipe middle |
| d | Diameter of stipe bottom |
| e | Diameter of thickest hapteron originating from the stipe. |


b
a
c
d
e

Arm were finely ridged or nearly smooth (Figs. 7, 14A-C). Many stipes with coarse ridges also had small protuberances on the crest of the ridges (Fig. 14D). Except on Indian Arm plants, fine ridges sometimes continued up the projecting side of ribs a few cm beyond the top of the stipe (Fig. 14B, C).

Indian Arm stipes were very flexible, and when a plant was out of the water they gave the blade no support. At the other three places the stipe was more rigid and gave blades some support when the plant was emerged.

Stipe anatomy:

Stipe anatomy was similar in all plants studied. It was difficult to determine where the outer layers (epidermal meristem of Smith, 1939) end, and cortex begins. The cells of the outer layers were pigmented and densely packed. The outermost cortical cells were similar to the outer layers, but the inner cortical cells became larger, unpigmented and less densely packed towards the centre of the stipe. The medulla was elliptical and the filaments more tightly packed than in the medulla of the blade or ribs (Fig. 15). In cross section cells of the stipe ridges were small and densely packed like the cells of the outer layers of the stipe elsewhere. Ridges appeared higher where protuberances occurred.

Fig. 14 Stipe morphology of mature Costaria from Indian Arm, Sooke and Point No Point, showing nearly smooth (A) and coarsely ridged stipes (B-D). Ridges may continue up projecting sides of ribs (B, C).

A Indian Arm, June 18, 1970.

B Sooke, June 17, 1970.

C Point No Point, June 17, 1970

D Sooke, June 17, 1970

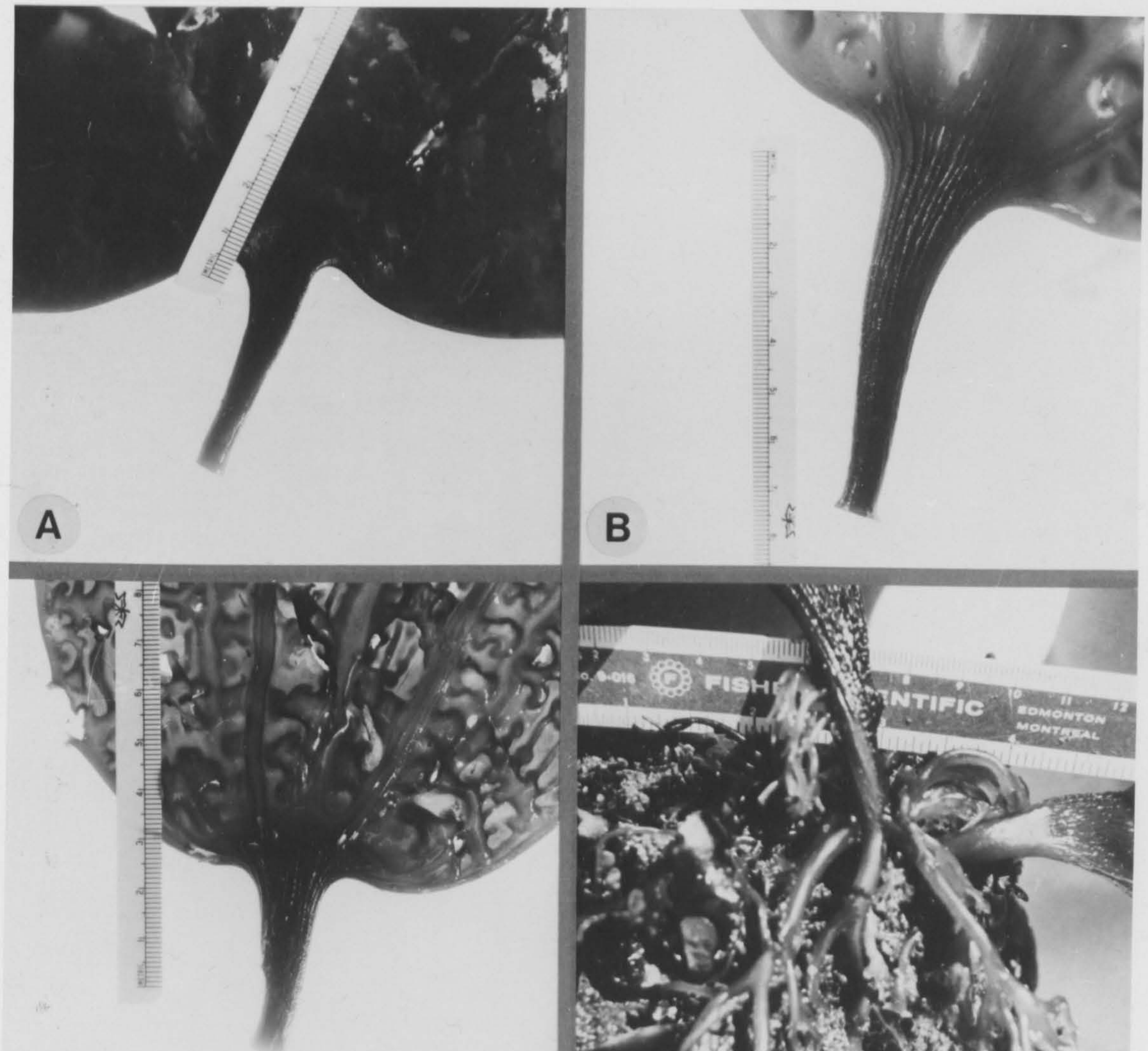

A
B
C
D
FISHER SCIENTIFIC
EDMONTON
MONTREAL

Fig. 15 Transverse sections of stipes from Indian Arm, Sooke and Point No Point showing internal structure and ridges. (Sections taken from near the top of the stipes).

A Indian Arm, June 18, 1970.

B Sooke, June 17, 1970.

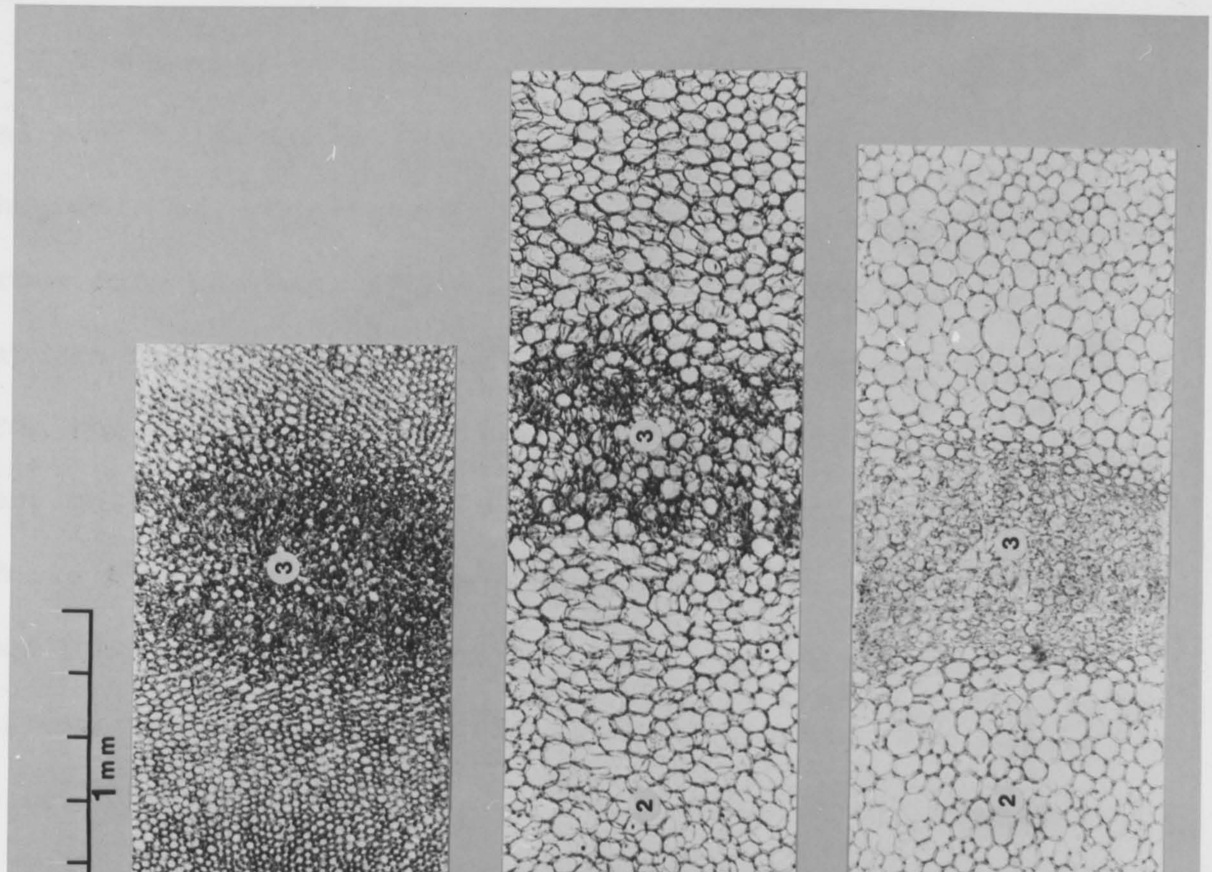
C Point No Point, June 17, 1970.

1 Epidermis

2 Cortex

3 Medulla

4 A ridge


1 mm
A
B
C
1
2
3
4

Hapteron morphology:

The number of haptera originating from the stipe base was similar at Sooke, Point No Point and Cape Beale, whereas they were more numerous at Indian Arm (Table I). The haptera arose from the base of the stipe and above the base in whorls. Haptera higher up were usually thicker than those which arose from the base. The diameters of the thickest haptera, measured near their origin (Fig. 13e), were similar at all four places (Table I). Haptera branch dichotomously and branching was most profuse at Indian Arm (Fig. 16). At this location haptera were attached loosely to the substrate, but firmly to boulders and rock at Sooke, Point No Point and Cape Beale.

Hapteron anatomy:

The outer layers and cortex of haptera were similar to those of the stipe. It was not easy to distinguish the medulla, which consisted of tightly packed cells.

In summary, the main morphological and anatomical characters of Costaria that differed between the four sites were rib thickness, bullations, blade texture, perforations, thickness of the stipe top, amount of ridging on the stipe surface and branching of the haptera.

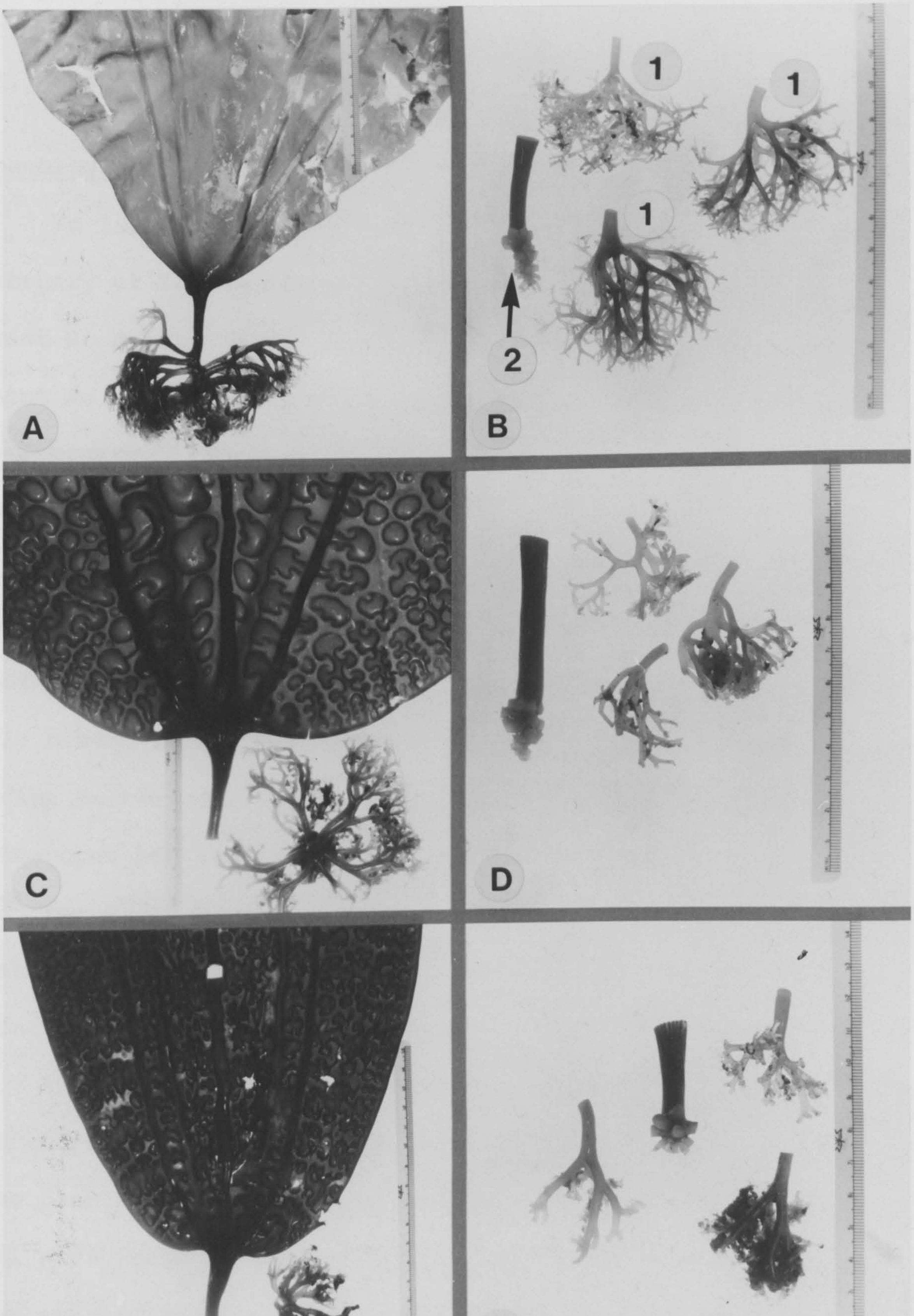
Fig. 16 Comparison of hapteron arrangement on stipes and degree of branching of the main haptera of *Costaria* from Indian Arm, Sooke and Point No Point.

A and B Indian Arm, June 18, 1970.

C and D Sooke, June 17, 1970.

E and F Point No Point, June 17, 1970.

A, C and E show the entire holdfast. In B, D and F the main haptera (1) have been cut off to show their arrangement on the stipe (2).


1
1
1
2
A
B
C
D
E
F

## II. Phenology and ontogeny

### Phenology:

In 1969 young *Costaria* plants were first found early in February at Indian Arm and Sooke and late in February at Point No Point. Since there were always fewer *Costaria* at Point No Point, small plants may not have been seen earlier in February. Plants grew rapidly until the sori appeared in mid-May at Indian Arm and Sooke and mid-June at Point No Point. Sori were found on *Costaria* as early as the end of April at Stanley Park, in Burrard Inlet. Blade length and width increased up to June or July (Tables III-V), but after July blades became very torn and mean blade lengths and widths decreased. Sporophytes began to disappear after meiospores had been released from mid-August at Indian Arm, and from early September at Sooke. There were always fewer plants at Point No Point, and they remained in good condition even in September and October.

A few old plants were still present at Indian Arm at the end of October and beginning of November. In addition, some plants up to 30 cm long with nearly entire blades and sori were found at this time (UBC 45632-7). These seemed to have started growing late in the season because the blades were nearly entire, were not covered by epiphytes and the meiospores had not been released. A similar combination of old plants and late developers were found at Sooke in mid-October and at the end of November. It was difficult to tell if there were late developers at Point No Point as plants there remained in good condition. Some late developers were still found at Indian Arm early in December (UBC 45638), but there is no information for Sooke and Point No Point for that time as no observations could be made due to rough weather.

Ontogeny:

The following account of the ontogeny of *Costaria* is based on monthly observations and collections from Indian Arm, Sooke and Point No Point. The development of *Costaria* was followed by describing selected characters of specimens without sori in groups based on blade length (less than 5 cm, 5-10 cm, 10-20 cm, 20-30 cm, and longer than 30 cm), and of larger specimens with sori in groups based on the month collected. The ends of blades up to 30 cm long were usually little torn, and so the groups could be described on the basis of blade length. Larger plants usually have very torn ends, and so another criterion was needed to distinguish the groups. The largest measurements of blade length and blade width recorded at Indian Arm, Sooke and Point No Point in 1968 and 1969 were as follows:

| | Indian Arm | Sooke | Point No Point |
|---|---|---|---|
| Blade length (cm) | 170 | 230 | 250 |
| Blade width (cm) | 75 | 60 | 25 |

Proportional increases in blade length and blade width partly explain the shape of the blade base. Up to the 30+ cm group without sori blade width increased. Indian Arm plants became wider than Sooke plants, which on the whole were wider than Point No Point plants (Tables III-V). Mature Indian Arm plants were slightly wider than mature Sooke plants, and mature Point No Point plants were considerably narrower. Blade width usually ceased to increase after sori were produced.

Only the smallest plants at Indian Arm, less than 5 cm long, were cuneate. The blade bases soon became obtuse and the angle increased until mature plants were obtuse or cordate, and some were even auriculate (Table III). The angle of the blade base may continue to increase slightly after the appearance of sori. Most Sooke plants were still cuneate in the 30+ cm group, but they then became obtuse, and mature plants were mainly obtuse and cordate, while some were auriculate (Table IV). Some Point No Point plants remained cuneate even with sori, but most became obtuse, and a few cordate when mature (Table V).

The development of the blade base and blade shape of typical Indian Arm, Sooke and Point No Point plants is shown in composite diagrams (Fig. 17).

The three middle ribs developed first, and then the two outermost ones. All initially appeared near the blade base. At Indian Arm a few 10-20 cm plants still had only three ribs whereas only a few 5-10 cm Sooke plants had three ribs, and some plants less than 5 cm at Point No Point already had five ribs. The ribs of Indian Arm *Costaria* were never prominent and usually became very flattened in mature blades whereas the ribs started and remained prominent at Sooke and Point No Point. The smallest plants recognizable as *Costaria* had the following dimensions:

| | Indian Arm | Sooke | Point No Point |
|---|---|---|---|
| Blade length (cm) | 2·8 | 1·9 | 1·8 |
| Blade width (cm) | 0·8 | 0·7 | 0·6 |

Most Indian Arm blades remained nearly smooth up to 10-20 cm long. Sooke and Point No Point blades less than 5cm

Fig. 17 Composite diagrams showing four stages in the development of blade shape and blade base shape of typical *Costaria* at Indian Arm, Sooke and Point No Point.

A Indian Arm

B Sooke

C Point No Point

1 February

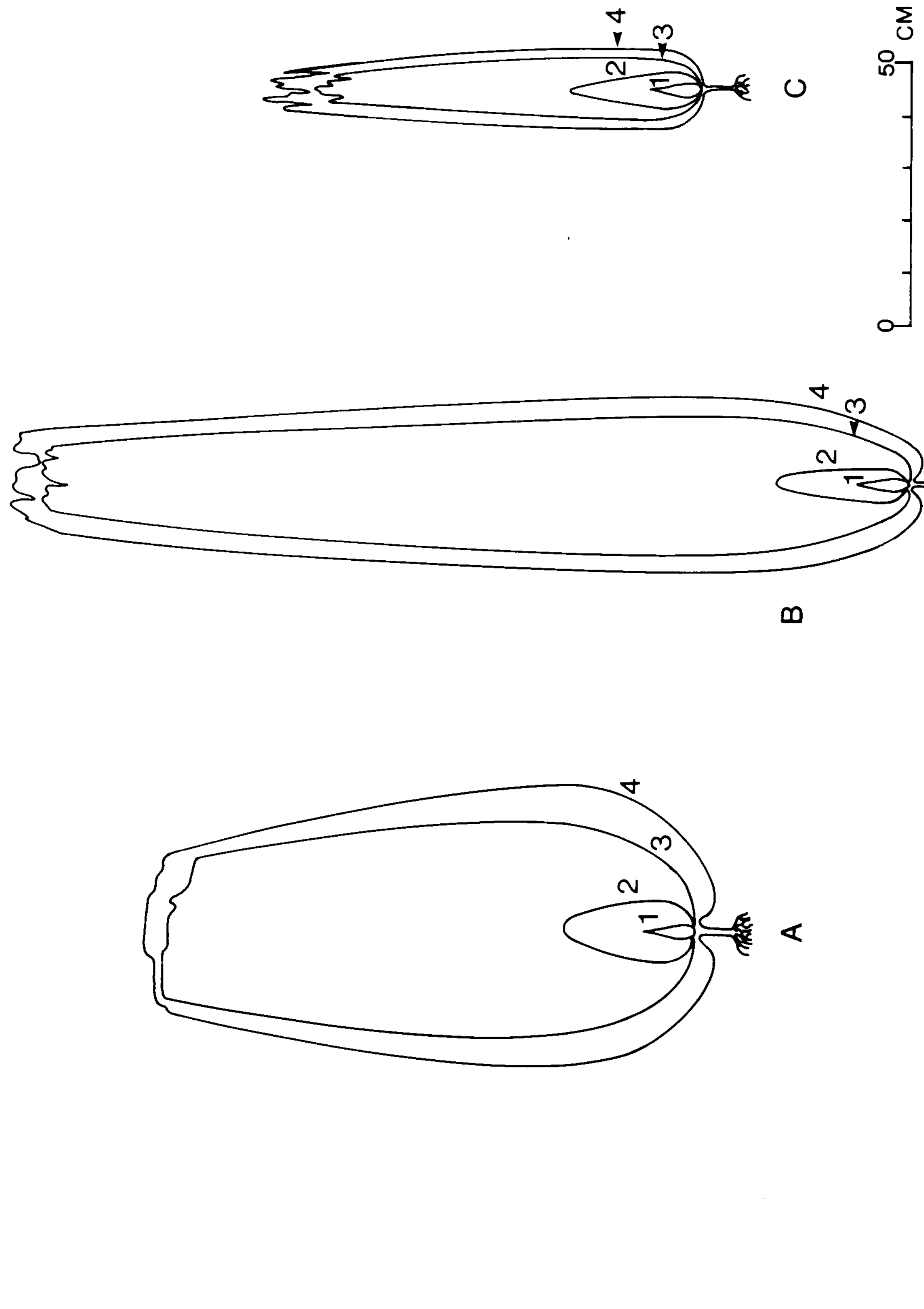
2 March

3 May

4 July

1-3 *Costaria* without sori

4 *Costaria* with sori


A
B
C
1
2
3
4
0
50
CM

long were smooth or had only small bullations near the blade base. Bullations first appear near the blade base and then grow in size as the plants grow. Indian Arm plants had fewer bullations per unit area than Sooke plants, which in turn had fewer bullations than those from Point No Point. At Indian Arm and Sooke mature plants appeared less bullate where there was a continuous soral cover. At Point No Point, soral cover was not continuous and the blades remained bullate.

At Indian Arm sori first appeared along the ribs of the top and middle thirds of the blade in patches or almost continuously. They then appeared on the fold side of ribs, and finally on the ridge side. In both cases, they either spread towards the midline of the ribs or started in patches on the ribs. There were very few patches of sori between the ribs on the top third of the blades, but more between the ribs on the middle third. Sori developed last on the bottom third. The ridge side of the middle ribs tended to be covered before the ridge side of the outer ribs. Indian Arm blades usually had large bullations and sori were nearly continuous on both sides of the blade, particularly on the bottom third. Where covered by sori the ribs became even more flattened than usual.

At Sooke the sequence of development was similar to that at Indian Arm, but where the sori first appeared between the ribs they tended to occur in the hollows of bullations on one side of the blade only. The ridge side of ribs was generally free of sori. Sori developed last outside the outermost ribs. Blades were less bullate and ribs slightly flattened where sori were nearly continuous on the lower half of the blade.

Unlike Indian Arm and Sooke plants, at Point No Point sori did not develop on the top third of the blade first, and were not usually found there. Sori appeared along the ribs of the bottom and middle thirds and between the ribs in the hollows of bullations on the bottom third. They were not usually found on the ridge side of ribs. Sori became nearly continuous between the ribs, but were more patchy outside the outermost ribs. Ribs remained prominent and the blade bullate even where covered by sori.

After meiospore release, the plants became colonized by epiphytes such as diatoms, filamentous algae, bryozoans and hydrozoans. Blades of Indian Arm plants tended to be covered more extensively by bryozoans than Sooke or Point No Point blades. Finally, large portions of blade tore off. Plants at Indian Arm became very torn and brittle, but at Sooke ribs projected from the torn blades. Costaria at Point No Point tended to remain in better condition.

Stipe length increased up to 30+ cm group, and was quite variable in mature plants (Tables III-V). At Indian Arm the stipe surface remained smooth up to and including the 20-30 cm group. Some of the plants in the 30+ cm group and nearly all the mature plants had finely ridged stipes. Many Sooke plants of 10-20 cm still had smooth stipes. They then became finely ridged, and when longer then 30 cm, coarsely ridged. Point No Point plants were similar to Sooke plants, but fine ridges were found on the stipes of plants 5-10 cm long, and coarse ridges on larger plants. Short stiped plants at Point No Point tended to be somewhat less coarsely ridged.[1]

In summary, the three populations had slightly different phenology.

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[1] Voucher specimens to illustrate the ontogeny of Costaria at the three sites are as follows: Indian Arm plants without sori, UBC 45743-45752; Indian Arm plants with sori, UBC 45621-8; Sooke plants without sori, UBC 45753-4 and UBC 45756-45770; Sooke plants with sori, UBC 45639-45654; Point No Point plants without sori, UBC 45771-45781; and Point No Point plants with sori UBC 45657-45673.

Some late developers were found at Indian Arm and Sooke, and plants at Point No Point remained in good condition late in the year. Differences in the ontogeny of Indian Arm, Sooke and Point No Point plants were seen in the development of the angle of the blade base, ribs, bullations and ridges on the stipe. The pattern of sorus appearance on Point No Point blades was also different from that on Indian Arm and Sooke plants.

III. Transplants and controls

In this section the development of the controls will be commented upon, and the way in which the transplants differed from the controls will be described. Emphasis is placed on transplants that had an initial blade length of less than 20 cm, and which were started early in the year, usually between February and April. Data are mainly from transplants made in 1969.

Transplants and controls were considered to have grown well if they were in similar condition and reached dimensions similar to naturally growing plants. There was a high loss of plants after transplanting and although statistical comparisons could not be made, some conclusions could be drawn.

Indian Arm *Costaria* controls (Fig. 18; UBC 45735-41)

Fig. 18 Transplant studies: Indian Arm *Costaria* controls started on February 27, March 6 and March 20, 1969, photographed at later dates to show development.

A Started on February 27.

1 Photographed on May 9.

2 " " June 11.

3 " " August 13.

B Started on March 3.

1 Photographed on May 9.

2 " " August 13.

C Started on March 20.

1 Photographed on June 18.

2 " " July 15.

3 " " August 13.


A1
A2
A3
B1
B2
C1
C2
C3

started on February 27, 1969, reached larger dimensions than did plants started on March 6 and March 20 (Tables VI-VIII), but otherwise their development was similar to that of Indian Arm plants described in Section II (Table III). Of the plants started on February 27, sori were first recorded on the four Costaria with the largest blade base angles on June 11. Sori probably appeared in May but the plants were not examined at that time. Plants started on March 6 and March 20 produced sori by July 15.

Indian Arm Costaria transplanted to Sooke on February 22 did not grow well in blade length and width compared to the controls (Table VI - IX). The plants became very torn, though what was left of the torn plant tended to be healthy. Plants started on March 30 grew even less (Table X). Some of the blades appeared to be less bullate than the controls. The angle of the blade base decreased rather than increased. Stipes became finely ridged a little earlier than those of the controls. No sori were produced as the plants did not survive long enough.

Indian Arm Costaria transplanted to Point No Point in 1969 did not survive. Two larger plants with initial blade lengths of 25·5 and 45·0 cm were started on March 29 and had become very torn within two weeks. Some plants in 1968 survived somewhat longer than this (Tables XI-XIII). The plants grew little and the shape of the blade base remained obtuse (Fig. 19; UBC 45719-21, 45723). The blades became very torn and were less bullate than usual. One 8 cm long plant started on July 9 had developed sori by September 28 (Table XIII; UBC 45723).

Sooke Costaria controls (Fig. 20; UBC 45728-9) started on March 30 and April 26 did not grow as well as plants started on February 22 (Tables XIV-XVI). However their developmental pattern was similar to that of naturally growing Sooke plants (Table IV). Of the plants started on February 22, sori were first seen on the two Costaria with the largest blade base angles in June (Table XIV). No sori were produced on plants started on March 30 and April 26.

Sooke Costaria transplanted to Indian Arm (Fig. 21; UBC 45731-4) on February 20 grew well until April 24 (Table XVII). There was less growth of plants started on February 27 (Table XVIII). Most of the blades of both sets of plants became brittle and unhealthy by May and June. Transplants produced slightly greater blade base angles earlier than did the controls. Like the controls, coarse ridges developed on the stipes. Sori

Fig. 19 Transplant studies: Indian Arm Costaria transplanted to Point No Point on May 13, 1968 and photographed on June 13, 1968.


36 ①
36 ②
36
0
5
10
15 cm

Fig. 20 Transplant studies: A Sooke Costaria control started on February 22, 1969, photographed at later dates to show development.

| | | |
|---|---|---|
| 1 | Photographed on | May 18. |
| 2 | " " | July 12. |
| 3. | " " | August 2. |

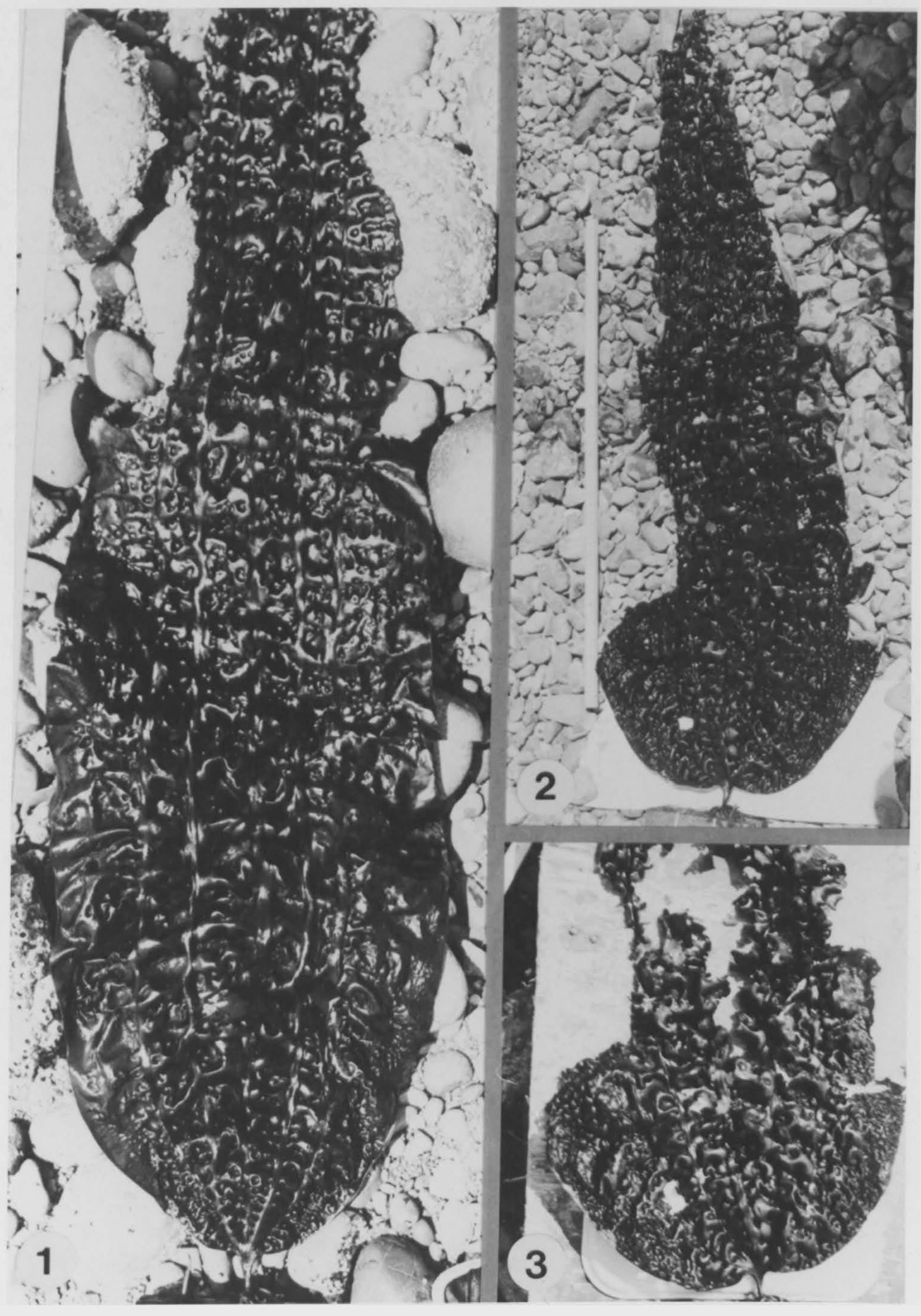
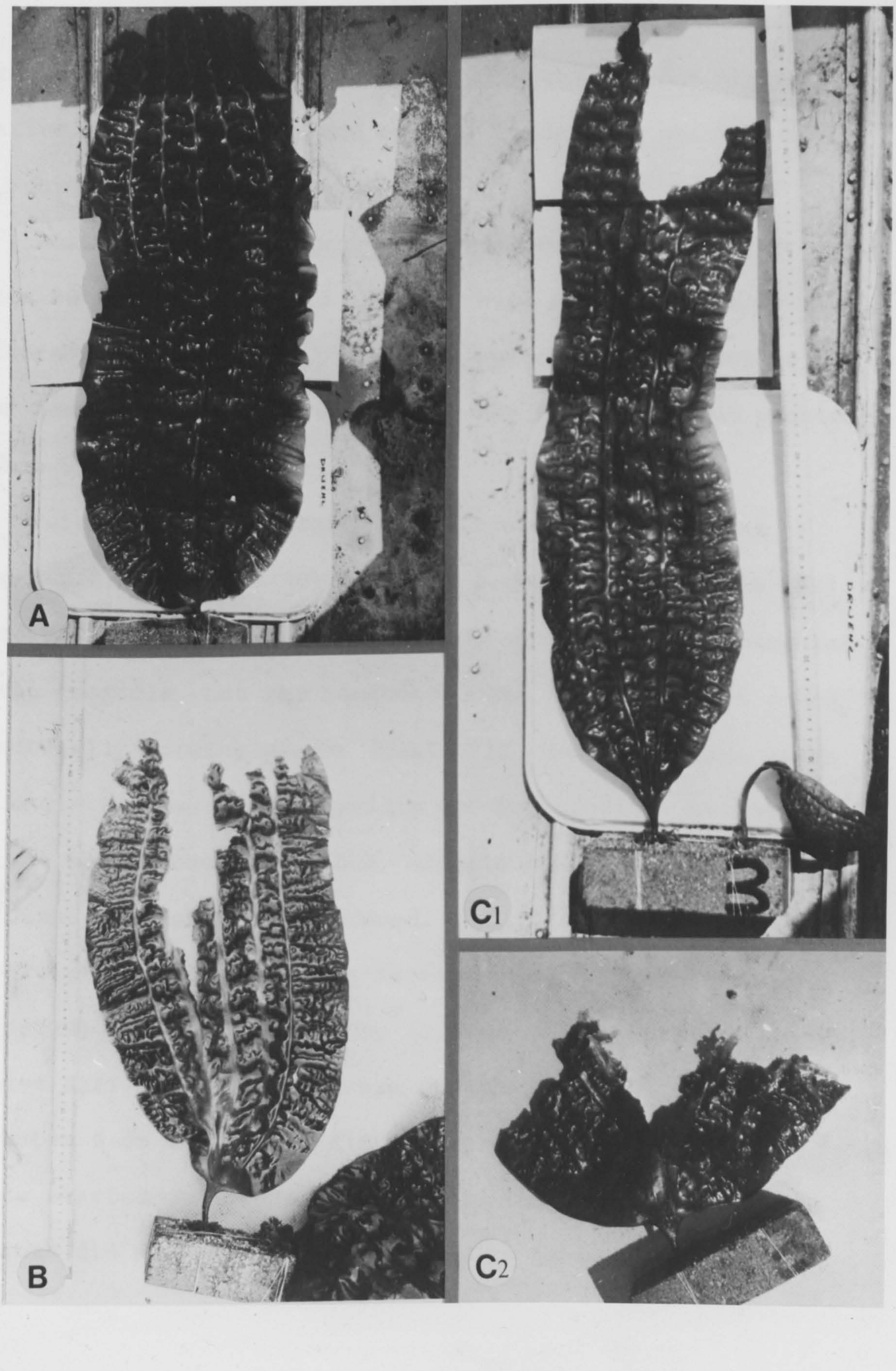

1
2
3

Fig. 21 Transplant studies: Sooke Costaria transplanted to Indian Arm on February 20 and February 27, 1969, photographed at later dates to show development.

A Started on February 20.
Photographed on May 9.

B Started on February 20.
Photographed on June 11.

C Started on February 27.
1 Photographed on May 9.
2 " " July 15.


A
B
C1
C2

were seen on June 11 on the plant with the largest angle started on February 20, and on July 15 on both plants started on February 27.

Point No Point _Costaria_ controls (Fig. 22A) started on March 29 and April 25 did not grow well and were lost or very tattered (Tables XIX-XX). The development of the controls was poor compared to the naturally growing Point No Point plants (Table V).

Point No Point _Costaria_ transplanted to Indian Arm (Figs. 22B, C; UBC 45730) on April 3 grew little (Table XXI). There was a slight increase in blade width and angle compared to the controls, but the increases were less than that found in naturally growing plants (Table V). However, blade width and angle increased in naturally growing plants. At Indian Arm the blades became twisted, brittle and unhealthy in May and June. No sori were produced.

Point No Point _Costaria_ transplanted to Sooke (Fig. 23; UBC 45727) on March 30 and May 18 grew better than the controls (Tables XXII-XXIII). Sori were produced on July 12 and September 6 on the lower half of the blades of the two remaining plants started on March 30 and May 18 respectively. The controls did not survive long enough to produce sori.

Fig. 22 Transplant studies: A Point No Point *Costaria* control started on April 25, (A) and Point No Point *Costaria* transplanted to Indian Arm on April 3, 1969 (B, C), photographed at later dates to show development.

| | |
|---|---|
| A | Point No Point control started on April 25. |
| 1 | Photographed on July 13. |
| 2 | " " August 3. |
| B and C | Point No Point *Costaria* transplanted to Indian Arm on April 3. |
| B 1 | Photographed on May 9. |
| 2 | " " June 11. |
| C 1 | Photographed on May 9. |
| 2 | " " June 11. |

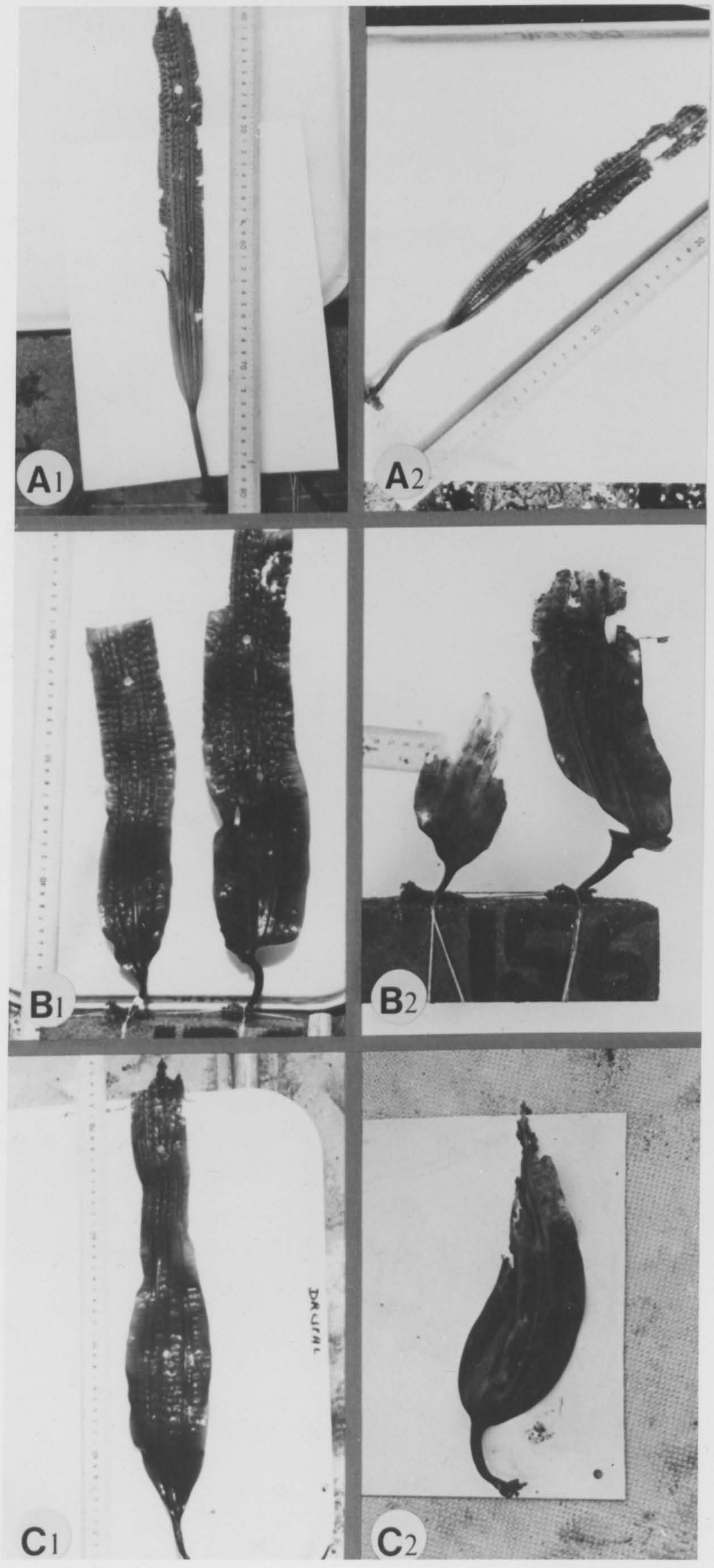
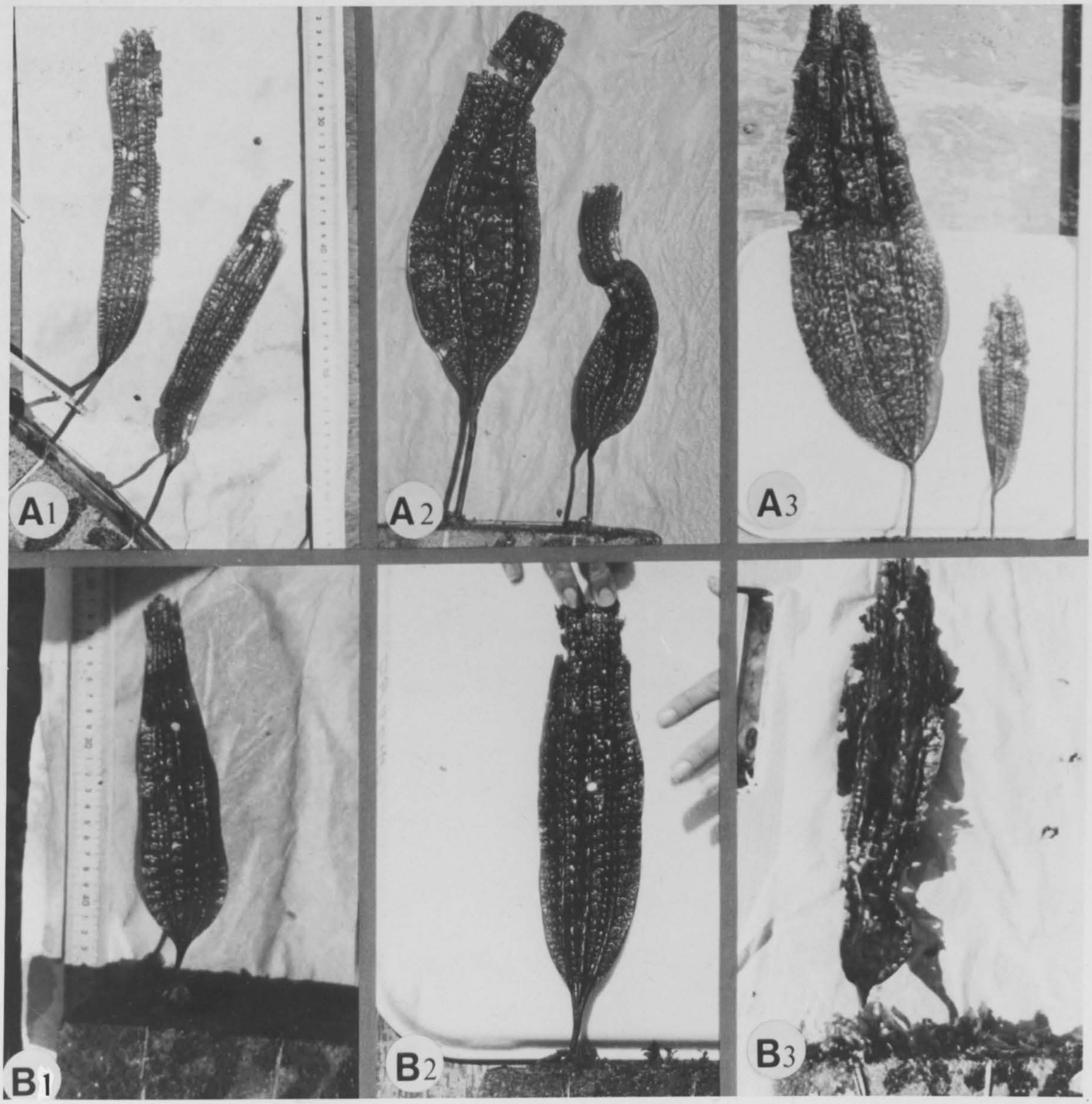

A1
A2
B1
B2
C1
C2

Fig. 23 Transplant studies: Point No Point *Costaria* transplanted to Sooke on May 18, 1969, photographed at later dates to show development.

| | |
|---|---|
| A | Started on May 18. |
| 1 | Photographed on June 15. |
| 2 | " " July 12. |
| 3 | " " August 2. |

| | |
|---|---|
| B | Started on May 18. |
| 1 | Photographed on July 12. |
| 2 | " " August 2. |
| 3 | " " September 6. |


A1
A2
A3
B1
B2
B3

The haptera of all the transplants were similar to the controls and to the naturally growing plants. Costaria with blade lengths initially greater than 20 cm, whether controls or transplants, tended to grow better than plants with initial blade lengths less than 20 cm. For example, Point No Point controls started on May 17 and June 14, 1969, grew quite well with a change in blade base shape from cuneate to obtuse and with the production of sori on some blades. Initially larger Sooke and Point No Point plants also grew better at Indian Arm, but they still became brittle and unhealthy in May and June.

In summary, the transplants generally grew and survived less well than did the controls. The angle of the blade base and bullations of some transplants tended to develop differently from those of the controls. There was little or no change in the prominence of the ribs, stipe length, ridges on the stipe surface or time of sori appearance in the transplants.

## IV. Morphology of Costaria in the northeast Pacific, and a study of historically important specimens.

### Study of Costaria in the northeast Pacific from herbarium specimens:

Most Costaria in the northeast Pacific had prominent ribs and coarsely ridged stipes. The bullations were difficult to determine on pressed specimens, but appeared to be variable. These plants were grouped according to the angle of their blade base and whether the blades had regular perforations or not. The different groups (cuneate/perforated, cuneate/ not perforated, obtuse/perforated, obtuse/ not perforated, cordate/not perforated and auriculate/not perforated) were plotted on a map of the northeast Pacific (Fig. 24).

Perforated plants were generally found on the outermost coasts. The only cordate/perforated specimen (UBC 22801) collected came from Klokachef I., Alaska (57°24'05"N, 136°52' W). Non-perforated plants showed no clear distribution pattern (Fig. 24). The existing wave exposure data are subjective observations made by earlier collectors. These data indicated that collections of Costaria were made mainly in moderately exposed and exposed areas.

Collections of Costaria at San Juan I., Washington, and in southwest British Columbia:

Observations on Costaria collected at San Juan I., Washington, and in southwest British Columbia are summarized in Table XXIV. Large immature and mature Costaria from Second Narrows and Stanley Park were similar. These plants, particularly

Fig. 24 Distribution in the northeast Pacific of mature *Costaria* with prominent ribs, variable bullations and coarsely ridged stipes, grouped according to the shape of the blade base and the presence or absence of perforations. (Data from herbarium specimens).

1 Cuneate/perforated

2 Cuneate/not perforated

3 Obtuse/perforated

4 Obtuse/not perforated

5 Cordate/not perforated

6 Auriculate/not perforated

MS Moderately sheltered

ME Moderately exposed

E Exposed


125°W
60°N
55°N
50°N
160°W
3
6
6 MS
5
5
3
4
5
6
2
4
1
3
2
3
4
5
6
3
4
5
6
5
2
3
3
4
1
2
3
1
4
2
4
2
4
3
5
3
4
4
2
4
5E
6ME
4 MS
6 MS
5 MS
1
ME 3
ME 1
ME 2
3
ME,E 4
ME 1
ME,E 2
3
E4
ME2
E 2
4
4
ME 5
ME 6
MS 1
MS,ME,E 2
3
MS,ME 4
MS 5
E3
E1
ME 5
E4
ME2
2
4
5
5
4
6 ME
2

from Second Narrows (where there is a strong current), tended to have long stipes which were fairly coarsely ridged. San Juan I. plants resembled them but had longer, more coarsely ridged stipes and more prominent ribs. Mature Hammond Bay and Thormanby I. plants were similar to each other and had short, not very coarsely ridged stipes. The main difference between Costaria in the vicinity of Bamfield, and Costaria at Port Renfrew and Amphitrite Point was that more plants had perforated blades in the former area (Table XXIV).

Young Costaria from San Juan I. (UBC 45686), Second Narrows (UBC 45674) and Stanley Park (UBC 45679) had large bullations, inconspicuous ribs and smooth stipes. At Hammond Bay (UBC 45690) and Thormanby I. (UBC 45694-5) young plants were similar, but had shorter stipes. However, at Port Renfrew (UBC 45702-5, 45707), the Bamfield vicinity (UBC 45708) and Amphitrite Point (UBC 45712) young Costaria had more bullations, prominent ribs and ridged stipes.

Study of historically important specimens:

Many of the specimens listed by Scagel (1957) were immature. From Table XXV it can be seen that C. costata and C. mertensii both with and without sori have a variable blade base, coarsely ridged stipe (except for some young plants), prominent ribs, and bullations variable in size. None of the plants are perforated (Figs. 25, 26). Specimens are either similar to Costaria at Sooke and Point No Point (Figs. 25A, B, 26A, B), or to a form of Costaria which grows around Oak Bay, Victoria (Figs. 25C, 26C).

There is no difference between specimens from the Dudley Herbarium labelled C. costata and C. mertensii by Doty (Fig. 27; Table XXV). Only one plant has sori. All have cuneate or obtuse blade bases, coarsely ridged stipes, prominent ribs, many small bullations (except for one plant) and are not perforated. They resemble Costaria from Sooke or Point No Point.

The type of Turner's Fucus costatus (1819) which I studied at the British Museum, London, was collected by Menzies at Port Trinidad, California, and has an obtuse blade base (Fig. 3). It is similar to Costaria at Point No Point. Another specimen, at the Royal Botanic Garden, Edinburgh, collected by Menzies on the northwest coast of America in 1788 is similar to the type specimen, but has a more cuneate blade base. Turner's illustration, copied from a drawing by Menzies, may have been a composite of these two specimens.

In summary, most herbarium specimens of mature Costaria from the northeast Pacific had many small bullations, prominent ribs and coarsely ridged stipes. Perforated plants generally

Fig. 25 *Costaria* cited as *C. costata* by Scagel (1957), showing variation in blade morphology. Compare with Fig. 26.

A UC 132658

B CAN 1642

C UC 777300

Magnification x 1/4

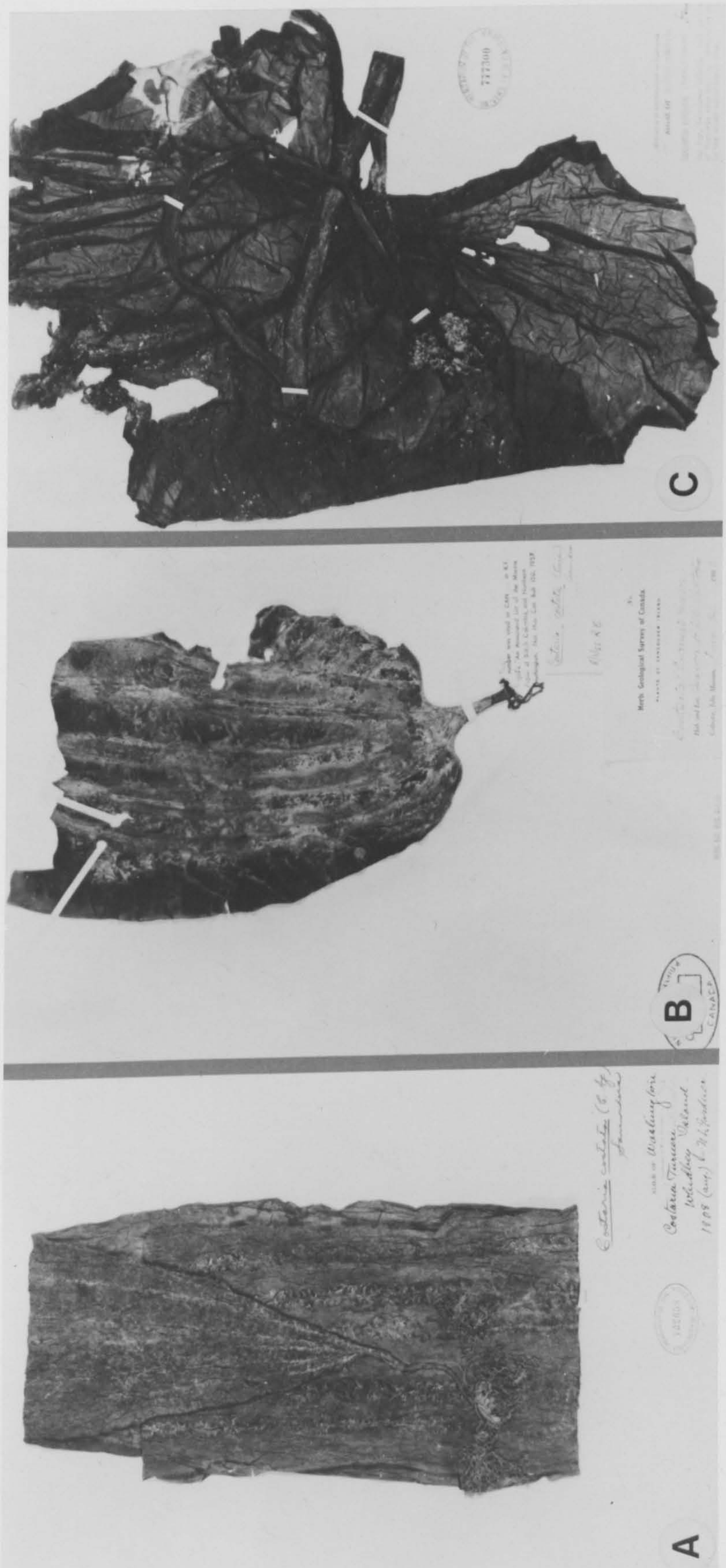

A
B
C

Fig. 26 *Costaria* cited as *C. mertensii* by Scagel (1957), showing variation in blade morphology.

A CAN 1638

B UBC 242

C UBC 243

Magnification x 1/4

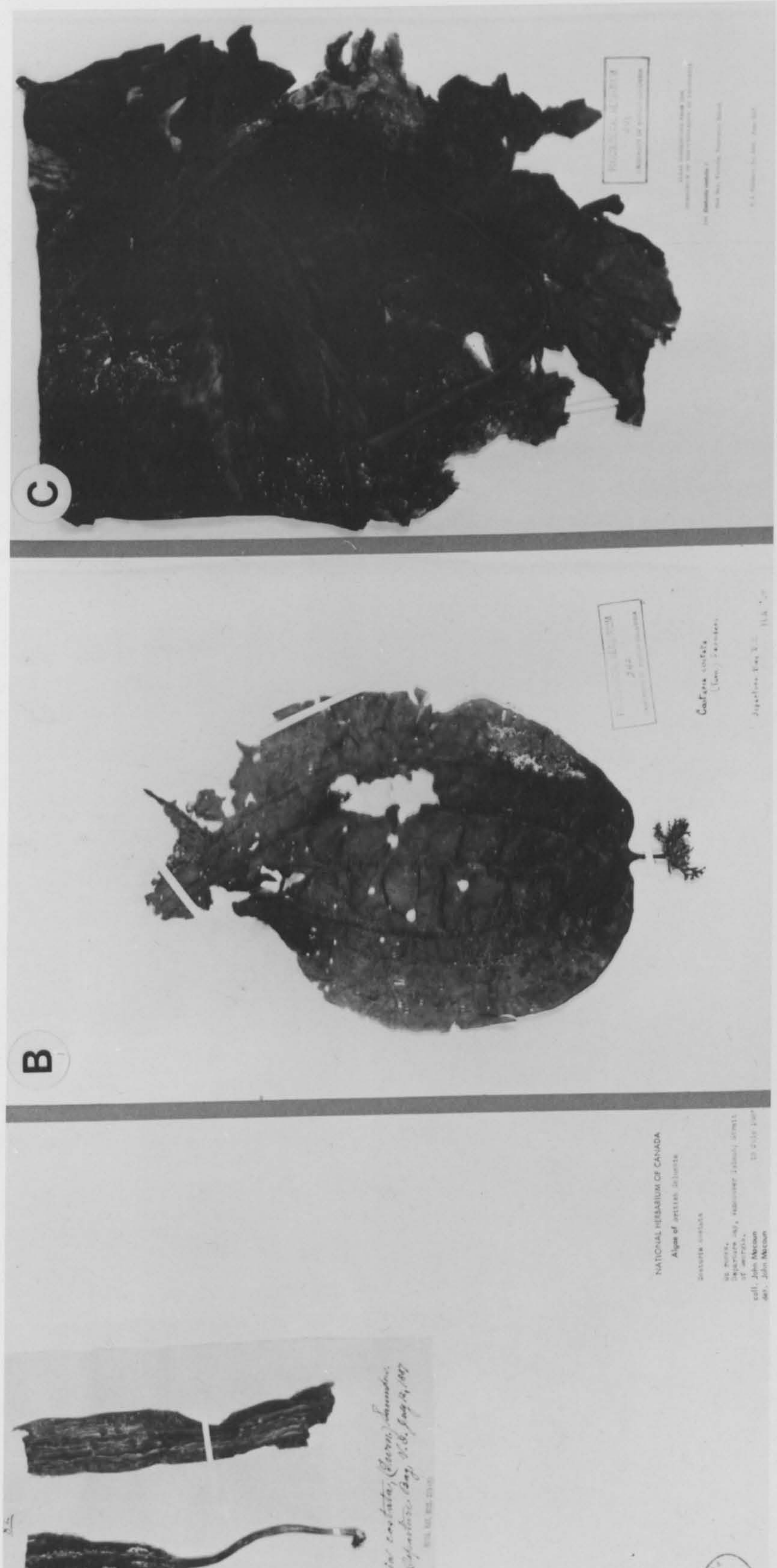

A
B
C

Fig. 27 *Costaria* from the Dudley Herbarium determined as *C. costata* and *C. mertensii* by Doty.

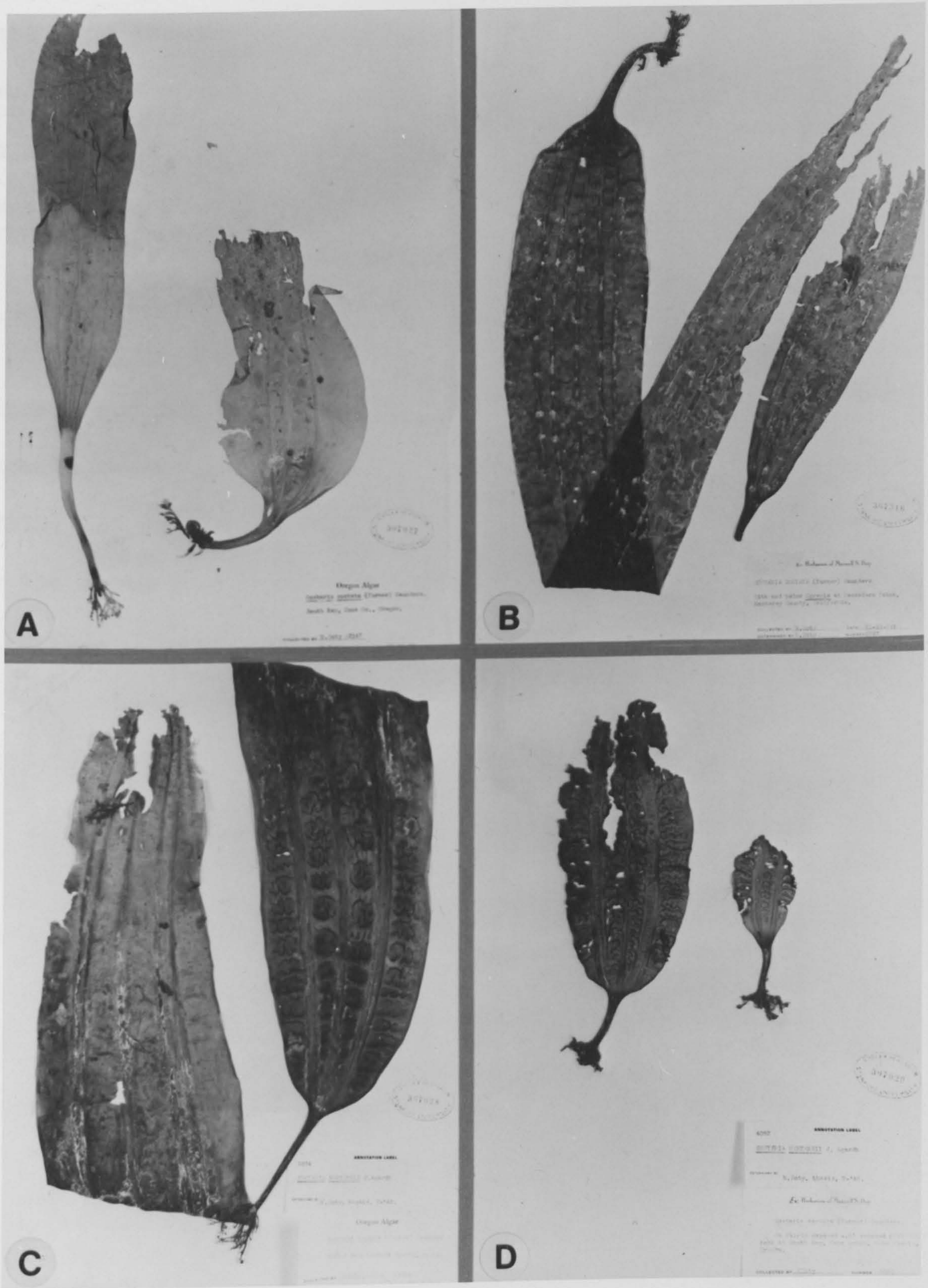
A *C. costata* (DUD 307027)

B *C. costata* (DUD 307316)

C *C. mertensii* (DUD 307028)

D *C. mertensii* (DUD 307029)

Magnification x 1/4


A
B
C
D

came from the outermost coasts. Costaria collected at San Juan I. and in southwest British Columbia were quite variable morphologically. The historically important specimens were also variable.

V. Study of Japanese specimens.

Costaria from Tsugaru Strait and Muroran, Hokkaido, were mature, and had linear blades with prominent ribs, perforations, cuneate bases, and coarsely ridged stipes (UC 200176, UBC 42819, UBC 45831-3). One specimen from Hokkaido was similar to the above plants, but had an auriculate blade base (UC 96714).

## DISCUSSION AND CONCLUSIONS

The results of observations and some experimental work on *Costaria*, particularly at the four study sites in southwest British Columbia, demonstrate two main morphological forms.

One morphological form, which will be called the Sooke/Point No Point form (=S/PNP form), has prominent ribs, small bullations, may have perforations, and has a tough blade which does not tear readily and a coarsely ridged stipe. This is typified by *Costaria* at Sooke, Point No Point and Cape Beale (Figs. 5-7). In addition the ribs are thick with about 30 cell layers in the cortex on the ridge side (Table II; Fig. 12). Sori are rarely found continuously over the blades of the S/PNP form and do not extend over the ridge side of ribs. The haptera are not very branched (Figs. 16). Blade shape varies from narrow linear to ovate and blade base shape usually varies from cuneate to cordate (Tables I, IV, V; Figs. 5-7).

Since Turner (1819), the S/PNP form has been the form of *Costaria* most frequently described, whether as one variable species (Mertens, 1829; Postels and Ruprecht, 1840; Kutzing, 1849; Harvey, 1852, 1862; Ruprecht, 1852; Areschoug, 1883; Setchell and Gardner, 1903; Tilden, 1935; Smith, 1944) or as two or more taxa (Agardh, 1848; Kjellman, 1893; Saunders, 1895;

De Toni, 1895). The descriptions have been of plants with prominent ribs, regular bullations and coarsely ridged stipes. Most authors have also said that perforations may be present. The morphological features used to distinguish species or different forms of Costaria have been the shape of the blade and blade base. However, the complete range of variation in shape can be seen in the S/PNP form (Tables I, IV, V; Figs. 5-7).

Specimens of Costaria collected in Oregon and California and determined by Doty (Table XXV; Fig. 27) fall within the range of the S/PNP form. Specimens of C. costata and C. mertensii from British Columbia and Northern Washington listed by Scagel (1957) were mostly of the S/PNP form (Table XXV; Figs. 25A, B, and 26A, B). Descriptions and illustrations of Costaria by Japanese authors (Okamura, 1892; 1928, Pl. 226; 1936, Pl. 143; Nagai, 1940; Tokida, 1954; Segawa, 1967, Pl. 23) are also of this form. Herbarium specimens from Tsugaru Strait (UC 200176) and Hokkaido (UC 96714, UBC 42819, UBC 45831-3) clearly fit the S/PNP form and are perforated.

The second morphological form is typified by Costaria at Indian Arm (Fig. 4). This form (=IA form) has flattened ribs, large bullations, no perforations, a crisp blade which tears readily and a finely ridged stipe. The ribs are thin with about 15 cell layers in the ridge side cortex (Table II; Fig. 12). Sori may be continuous over the surface of blades including the ridge side of ribs. The haptera are extensively branched (Fig. 16). Blade shape is usually ovate and blade base shape obtuse or cordate (Tables I, III; Fig. 4).

To date there has been no description or illustration of the IA form. Setchell and Gardner's (1925) broad description of variation in the genus did not include this form, although one of their illustrations (Pl. 79a) is closer to an IA form than to a S/PNP form.

The phenology of the S/PNP and IA forms was similar. Differences in the ontogeny of the two forms lay in the development of the same characters which distinguish the mature plants (Tables II-V). The time of development of the different characters was also distinctive: The IA form became relatively wider and developed an obtuse or cordate blade base earlier than did the S/PNP form, whereas bullations and ridges on the stipe developed earlier on the S/PNP form.

Each of the four populations of Costaria examined had some distinctive features of their own. The Indian Arm plants were quite distinct, as described above. Included in the

S/PNP form, *Costaria* at Sooke were usually large plants with relatively broad blades. At Point No Point, the plants were smaller with narrower blades, smaller bullations and a different pattern of sorus development. *Costaria* at Cape Beale were distinguished by their much perforated blades. These four populations form a series as regards blade shape, amount of bullation and presence of perforations as follows: Indian Arm ⟶ Sooke ⟶ Point No Point ⟶ Cape Beale (Tables I, III-V; Figs. 4-7).

Small collections of *Costaria* were made from other sites in southwest British Columbia and San Juan I., Washington. These were found to fit into this series (Table XXIV). *Costaria* at Second Narrows and Stanley Park were similar to plants at Indian Arm although plants with long stipes were fairly coarsely ridged. Some plants at Oak Bay, Victoria (Figs. 25C, 26C) resembled the IA form, but had longer, more coarsely ridged stipes and more prominent ribs, as had some specimens at San Juan I. Other *Costaria* from different localities on San Juan I. were of the S/PNP form. *Costaria* at Hammond Bay and Thormanby I. were similar to plants at Sooke but had short stipes with fine ridges. Plants at Port Renfrew, in the vicinity of Bamfield and at Amphitrite Point resembled *Costaria* at Point No Point or Cape Beale depending on whether the blades were perforated or not.

For convenience, in Table XXV, specimens were designated as similar to Costaria at Oak Bay, Victoria, if they had broad blades with large bullations and flattened ribs, and had a long coarsely ridged stipe (Figs. 25C, 26C). These plants are closer to the IA form than to the S/PNP form, and were only listed by Scagel for San Juan I. and Oak Bay. No Costaria having a long stipe was ever found without being at least fairly coarsely ridged.

The morphological series in southwest British Columbia has the appearance of a discontinuous cline with the IA form at one extreme. The S/PNP form has several rather indistinct subgroups, with Costaria at Cape Beale at the other extreme from the IA form. Experimentally, transplanting between different environments in the field has been used to determine the stability or plasticity of morphological characters in any one population (Sundene, 1962a, 1962b; Druehl, 1967b; Norton, 1969). In the present study, transplants of Costaria were made between Indian Arm, Sooke and Point No Point. The Sooke and Point No Point sites are more exposed to wave action than the Indian Arm site. The salinity is higher at the first two sites, and both surface temperature and salinity are fairly constant. At Indian Arm there is considerable fluctuation annually in surface temperature and salinity.

There were no major changes in Costaria transplanted between Indian Arm, Sooke and Point No Point, but there were a few trends. The angle of the blade base of Indian Arm plants at Sooke decreased, and some blades became slightly smoother than usual (Tables IX, X). The smoother blades may be explained as follows. Growth of the blades may have been better than was apparent insofar as distal erosion of the blade could have obscured an increase in length. Bullations would have increased proportionately in size; and since the blades were very torn, only a few bullations would be seen on the remaining pieces of blade.

Blade base shape of Indian Arm plants did not seem to change at Point No Point, but exact measurements were not made (Tables XI-XIII; Fig. 19). As at Sooke, some Indian Arm blades looked smoother than usual at Point No Point. The poor survival of Indian Arm plants at Sooke and Point No Point (Tables IX-XIII) and of the Point No Point controls themselves (Tables XIX, XX) was probably due to mechanical damage to the blades as they were beaten against the sides of the transplant bricks and sand was washed over them by the greater water movement. Norton (1969) found that Saccorhiza polyschides transplanted from a sheltered area to an area with strong current did not survive because they soon were severely torn.

Sooke plants at Indian Arm developed a greater blade base angle earlier than did Sooke controls (Tables XIV, XVII, XVIII). The sheltered environment of Indian Arm may have induced this, as the blades of some Laminariales tend to be broader in sheltered than in exposed areas (Sundene, 1962b, 1964; Norton, 1969). Sooke plants at Indian Arm became very unhealthy in May and June (Fig. 21).

Point No Point plants at Indian Arm grew better than did their controls initially, but like the Sooke plants their blades became brittle and translucent in May and June when the plants were dying (Tables XIX-XXI; Fig. 22B, C). Sundene (1962b) found that Alaria esculenta transplanted to a fjord where it did not normally occur, grew well during the winter and early spring but degenerated and disappeared during the summer and early autumn. He attributed this to the low salinity and particularly the high summer temperatures in the fjord. Sundene (1964) and Druehl (1967b) obtained similar results with transplanted Laminaria digitata and L. groenlandica respectively.

Apart from exposure, temperature and salinity were the only factors considered that differed between the sites. The deterioration of the Sooke and Point No Point Costaria at Indian Arm may have been caused by high summer temperatures and low salinities. There is no experimental evidence for this, and the deterioration may have been caused in part or wholly by other factors, such as nutrients, pollution or disease.

Point No Point Costaria transplanted to Sooke grew better than did the controls and remained healthy (Tables XXII, XXIII; Fig. 23). Some plants produced sori. Sooke is less exposed than Point No Point, which may account for the better survival and growth of these transplants.

Variation in blade morphology has usually been associated with differences in exposure to waves, and so transplanting techniques have been carried out to investigate this (Sundene, 1962a, 1962b, 1964; Norton, 1969). However, in Costaria blade and blade base shape are partly related to the stage of development (Tables III-V; Fig. 17). Small Indian Arm plants had cuneate bases which soon became obtuse and eventually cordate before reaching maturity (Table III), whereas S/PNP forms remained cuneate longer and the mature plants were obtuse or cordate (Tables IV, V). Agardh (1848) was the first to realize that the shape of Costaria changes with age. Parke (1948) and Burrows (1964) found that the shape of the blade base of two Laminaria species was a function of growth rate. Fallis (1916) measured growth rates in Costaria but did not relate tham to change in blade shape.

Other authors explained the variable shape of the blade base in terms of the stage of development of Costaria and/or the effect of the environment, particularly exposure to waves (Setchell, 1893; Setchell and Gardner, 1925; Okamura, 1928, 1936; Kanda, 1936; Nagai, 1940; Tokida, 1954). Mature Costaria at Cape Beale and Point No Point tend to have streamlined linear blades with cuneate or obtuse bases (Table I; Figs. 6,7). The plants are usually not very large. If they are large, the blades are much longer than broad, and the plants tend to grow subtidally. These plants are well adapted for much tossing about in exposed areas. At Sooke and Indian Arm, the blades tend to be more ovate, broader and larger (Table I; Figs. 4,5).

Nearly all the herbarium specimens of mature Costaria examined from the northeast Pacific were of the S/PNP form, and were collected from moderately exposed and exposed areas. No pattern emerged when groups of Costaria were plotted according to blade base shape (Fig. 24). However, more perforated plants were found on the outermost coasts. The IA form may have appeared rare because few of the collections were made in mainland inlets. Costaria was found to grow subtidally up Indian Arm whereas it grew in the low intertidal as well as subtidally in open coastal areas (Druehl, 1967a).

Variation in characters other than blade shape have also been related to exposure. Widdowson (1965b) studied morphological variation in Hedophyllum sessile. In this species the presence of bullations and degree of splitting of the blade vary with the stage of development as well as with exposure to waves and sunlight. The size of bullations in Costaria seems to decrease with increasing exposure from Indian Arm to Point No Point (Fig. 8). Small bullations may strengthen the blade, allow water to pass more easily over the blade, and increase the surface area for photosynthesis. The tough blades of Cape Beale Costaria were nearly smooth between the ribs and had bullations outside the outermost ribs (Figs. 7, 8D). The bullations on either side of the middle rib may have become perforated, making that part smoother. Costaria blades may offer less resistance to water movement if they are perforated.

Norton (1969) found that the blades of Saccorhiza polyschides growing in sheltered places tore under their own weight when removed from the water, whereas _S. polyschides_ in more exposed sites had tough blades. Similarly IA form _Costaria_ tore readily when handled, but the S/PNP form was tough. Norton and Burrows (1969) also found that tough, thick _S. polyschides_ had a larger number of cortical cells than did plants in a sheltered area. The thickness of _Costaria_ blades between the ribs did not vary much at the different sites (Table II; Fig. 10). However, the ribs of the S/PNP form were nearly twice as thick as the ribs of the IA form, and most of the extra thickness came from the increased number of cell layers in the ridge side cortex (Table II; Fig. 12). These thicker ribs probably give added strength to the blade, as they run the length of the blade and are not easily torn across. The thicker ribs would also explain why _Costaria_ blades become more eroded longitudinally with increasing exposure to waves, rather than eroded at right angles to the longitudinal axis, as tended to occur at Indian Arm.

Sorus appearance and distribution on the blade may be explained as follows. At Indian Arm and Sooke, blades are less torn than at Point No Point or Cape Beale and sori are first visible on the upper and older portions of the blades; they later cover more of the lower parts. Due to erosion of the blade ends in plants from Point No Point and Cape Beale, sori seem to develop chiefly on the lower half of blades. Sori are distributed almost continuously on the comparatively smooth blade surfaces of the IA form. However, the S/PNP form shows a discontinuous distribution of sori. The more sheltered micro-environment of the hollows of the bullations may favour sorus development.

It is difficult to relate stipe length of Costaria to exposure, but a longer stipe may allow a plant freer movement in an exposed area. Druehl (1967b) found the short stipe form of Laminaria groenlandica to occur in quiet waters and the long stipe form in more exposed areas. The IA form Costaria had finely ridged, more slender stipes than the S/PNP form which were coarsely ridged (Table I; Figs. 14,15). Like the thicker ribs on the blades, coarse ridges may similarly add to the strength of the stipe. The added strength would be particularly advantageous where the stipe becomes flattened at the junction of the stipe and blade. Ridges also increase surface area, possibly for photosynthesis. On the whole, short stipes tended to be less ridged than long stipes even in exposed areas and long stipes were always fairly coarsely ridged or coarsely ridged even in less exposed areas.

Indian Arm form Costaria had numerous, profusely branched haptera loosely attached to the substrate. The S/PNP form had fewer, less branched haptera which attached tightly to the substrate. The many haptera of the IA form seemed to bind the mud without adhering to a solid substrate. The tightly attached haptera may be correlated with greater water movement, as loosely attached plants in an exposed area would get washed away.

Changes in morphology have usually been associated with water movement (Knight and Parke, 1950; Burrows and Lodge, 1951; Kain, 1962; Sundene, 1962a, 1962b, 1964; Druehl, 1967b; Norton, 1969). However, Burrows (1964) has related variation in texture, mucilage ducts and anatomy of laminarialean blades to differences in temperature. The effect of salinity on morphological characters of kelp sporophytes has not been studied, although Sundene (1962b, 1964) attributed the deterioration of transplanted Alaria and Laminaria partly to low fjord salinities.

An interesting small collection of Costaria was made in June, 1971, at Bamfield at about 12 m below the extreme low tide level. Here Costaria was growing with Laminaria saccharina and Zostera marina which are usually found in more sheltered places (Druehl, pers. comm.). The blades of the Costaria were more delicate than usual for that area with large bullations, flattened ribs and no perforations (UBC 45795-9). There were sori along the ribs on the upper part of some blades (UBC 45795-6). The stipes were coarsely ridged and the haptera quite branched. Except for the coarsely ridged stipes, the plants resembled the sheltered IA form <u>Costaria</u> (Fig. 28). However, the deep growing plants were most similar to <u>Costaria</u> from Second Narrows. Sundene (1962a) and Kain (1962) found that some other members of the Laminariales growing in deep water in more exposed areas tended to have the same form as plants growing in more sheltered places. Second Narrows is sheltered but has a strong current, and a plant with a long stipe would be better adapted for survival in a current than a plant with a short stipe. As noted earlier, long stipes are always ridged. The presence of a current where the collection was made at Bamfield would explain the long, coarsely ridged stipe.

Trends in the morphology of mature <u>Costaria</u> as related to a wave exposure gradient from sheltered to fully exposed may be summarized as follows:

| <u>Sheltered</u> | <u>Fully exposed</u> |
|---|---|
| Broad blade | Narrow blade |
| Large angle of blade base | Small angle of blade base |

Fig. 28 *Costaria* collected in June, 1971, about 12 m below extreme low tide level at Bamfield (UBC 45795).

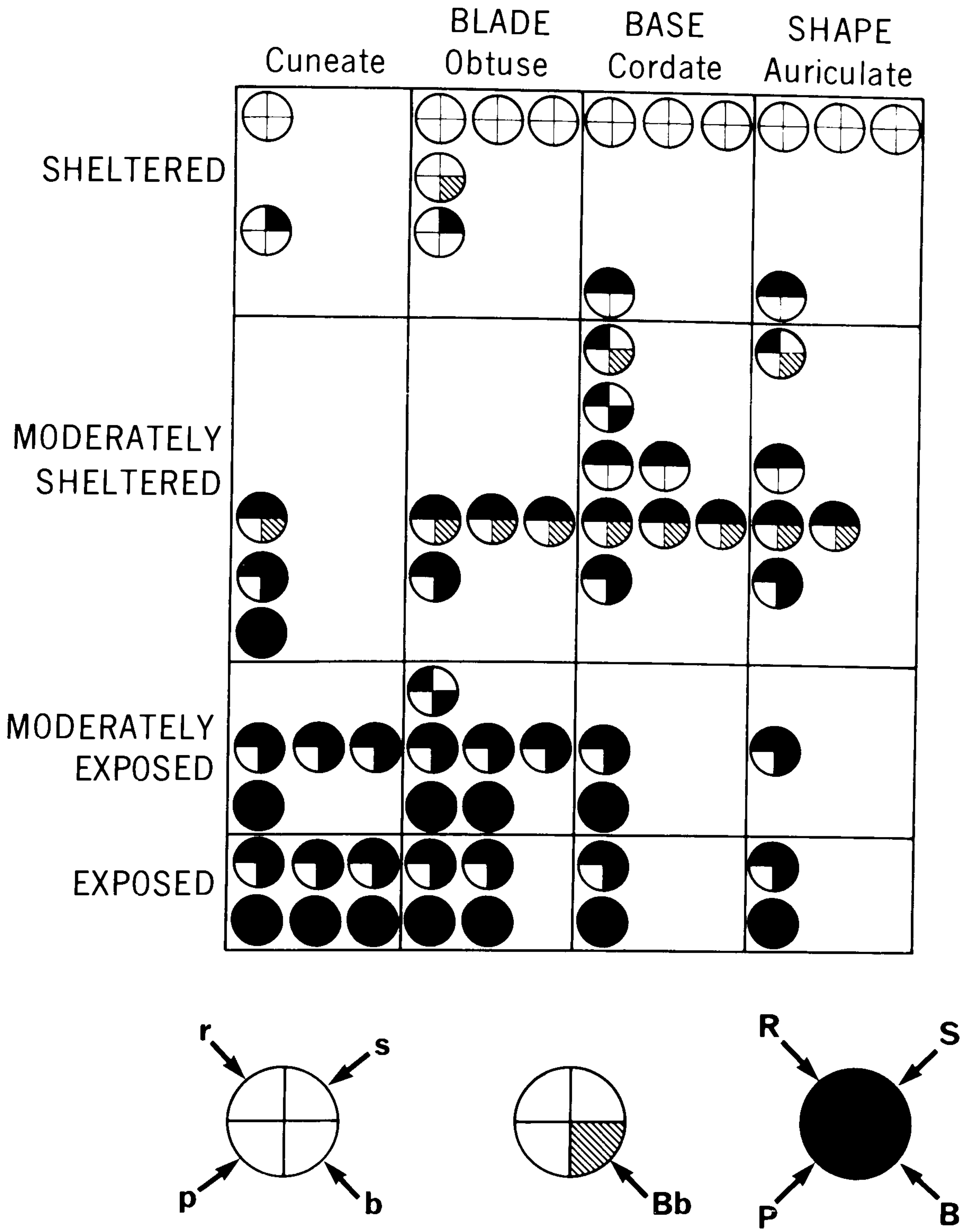
| | |
|---|---|
| Ribs flattened | Ribs prominent |
| Bullations large | Bullations small |
| Crisp blade, tears easily | Tough blade, does not tear easily |
| No perforations | Perforations |
| Stipe surface smooth or finely ridged | Stipe surface coarsely ridged |
| Haptera extensively branched | Haptera not extensively branched |

Taken individually, these are not good taxonomic characters because they regularly intergrade. Combinations of characters make the extreme forms of <u>Costaria</u> (e.g. from Indian Arm and Cape Beale) quite distinctive, but the intermediate forms (e.g. from San Juan I. and Oak Bay, Victoria) complicate the pattern. Because only four (geographically separated) populations were studied extensively, more intermediates may be found around the islands of the Strait of Georgia and along the British Columbia mainland and east coast of Vancouver I. The range of variation is summarized in Fig. 29 and the relative frequencies of each morphological variant is given for <u>Costaria</u> from the major collection sites.

The variation seen within any one population may partly be explained by the breeding system of <u>Costaria</u>; sexual reproduction would favour outbreeding. Meiospores are released

Fig. 29 Summary of the range of variation in prominence of ribs, ridges on the stipe surface, bullations and perforations in Costaria from areas of different wave exposures, arranged according to blade base shape. At the major collection sites (Indian Arm, Sooke, Point No Point and Cape Beale) the more frequent morphological variants are shown by duplicate and triplicate symbols. Some data come from the small collections in southwest British Columbia and from herbarium specimens from the northeast Pacific, wherever wave exposure data were available.

| | |
|---|---|
| r | Ribs not prominent |
| s | Stipe smooth or finely ridged |
| b | Bullations few and large |
| p | Perforations absent |
| Bb | Bullations variable |
| R | Ribs prominent |
| S | Stipe coarsely ridged |
| B | Bullations many and small |
| P | Perforations present |


BLADE BASE SHAPE
Cuneate
Obtuse
Cordate
Auriculate
SHELTERED
MODERATELY SHELTERED
MODERATELY EXPOSED
EXPOSED
r
s
p
b
Bb
R
S
P
B

over several months. They are motile and would be dispersed by water movements. Male gametes are also motile. In theory there is a potential for gene exchange between all populations of Costaria, but it is not known how far meiospores can be dispersed nor for how long they are viable.

Differences in Costaria plants may be accounted for by phenotypic plasticity or ecotypic variation. Phenotypic plasticity is indicated where morphological characters vary widely in response to variations in environment. Experimentally, transplants should distinguish between phenotypic plasticity and ecotypic variation. The Costaria transplants did not give definite results as to the plasticity of the various characters studied. However the sporophytes used in the transplant experiments already had blades up to 20 cm long and so had probably spent several weeks in their first environment. Thus, the reaction of the transplants to the second environment may have been conditioned physiologically and/or morphologically by their experience in the first. Hence the IA form could not survive mechanical damage from wave action in the upper subtidal of moderately exposed and exposed coasts while the S/PNP form could not survive the high summer temperatures and low salinities of a mainland inlet. To distinguish between phenotypic plasticity and ecotypic variation, ideally meiospores should be transplanted.

Natural selection of those meiospores, gametophytes or young sporophytes most suited to each environment could also contribute to observed variation in the cline; to find the effect of selection, survival and development of these stages would have to be followed individually.

On the southwest and west coasts of Vancouver I. ecotypic variation of Costaria would seem unlikely because distinctive habitats are not isolated, suggesting that phenotypic plasticity would be responsible for the variation. However, Indian Arm could be considered environmentally distinct, and the population there could either be ecotypically divergent or else strongly phenotypically plastic. At Bamfield the deep growing Costaria, which were similar to Costaria at Indian Arm and Second Narrows, were spatially close to an exposed area and geographically separated from sheltered Indian Arm and Burrard Inlet. The temperature and salinity ranges at Bamfield were also quite different from Indian Arm. In this case ecotypic divergence seems unlikely.

In conclusion, from my observations and transplanting experiments, it is not possible to say with certainty what causes variation in *Costaria*, but phenotypic plasticity seems most likely with wave exposure the major factor determining morphology.

Since variation in blade and blade base shape has been the feature most commonly used to distinguish between *Costaria costata*, *C. mertensii* and/or other taxa of *Costaria*, and since the *Costaria* described to date have been of the S/PNP form, the various names should be reduced to synonomy with *C. costata*. Turner's *Fucus costatus* (1819) is the type specimen for the genus *Costaria* and the species *C. costata* (Fig. 3). Although the IA form has not been described or illustrated previously, it fits the sheltered extreme of the wave exposure gradient in variation. Thus the S/PNP form could be called a 'wave exposed morphological form' and the IA form a 'sheltered morphological form'. Because of wide polymorphism in the different populations and between populations, the morphological forms should not be given taxonomic status.

# APPENDIX

In Tables I - XXV the following abbreviations are used:

| | |
|---|---|
| Mean | Mean measurement |
| S.D. | Standard deviation |
| CUN | Cuneate |
| OBT | Obtuse |
| COR | Cordate |
| AUR | Auriculate |
| No. of plants | Number of plants used to calculate means and standard deviations (Tables VI - XXIII). Higher number represents sample size; lower number represents fewer measurements made because parts of some plants in the sample were damaged. |

TABLE I

Blade, stipe and hapteron measurements used in the morphological comparison of mature <u>Costaria</u> collected from Indian Arm, Sooke and Point No Point in June 1970, and from Cape Beale in July 1970 (see Fig. 13 a-e).

| Number of plants examined | INDIAN ARM | | | SOOKE | | | POINT NO POINT | | | CAPE BEALE | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 19 | | | 30 | | | 7 | | | 6 | |
| | Range | Mean | St. Dev. | Range | Mean | St. Dev. | Range | Mean | St. Dev. | Range | Mean | St. Dev. |
| Blade length (cm) | 109-170 | 136 | 17.6 | 80-197 | 144 | 33.0 | 44-113 | 81 | 23.0 | 112-155 | 127 | 16.6 |
| Maximum blade width (cm) | 43- 73 | 55 | 9.6 | 31- 64 | 46 | 9.6 | 14- 24 | 18 | 3.6 | 8.0-11.5 | 9.6 | 1.4 |
| Blade base angle | 100-250 | 178 | 48 | 140-290 | 214 | 37 | 110-200 | 151 | 27 | 40- 90 | 68 | 17 |
| Width of middle rib 15 cm from blade base (cm) | 0.8-1.4 | 1.1 | 0.2 | 0.5-1.5 | 0.9 | 0.3 | 0.4-0.6 | 0.6 | 0.1 | 0.3-0.6 | 0.4 | 0.1 |
| Stipe length (cm) | 2.5-8.0 | 5.2 | 1.5 | 3.0-14.0 | 6.9 | 2.6 | 3.0-7.5 | 4.8 | 1.7 | 6.0-15.0 | 9.7 | 3.4 |
| Least diameter of stipe top (a) (mm) | 3.3-4.0 | 3.6 | 0.3 | 4.2-6.9 | 5.7 | 0.7 | 5.7-6.9 | 6.1 | 0.5 | 3.7-6.3 | 5.0 | 1.0 |
| Greatest diameter of stipe top (b) (cm) | 0.9-2.5 | 1.6 | 0.4 | 1.5-3.2 | 2.4 | 0.5 | 1.2-2.0 | 1.7 | 0.3 | 1.1-1.6 | 1.4 | 0.2 |
| Diameter of stipe middle (c) (cm) | 0.5-1.0 | 0.7 | 0.1 | 0.7-1.8 | 1.1 | 0.3 | 0.8-1.2 | 1.0 | 0.1 | 0.6-1.1 | 0.9 | 0.2 |
| Diameter of stipe bottom (d) (cm) | 0.4-0.7 | 0.6 | 0.1 | 0.6-1.0 | 0.8 | 0.1 | 0.7-0.8 | 0.8 | 0 | 0.6-0.9 | 0.8 | 0.1 |
| Number of main haptera | 13- 32 | 19 | 4 | 8- 19 | 13 | 3 | 9- 16 | 12 | 3 | 12- 17 | 14 | 2 |
| Diameter of thickest hapteron (e)(mm) | 1.8-3.8 | 2.9 | 0.6 | 3.0-4.3 | 3.4 | 0.4 | 2.8-4.1 | 3.5 | 0.5 | 2.7-3.8 | 3.2 | 0.4 |

TABLE II

Blade and rib measurements used in the anatomical comparison of mature *Costaria* collected from Indian Arm, Sooke and Point No Point in June 1970 and from Cape Beale in July 1970 (see Fig. 9 a-g). Measurements were made 15 cm from the blade base.

| | INDIAN ARM | | | SOOKE | | | POINT NO POINT | | | CAPE BEALE | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of plants examined | 6 | | | 9 | | | 6 | | | 6 | | |
| | Range | Mean | St. Dev. | Range | Mean | St. Dev. | Range | Mean | St. Dev. | Range | Mean | St. Dev. |
| Blade thickness (a) (μ) | 373- 698 | 525 | 114 | 435- 646 | 542 | 59 | 325- 694 | 547 | 130 | 389- 652 | 475 | 93 |
| Cortex thickness. Mean of b and $b_1$ (μ) | 136- 266 | 196 | 40 | 143- 246 | 207 | 27 | 88- 246 | 192 | 50 | 151- 322 | 210 | 58 |
| Cortex-number of cell layers. Mean of b and $b_1$ | 4- 6 | 5 | 1 | 4- 5 | 5 | 1 | 4- 6 | 5 | 1 | 4- 6 | 5 | 1 |
| Medulla thickness (c) (μ) | 57- 130 | 91 | 29 | 53- 143 | 87 | 29 | 57- 197 | 136 | 48 | 97- 171 | 129 | 29 |
| Rib thickness (d)(μ) | 849-1369 | 1179 | 185 | 1687-2103 | 1897 | 155 | 1717-2263 | 1977 | 206 | 1637-3196 | 2063 | 580 |
| Cortex thickness-ridge side (e) (μ) | 322- 739 | 619 | 169 | 1085-1394 | 1211 | 115 | 1051-1583 | 1285 | 196 | 955-1430 | 1215 | 171 |
| Cortex-number of cell layers-ridge side | 9- 21 | 15 | 5 | 24- 34 | 28 | 4 | 23- 35 | 29 | 4 | 24- 40 | 33 | 5 |
| Cortex thickness-fold side (f) (μ) | 249- 380 | 327 | 49 | 429- 553 | 495 | 63 | 406- 549 | 467 | 58 | 413- 605 | 517 | 78 |
| Cortex-number of cell layers-fold side | 5- 9 | 7 | 1 | 7- 12 | 9 | 2 | 6- 9 | 8 | 1 | 7- 10 | 9 | 1 |
| Rib medulla thickness (g) (μ) | 159- 222 | 192 | 26 | 114- 192 | 161 | 28 | 152- 227 | 196 | 28 | 149- 399 | 240 | 82 |

TABLE III

The ontogeny of Costaria at Indian Arm compiled from collections of plants in the natural population during 1968 and 1969. (Compare with Tables 4 and 5).

| | WITHOUT SORI | | | | | | | | | | WITH SORI | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Size classes based on blade length | Less than 5 cm | | 5-10 cm | | 10-20 cm | | 20-30 cm | | 30 + cm | | ---- | | ---- | | ---- | | ---- | |
| Classes based on when plants collected | ---- | | ---- | | ---- | | ---- | | ---- | | June | | July | | Aug. | | Sept. | |
| Months when plants most commonly found | Feb.-Apr. | | Feb.-Apr. | | Mar.-May | | Mar.-May | | Apr.-Jun. | | ---- | | ---- | | ---- | | ---- | |
| Number of plants examined | 56 | | 48 | | 40 | | 9 | | 13 | | 9 | | 6 | | 9 | | 6 | |
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 3.3 | 0.9 | 7.3 | 1.3 | 13.2 | 2.1 | 25.5 | 3.7 | 74.1 | 41.0 | 104.9 | 11.0 | 120.5 | 27.6 | 78.1 | 10.3 | 43.8 | 20.7 |
| Maximum blade width (cm) | 1.0 | 0.4 | 2.4 | 0.7 | 4.7 | 1.4 | 11.4 | 3.2 | 29.9 | 17.1 | 49.4 | 11.4 | 32.7 | 4.7 | 27.4 | 7.0 | 29.4 | 5.7 |
| Blade base angle | 90 | 19 | 116 | 19 | 134 | 18 | 151 | 23 | 143 | 35 | ---- | | 180 | 58 | 197 | 35 | 217 | 53 |
| Blade base shape (number of plants) | CUN<br>OBT | (45)<br>(11) | CUN<br>OBT | (15)<br>(33) | CUN<br>OBT<br>COR | (1)<br>(38)<br>(1) | OBT<br>COR | (8)<br>(1) | CUN<br>OBT<br>COR | (2)<br>(10)<br>(1) | CUN<br>OBT<br>COR | (3)<br>(4)<br>(2) | OBT<br>COR | (4)<br>(2) | OBT<br>COR<br>AUR | (3)<br>(5)<br>(1) | OBT<br>COR<br>AUR | (1)<br>(3)<br>(2) |
| Stipe length (cm) | 0.5 | 0.2 | 0.9 | 0.3 | 1.9 | 0.9 | 3.8 | 1.9 | 5.1 | 1.8 | ---- | | 6.4 | 2.2 | 7.1 | 1.7 | 5.5 | 1.5 |

TABLE IV

The ontogeny of <u>Costaria</u> at Sooke compiled from collections of plants in the natural population during 1968 and 1969. (Compare with Tables 3 and 5).

| | WITHOUT SORI | | | | | | | | | | WITH SORI | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Size classes based on blade length | Less than 5 cm | | 5-10 cm | | 10-20 cm | | 20-30 cm | | 30 – cm | | ---- | | ---- | | ---- | | ---- | | ---- | |
| Classes based on when plants collected | ---- | | ---- | | ---- | | ---- | | ---- | | June | | July | | Aug. | | Sept. | | Oct. | |
| Months when plants most commonly found | Feb.-Mar. | | Feb.-Mar. | | Feb.-Apr. | | Feb.-Apr. | | Apr.-Jun. | | ---- | | ---- | | ---- | | ---- | | ---- | |
| Number of plants examined | 26 | | 36 | | 56 | | 18 | | 47 | | 4 | | 25 | | 10 | | 5 | | 10 | |
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 3.5 | 0.9 | 7.1 | 1.3 | 13.4 | 3.2 | 23.9 | 2.9 | 76.5 | 54.0 | approx. 200 | -- | 146.7 | 38.8 | 136.4 | 28.6 | 108.8 | 14.7 | 32.2 | 11.3 |
| Maximum blade width (cm) | 1.1 | 0.4 | 2.4 | 0.6 | 3.7 | 0.8 | 5.8 | 1.3 | 15.0 | 10.5 | 32.8 | 7.0 | 31.2 | 9.3 | 32.7 | 8.7 | 35.0 | 5.8 | 20.8 | 4.9 |
| Blade base angle | 77 | 15 | 77 | 14 | 72 | 13 | 62 | 15 | 70 | 41 | 163 | 40 | 193 | 31 | 196 | 34 | 208 | 28 | 203 | 23 |
| Blade base shape (number of plants) | CUN | (26) | CUN | (36) | CUN | (56) | CUN | (18) | CUN<br>OBT<br>COR | (41)<br>(5)<br>(1) | OBT<br>COR | (3)<br>(1) | OBT<br>COR<br>AUR | (9)<br>(15)<br>(1) | OBT<br>COR<br>AUR | (2)<br>(6)<br>(1) | OBT<br>COR | (2)<br>(3) | OBT<br>COR | (2)<br>(8) |
| Stipe length (cm) | 0.4 | 0.2 | 0.7 | 0.4 | 2.3 | 1.8 | 3.0 | 1.3 | 5.4 | 3.6 | 9.2 | 2.7 | 10.9 | 4.4 | 15.2 | 5.6 | 11.9 | 2.9 | 13.9 | 3.8 |

TABLE V

The ontogeny of <u>Costaria</u> at Point No Point compiled from collections of plants in the natural population during 1968 and 1969. (Compare with Tables 3 and 4).

| | WITHOUT SORI | | | | | | | | | | WITH SORI | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Size classes based on blade length | Less than 5 cm | | 5-10 cm | | 10-20 cm | | 20-30 cm | | 30 + cm | | ---- | | ---- | | ---- | | ---- | |
| Classes based on when plants collected | ---- | | ---- | | ---- | | ---- | | ---- | | June | | July | | Aug. | | Sept. | |
| Months when plants most commonly found | Mar.-Apr. | | Mar.-Apr. | | Mar.-Jun. | | Apr.-Jun. | | Apr.-Jun. | | ---- | | ---- | | ---- | | ---- | |
| Number of plants examined | 11 | | 16 | | 18 | | 7 | | 23 | | 2 | | 4 | | 13 | | 10 | |
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 2.9 | 0.7 | 6.5 | 1.4 | 12.8 | 2.4 | 24.2 | 3.6 | 62.3 | 31.4 | 64.5 | (52-77) | 72.3 | 23.9 | 99.8 | 57.7 | 58.2 | 11.0 |
| Maximum blade width (cm) | 0.9 | 0.3 | 2.2 | 0.5 | 2.8 | 0.5 | 7.4 | 4.3 | 11.7 | 5.7 | 9.8 | (7.5-12) | 15.0 | 6.3 | 14.3 | 7.5 | 11.6 | 4.8 |
| Blade base angle | 66 | 12 | 69 | 13 | 57 | 10 | 81 | 47 | 71 | 32 | 120 | (90-150) | 123 | 26 | 106 | 45 | 126 | 42 |
| Blade base shape (number of plants) | CUN | (11) | CUN | (16) | CUN | (18) | CUN<br>OBT | (6)<br>(1) | CUN<br>OBT | (19)<br>(4) | CUN<br>OBT | (1)<br>(1) | CUN<br>OBT | (1)<br>(3) | CUN<br>OBT<br>COR | (7)<br>(5)<br>(1) | CUN<br>OBT<br>COR | (4)<br>(5)<br>(1) |
| Stipe length (cm) | 0.5 | 0.1 | 1.1 | 0.6 | 2.0 | 0.9 | 2.5 | 0.8 | 7.9 | 8.4 | 2.5 | (2-3) | 4.4 | 1.2 | 9.0 | 7.5 | 6.9 | 3.7 |

TABLE VI

Transplant studies: Indian Arm *Costaria* controls started on February 27, 1969, showing blade and stipe measurements for successive sampling dates.

| | Feb. 27 | | Mar. 27 | | Apr. 24 | | June 11 | | July 15 | | Aug. 13 | | Sept. 17 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 13.2 | 3.6 | 34.8 | 5.7 | 74.1 | 15.2 | 92.3 | 37.5 | 82.6 | 7.2 | 55.4 | 13.5 | 19.5 | --- |
| Maximum blade width (cm) | 6.4 | 1.8 | 20.7 | 6.2 | 38.4 | 11.9 | 47.8 | 15.1 | 43.7 | 9.8 | 37.0 | 6.2 | --- | --- |
| Blade base angle | --- | --- | 168 | 15 | 141 | 23 | 175 | 48 | 183 | 40 | 208 | 33 | 225 | --- |
| Blade base shape | CUN<br>OBT | | OBT | | CUN<br>OBT | | CUN<br>OBT<br>COR | | CUN<br>OBT<br>COR | | OBT<br>COR<br>AUR | | COR | |
| Stipe length (cm) | 1.3 | 0.5 | 2.7 | 0.7 | 4.3 | 0.5 | 4.5 | 1.0 | 4.8 | 1.4 | 4.5 | 1.8 | 5.0 | 1.7 |
| No. of plants | 9 | | 4-7 | | 7 | | 6 | | 6-7 | | 3-5 | | 2-4 | |

TABLE VII

Transplant studies: Indian Arm *Costaria* controls started on March 6, 1969, showing blade and stipe measurements for successive sampling dates.

| | Mar. 6 | | May 21 | | June 18 | | July 15 | | Aug. 13 | | Sept. 9 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 8.1 | 1.1 | 64.8 | 17.1 | 41.5 | --- | 68.6 | 36.9 | 54.0 | 16.5 | 33.0 | --- |
| Maximum blade width (cm) | 3.3 | 0.6 | 27.8 | 5.6 | 21.3 | --- | 38.7 | 27.8 | 22.3 | --- | --- | --- |
| Blade base angle | --- | --- | 145 | 13 | 115 | --- | 140 | 25 | 153 | 31 | 170 | --- |
| Blade base shape | CUN<br>OBT | | OBT | | OBT | | OBT | | OBT | | OBT<br>COR | |
| Stipe length (cm) | 0.5 | 0.2 | 5.4 | 0.8 | 5.2 | --- | 5.2 | 0.3 | 5.2 | 0.2 | 5.8 | --- |
| No. of plants | 8 | | 4 | | 2 | | 4-5 | | 2-3 | | 2 | |

TABLE VIII

Transplant studies: Indian Arm _Costaria_ controls started on March 20, 1969, showing blade and stipe measurements for successive sampling dates.

| | Mar. 20 | | Apr. 10 | | May 21 | | June 18 | | July 15 | | Aug. 13 | | Sept. 17 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 9.5 | 1.7 | 22.2 | 4.7 | 52.7 | 20.1 | 46.9 | 22.8 | 63.4 | 12.8 | 50.0 | --- | 23.0 | --- |
| Maximum blade width (cm) | 3.9 | 0.9 | 10.9 | 1.9 | 22.6 | 10.2 | 21.4 | 10.7 | 30.7 | 9.1 | --- | --- | --- | --- |
| Blade base angle | 109 | 14 | 133 | 8 | 126 | 13 | 126 | 20 | 150 | 35 | 185 | --- | 220 | --- |
| Blade base shape | CUN<br>OBT | | OBT | | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT | | OBT<br>COR | | COR | |
| Stipe length (cm) | 0.9 | 0.4 | 2.3 | 1.2 | 4.9 | 1.0 | 5.2 | 1.2 | 6.1 | 2.1 | 5.0 | --- | 6.0 | --- |
| No. of plants | 21-26 | | 6-26 | | 19-20 | | 11-15 | | 4-6 | | 2 | | 1 | |

TABLE IX

Transplant studies: Indian Arm *Costaria* transplanted to Sooke on February 22, 1969, showing blade and stipe measurements for successive sampling dates.

| | Feb. 22 | | Mar. 9 | | Mar. 30 | | Apr. 13 | | Apr. 26 | | May 18 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 9.6 | 2.5 | 14.3 | 6.0 | 27.2 | 13.8 | 31.7 | 15.5 | 36.0 | --- | 18.5 | --- |
| Maximum blade width (cm) | 4.4 | 0.9 | 7.5 | 1.9 | 11.1 | 3.7 | 11.7 | 4.2 | --- | --- | 7.5 | --- |
| Blade base angle | --- | --- | 118 | 20 | 104 | 21 | 100 | 27 | 85 | --- | --- | --- |
| Blade base shape | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT | | ---<br>--- | |
| Stipe length (cm) | 0.6 | 0.2 | 1.3 | 0.5 | 2.7 | 0.9 | 3.5 | 0.9 | 5.1 | --- | 4.0 | --- |
| No. of plants | 8 | | 7-8 | | 8 | | 3-6 | | 2 | | 1 | |

TABLE X

Transplant studies: Indian Arm Costaria transplanted to Sooke on March 30, 1969, showing blade and stipe measurements for successive sampling dates.

| | Mar. 30 | | Apr. 13 | | Apr. 26 | |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 11.0 | 2.9 | 7.6 | 2.4 | 7.0 | 2.1 |
| Maximum blade width (cm) | 5.2 | 1.9 | 4.4 | 1.0 | 3.1 | 1.2 |
| Blade base angle | 123 | 27 | 80 | 14 | 87 | 25 |
| Blade base shape | CUN OBT | | CUN | | CUN OBT | |
| Stipe length (cm) | 1.2 | 0.3 | 1.3 | 0.2 | 1.6 | 0.7 |
| No. of plants | 8 | | 4-8 | | 3-5 | |

TABLE XI

Transplant studies: Indian Arm Costaria transplanted to Point No Point on May 13, 1968, showing blade and stipe measurements for successive sampling dates.

| | May 13 | | June 13 | | July 9 | |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 7.9 | --- | 14.5 | --- | 18.8 | --- |
| Maximum blade width (cm) | 7.1 | --- | 6.5 | --- | 7.2 | --- |
| Blade base angle | --- | --- | --- | --- | --- | --- |
| Blade base shape | OBT | | OBT | | OBT | |
| Stipe length (cm) | 1.8 | --- | 3.5 | --- | 4.6 | --- |
| No. of plants | 1 | | 1 | | 1 | |

TABLE XII

Transplant studies: Indian Arm <u>Costaria</u> transplanted to Point No Point on June 13, 1968, showing blade and stipe measurements for successive sampling dates.

| | June 13 | | July 9 | |
|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 7.2 | --- | 8.5 | --- |
| Maximum blade width (cm) | 5.1 | --- | 3.5 | --- |
| Blade base angle | --- | --- | --- | --- |
| Blade base shape | OBT | | OBT | |
| Stipe length (cm) | 2.3 | --- | 2.4 | --- |
| No. of plants | 2 | | 2 | |

TABLE XIII

Transplant studies: Indian Arm <u>Costaria</u> transplanted to Point No Point on July 9, 1968, showing blade and stipe measurements for successive sampling dates.

| | July 9 | | Aug. 23 | | Sept. 28 | |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 9.2 | 6.0 | 14.9 | 11.8 | 7.9 | --- |
| Maximum blade width (cm) | 4.6 | 1.7 | 5.6 | 3.1 | 5.2 | --- |
| Blade base angle | --- | --- | --- | --- | --- | --- |
| Blade base shape | OBT | | OBT | | OBT | |
| Stipe length (cm) | 1.5 | 1.0 | 2.3 | 1.7 | 4.6 | |
| No. of plants | 5 | | 5 | | 1 | |

TABLE XIV

Transplant studies: Sooke *Costaria* controls started on February 22, 1969, showing blade and stipe measurements for successive sampling dates.

| | Feb. 22 | | Mar. 9 | | Mar. 30 | | Apr. 13 | | Apr. 26 | | May 18 | | June 15 | | July 12 | | Aug. 2 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 11.7 | 3.2 | 27.0 | 8.9 | 70.1 | 19.2 | 61.0 | 41.8 | 50.9 | 33.4 | 100.5 | 69.3 | 91.7 | 68.2 | 80.3 | 69.9 | 73.0 | --- |
| Maximum blade width (cm) | 4.0 | 0.8 | 7.0 | 1.8 | 18.1 | 4.0 | 13.0 | 7.5 | 17.4 | 10.1 | 33.7 | 18.8 | 38.0 | 22.1 | 38.5 | 22.C | 34.8 | --- |
| Blade base angle | --- | --- | 65 | 12 | 70 | 18 | 70 | 8 | 82 | 33 | 167 | 70 | 190 | 72 | 223 | 25 | 210 | --- |
| Blade base shape | CUN | | CUN | | CUN | | CUN | | CUN OBT | | OBT COR | | OBT COR | | COR AUR | | COR | |
| Stipe length (cm) | 0.8 | 0.3 | 1.8 | 0.5 | 3.1 | 0.5 | 3.8 | 1.2 | 3.6 | 0.8 | 4.3 | 1.2 | 4.7 | 1.4 | 4.3 | 0.8 | 4.0 | |
| No. of plants | 8 | | 6-8 | | 4-5 | | 4-6 | | 4-5 | | 3 | | 3 | | 3 | | 2 | |

TABLE XV

Transplant studies: Sooke *Costaria* controls started on March 30, 1969, showing blade and stipe measurements for successive sampling dates.

| | Mar. 30 | | Apr. 26 | | May 18 | |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 11.1 | 4.7 | 18.8 | 10.8 | 32.8 | 20.9 |
| Maximum blade width (cm) | 3.7 | 1.1 | 4.8 | 1.7 | 5.9 | 2.9 |
| Blade base angle | 54 | 6 | 50 | 16 | 53 | 15 |
| Blade base shape | CUN | | CUN | | CUN | |
| Stipe length (cm) | 1.1 | 0.6 | 2.9 | 1.1 | 4.5 | 1.3 |
| No. of plants | 5 | | 4-5 | | 4 | |

TABLE XVI

Transplant studies: Sooke *Costaria* controls started on April 26, 1969, showing blade and stipe measurements for successive sampling dates.

| | Apr. 26 | | May 18 | | June 15 | | July 12 | | Aug. 2 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 14.1 | 4.7 | 32.7 | 13.9 | 24.3 | 15.1 | 23.4 | 10.9 | 19.3 | 6.4 |
| Maximum blade width (cm) | 3.9 | 1.3 | 6.0 | 2.3 | 5.4 | 3.8 | 7.3 | 6.4 | 6.7 | --- |
| Blade base angle | 55 | 8 | 53 | 14 | 67 | 15 | 78 | 34 | 77 | 23 |
| Blade base shape | CUN | | CUN | | CUN OBT | | CUN OBT | | CUN OBT | |
| Stipe length (cm) | 4.9 | 2.9 | 6.8 | 3.5 | 7.4 | 4.5 | 6.9 | 2.7 | 7.9 | 3.3 |
| No. of plants | 12 | | 12 | | 9 | | 5 | | 2-3 | |

TABLE XVII

Transplant studies: Sooke _Costaria_ transplanted to Indian Arm on February 20, 1969 showing blade and stipe measurements for successive sampling dates.

| | Feb. 20 | | Mar. 13 | | Mar. 27 | | Apr. 24 | | June 11 | | July 15 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 14.9 | 4.5 | 36.7 | 17.6 | 64.4 | 4.4 | 83.0 | 21.4 | 55.0 | 22.6 | 32.5 | --- |
| Maximum blade width (cm) | 4.5 | 1.3 | 9.0 | 3.4 | 19.0 | 3.3 | 23.1 | 5.1 | 24.8 | 11.5 | --- | --- |
| Blade base angle | --- | --- | 95 | --- | 100 | 20 | 110 | 14 | 150 | 50 | 165 | --- |
| Blade base shape | CUN | | CUN | | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT<br>COR | | OBT<br>COR | |
| Stipe length (cm) | 1.2 | 0.4 | 1.7 | 1.0 | 3.2 | 0.6 | 4.3 | 1.3 | 4.8 | 1.3 | 6.0 | --- |
| No. of plants | 7 | | 2-3 | | 4 | | 7 | | 3 | | 2 | |

TABLE XVIII

Transplant studies: Sooke *Costaria* transplanted to Indian Arm on February 27, 1969, showing blade and stipe measurements for successive sampling dates.

| | Feb. 27 | | Mar. 13 | | Mar. 27 | | Apr. 3 | | Apr. 10 | | May 21 | | July 15 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean. | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 10.6 | 3.9 | 14.1 | 3.1 | 42.2 | 12.2 | 24.5 | 8.7 | 41.8 | 1.8 | 44.8 | 8.7 | 28.0 | --- |
| Maximum blade width (cm) | 3.7 | 1.3 | 4.2 | 0.6 | 11.6 | 3.1 | 7.7 | 1.8 | 11.7 | 1.6 | 16.6 | 4.3 | --- | --- |
| Blade base angle | --- | --- | 84 | 8 | 94 | 17 | 102 | 15 | 103 | 12 | 114 | 22 | 195 | --- |
| Blade base shape | CUN | | CUN | | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT | | CUN<br>OBT | | OBT<br>COR | |
| Stipe length (cm) | 0.9 | 0.6 | 0.9 | 0.2 | 2.8 | 1.8 | 1.9 | 0.5 | 2.3 | 0.3 | 4.0 | 0.8 | 4.5 | --- |
| No. of plants | 16 | | 7 | | 9 | | 4 | | 3 | | 5 | | 2 | |

TABLE XIX

Transplant studies: Point No Point *Costaria* controls started on March 29, 1969, showing blade and stipe measurements for successive sampling dates.

| | Mar. 29 | | Apr. 25 | | May 17 | |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 11.9 | 3.8 | 11.4 | 2.3 | 12.0 | --- |
| Maximum blade width (cm) | 2.8 | 0.6 | 2.8 | 0.7 | --- | --- |
| Blade base angle | 56 | 5 | 56 | 6 | 60 | --- |
| Blade base shape | CUN | | CUN | | CUN | |
| Stipe length (cm) | 1.3 | 0.5 | 2.2 | 0.9 | 1.7 | --- |
| No. of plants | 8 | | 5-6 | | 1 | |

TABLE XX

Transplant studies: Point No Point *Costaria* controls started on April 25, 1969, showing blade and stipe measurements for successive sampling dates.

| | Apr. 25 | | May 17 | | June 14 | | July 13 | | Aug. 3 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 13.6 | 3.7 | 17.7 | 7.8 | 30.2 | 11.1 | 21.4 | 12.4 | 25.5 | --- |
| Maximum blade width (cm) | 3.6 | 0.4 | 3.4 | 1.0 | 4.5 | 1.4 | 4.5 | 1.0 | 3.5 | --- |
| Blade base angle | 60 | 17 | 64 | 9 | 57 | 18 | 48 | 12 | 40 | --- |
| Blade base shape | CUN | | CUN | | CUN | | CUN | | CUN | |
| Stipe length (cm) | 1.9 | 0.7 | 2.5 | 1.1 | 5.4 | 1.9 | 6.3 | 2.6 | 8.5 | --- |
| No. of plants | 11 | | 8-11 | | 8-9 | | 5-6 | | 1 | |

TABLE XXI

Transplant studies: Point No Point *Costaria* transplanted to Indian Arm on April 3, 1969, showing blade and stipe measurements for successive sampling dates.

| | Apr. 3 | | Apr. 24 | | June 11 | |
|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 11.0 | 4.1 | 18.4 | 6.5 | 17.0 | --- |
| Maximum blade width (cm) | 3.0 | 1.0 | 3.8 | 0.8 | 6.9 | --- |
| Blade base angle | 54 | 9 | 65 | 11 | 85 | --- |
| Blade base shape | CUN | | CUN | | CUN | |
| Stipe length (cm) | 1.5 | 0.6 | 2.0 | 0.7 | 3.0 | 0.7 |
| No. of plants | 14 | | 14 | | 2 | |

TABLE XXII

Transplant studies: Point No Point *Costaria* transplanted to Sooke on March 30, 1969, showing blade and stipe measurements for successive sampling dates.

| | Mar. 30 | | Apr. 3 | | Apr. 26 | | May 18 | | June 15 | | July 12 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 10.5 | 4.6 | 17.6 | 6.4 | 20.7 | 13.4 | 28.3 | 24.0 | 44.0 | --- | 42.0 | --- |
| Maximum blade width (cm) | 3.0 | 0.6 | 3.4 | 0.8 | 3.2 | 1.3 | 3.1 | 2.5 | 6.1 | --- | 6.5 | --- |
| Blade base angle | 57 | 13 | 56 | 11 | 35 | 6 | 30 | --- | 30 | --- | 40 | --- |
| Blade base shape | CUN | | CUN | | CUN | | CUN | | CUN | | CUN | |
| Stipe length (cm) | 1.4 | 0.7 | 2.1 | 0.9 | 2.7 | 1.5 | 3.4 | 1.9 | 5.5 | --- | 5.5 | --- |
| No. of plants | 9 | | 8-9 | | 4 | | 2-3 | | 1 | | 1 | |

TABLE XXIII

Transplant studies: Point No Point *Costaria* transplanted to Sooke on May 18, 1969, showing blade and stipe measurements for successive sampling dates.

| | May 18 | | June 15 | | July 12 | | Aug. 2 | | Sept. 6 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. | Mean | S.D. |
| Blade length (cm) | 13.9 | 4.7 | 16.4 | 7.8 | 19.6 | 7.0 | 26.8 | --- | 30.0 | --- |
| Maximum blade width (cm) | 3.3 | 0.6 | 3.1 | 0.7 | 4.6 | 2.4 | 6.7 | --- | 7.2 | --- |
| Blade base angle | 55 | 6 | 50 | 8 | 70 | 27 | 70 | --- | 110 | --- |
| Blade base shape | CUN | | CUN | | CUN | | CUN | | OBT | |
| Stipe length (cm) | 2.4 | 2.1 | 4.0 | 2.4 | 3.2 | 2.0 | 4.6 | --- | 3.0 | --- |
| No. of plants | 4 | | 4 | | 3 | | 2 | | 1 | |

TABLE XXIV

Some morphological features of Costaria collected at San Juan I., Washington, and in southwest British Columbia during 1968 and 1969, with wave exposure of the collection sites.

| PLACE COLLECTED | WAVE EXPOSURE | BLADE BASE SHAPE | STIPE SURFACE: COARSE RIDGE | STIPE SURFACE: SMOOTH OR FINE RIDGE | RIBS: PROM. | RIBS: NOT PROM. | BULLATIONS: MANY SMALL | BULLATIONS: FEW LARGE | PERFORATIONS: PRES. | PERFORATIONS: NOT PRES. | COMMENTS | ACCESSION NUMBERS OF EXAMPLES |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| SAN JUAN I. (48°30'N,125°05'W) Large, immature plants | Sheltered | COR-AUR | ✓ | | ✓ | | | ✓ | | ✓ | Long stipes | UBC 45687-9 |
| SECOND NARROWS (49°17'30"N,123°01'W) Large, immature plants | Sheltered | CUN-OBT | ✓ | | | ✓ | | ✓ | | ✓ | Long stipes fairly coarsely ridged | UBC 45674-7 |
| STANLEY PARK (49°18'N,123°07'30"W) Mature plants | Sheltered | CUN-OBT | ✓ | | | ✓ | | ✓ | | ✓ | Stipes fairly coarsely ridged | UBC 45680-1<br>UBC 45684-5 |
| THORMANBY I. (49°29'N,123°59'W) Mature plants | Moderately Sheltered | CCR-AUR | | ✓ | ✓ | | ✓ | ✓ | | ✓ | Short stipes, variable sized bullations | UBC 45696-8 |
| HAMMOND BAY (49°14'N,123°57'W) Mature plants | Moderately Sheltered | COR-AUR | ✓ | | ✓ | | | ✓ | | ✓ | Short stipes, fairly coarsely ridged | UBC 45691 |

TABLE XXIV
(continued)

| PLACE COLLECTED | EXPOSURE | BLADE BASE SHAPE | STIPE SURFACE: COARSE RIDGE | STIPE SURFACE: SMOOTH OR FINE RIDGE | RIBS: PROM. | RIBS: NOT PROM. | BULLATIONS: MANY SMALL | BULLATIONS: FEW LARGE | PERFORATIONS: PRES. | PERFORATIONS: NOT PRES. | COMMENTS | ACCESSION NUMBERS OF EXAMPLES |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PORT RENFREW ($48^\circ 32'$N, $124^\circ 27' 30''$W) Large, immature plants | Fully exposed | CUN-OBT | ✓ | | ✓ | | ✓ | | ✓ | ✓ | Some blades perforated | UBC 45702<br>UBC 45704-7 |
| VICINITY OF BAMFIELD ($48^\circ 50'$N, $125^\circ 09'$W) Mature plants | Moderately exposed | OBT-COR | ✓ | | ✓ | | ✓ | | ✓ | | | UBC 45709-11 |
| AMPHITRITE POINT ($48^\circ 55' 30''$N, $125^\circ 32' 30''$W) Mature plants | Fully exposed | OBT-AUR | ✓ | | ✓ | | ✓ | | ✓ | ✓ | Some blades perforated | UBC 45713-5 |

TABLE XXV

Some morphological features of Costaria cited as C. costata and C. mertensii by Scagel (1957), and specimens of Costaria from the Dudley Herbarium collected and determined by Doty.

| ACCESSION NUMBER | PLACE COLLECTED | DATE | SORI PRES: ✓ ABS.: X | BLADE BASE SHAPE | STIPE SURFACE COARSE RIDGE | STIPE SURFACE SMOOTH OR FINE RIDGE | RIBS PROM. | RIBS NOT PROM. | BULLATIONS MANY | BULLATIONS INTER-MEDIATE | BULLATIONS FEW | COMMENTS | SPECIMEN SIMILAR TO COSTARIA AT: |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C. COSTATA (Scagel, 1957) | | | | | | | | | | | | | |
| UC 132658 | Whidbey I. | Aug. 1908 | ✓ | CUN | --- | --- | ✓ | | ✓ | | | | Point No Point (Fig. 25A) |
| UC 395303 | Friday Hr., San Juan I. | July 1910 | ✓? | CUN | --- | --- | | ✓ | --- | --- | --- | Large specimen poorly preserved | --- |
| CAN 1639 | Beacon Hill, Victoria | June 1908 | ✓ | COR | ✓ | | ✓ | | ✓ | | | | Sooke or Point No Point |
| CAN 1642 | " | June 1909 | ✓ | COR | ✓ | | ✓ | | | ✓ | | | Sooke or Point No Point (Fig. 25B). |
| UC 277430 | Departure Bay | June 1908 | ✓ | OBT | ✓ | | ✓ | | --- | --- | --- | | Sooke or Point No Point |
| VIC 1251 | Comox | July 1915 | ✓ | CUN? | --- | --- | ✓ | | ✓ | | | Blade torn at base. Poorly preserved | --- |

TABLE XXV
(cont'd)

| ACCESSION NUMBER | PLACE COLLECTED | DATE | SORI PRES.: ✓ ABS.: X | BLADE BASE SHAPE | STIPE SURFACE COARSE RIDGE | STIPE SURFACE SMOOTH OR FINE RIDGE | RIBS PROM. | RIBS NOT PROM. | BULLATIONS MANY | BULLATIONS INTER-MEDIATE | BULLATIONS FEW | COMMENTS | SPECIMEN SIMILAR TO *COSTARIA* AT: |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UC 96720 (two specimens) | Whidbey I. | --- | X | CUN | --- | --- | ✓ | | ✓ | | | Young specimens | --- |
| UC 266488 | Near Roche Hr., San Juan I. | --- | X | --- | ✓ | | --- | --- | --- | --- | --- | Large specimen folded over on itself | Oak Bay, Victoria |
| UW 64615 | Canoe I. | July 1907 | X | CUN | ✓ | | ✓ | | --- | --- | --- | | Sooke or Point No Point |
| UW 70550 | False Bay, San Juan I. | 1928 | X | CUN | --- | --- | ✓ | | ✓ | | | | " |
| UC 974467 | Goose I. | July 1952 | X | CUN | | ✓? | ✓ | | ✓ | | | Young specimen | " |
| UC 763478 | Rocky Point opposite Tracyton | July 1897 | X | CUN | | ✓? | | ✓ | | | ✓ | " | Young Indian Arm |
| UC 395324 | Washington | --- | X | CUN | ✓ | | --- | --- | --- | --- | --- | Large specimen folded over on itself | --- |
| VIC 1250 | Beacon Hill, Victoria | July 1913 | X | CUN | --- | --- | ✓ | | ✓ | | | Poorly preserved | --- |

TABLE XXV
(cont'd)

| ACCESSION NUMBER | PLACE COLLECTED | DATE | SORI PRES: ✓ ABS.: X | BLADE BASE SHAPE | COARSE RIDGE | SMOOTH OR FINE RIDGE | RIBS PROM. | RIBS NOT PROM. | BULLATIONS MANY | BULLATIONS INTER-MEDIATE | BULLATIONS FEW | COMMENTS | SPECIMEN SIMILAR TO COSTARIA AT: |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| UC 402109 | Oak Bay, Victoria | June 1917 | X | COR | ✓ | | --- | --- | --- | --- | --- | Large specimen, poorly preserved | Oak Bay, Victoria |
| UC 777300 | " | " | X | COR/ AUR | ✓ | | --- | --- | --- | --- | --- | Large specimen, poorly preserved | " (Fig. 25C) |
| UC 96719 | Esquimalt | May 1901 | X | OBT/ COR | --- | --- | | ✓ | | ✓ | | Young specimen, poorly preserved | --- |
| CAN 1174 | Sidney | 1913 | X | COR | ✓? | | ✓ | | | ✓ | | Large specimen | --- |
| CAN 1640 | Departure Bay | June 1908 | X | OBT | ✓ | | ✓ | | | ✓ | | Large specimen | Sooke |
| *C. MERTENSII* (Scagel, 1957) | | | | | | | | | | | | | |
| UW 64510 | Oak Bay, Victoria | June 1917 | ✓? | COR/ AUR | ✓ | | --- | --- | | | ✓ | Large specimen folded over on itself | Oak Bay, Victoria |
| UW 137703 | " | " | ✓? | COR | ✓ | | | ✓ | | | ✓ | " | " |
| CAN 1638 | Departure Bay | July 1887 | ✓ | CUN | ✓ | | ✓ | | --- | --- | --- | | Point No Point (Fig. 26A) |
| UBC 239 | " | 1938 | ✓ | OBT | ✓ | | ✓ | | | | ✓ | | Sooke or Point No Point |

TABLE XXV
(cont'd)

| ACCESSION NUMBER | PLACE COLLECTED | DATE | SORI PRES.:✓ ABS.:X | BLADE BASE SHAPE | STIPE SURFACE COARSE RIDGE | STIPE SURFACE SMOOTH OR FINE RIDGE | RIBS PROM. | RIBS NOT PROM. | BULLATIONS MANY | BULLATIONS INTER-MEDIATE | BULLATIONS FEW | COMMENTS | SPECIMEN SIMILAR TO COSTARIA AT: |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| C. MERTENSII (Scagel, 1957) cont'd | | | | | | | | | | | | | |
| UBC 241 | Departure Bay | 1938 | ✓ | COR | --- | --- | ✓ | | | ✓ | | | Sooke or Point No Point |
| UBC 242 | " | " | ✓ | COR | --- | --- | ✓ | | | ✓ | | | " (Fig. 26B) |
| UW 63874 | San Juan I. | July 1915 | X | COR | --- | --- | ✓ | | | | ✓ | | Oak Bay, Victoria |
| UW 63875 | " | " | X | OBT | ✓ | | ✓ | | ✓ | | | | Sooke or Point No Point |
| UW 64499 | Friday Hr., San Juan I. | July 1904 | X | OBT | ✓ | | ✓ | | | ✓ | | | --- |
| UW 64614 (two speci-mens) | " | " | X | OBT | | ✓? | ✓ | | | | ✓ | Young specimens | --- |
| UBC 243 | Oak Bay, Victoria | June 1917 | X | COR | ✓ | | ✓ | | | | ✓ | Large specimen folded over on itself | Oak Bay, Victoria (Fig. 26C) |
| CAN 1666 | Comox | --- | X | CUN | | ✓? | | ✓ | | | ✓ | Young specimen | Young Indian Arm |

TABLE XXV
(cont'd)

| ACCESSION NUMBER | PLACE COLLECTED | DATE | SORI PRES.:✓ ABS.:X | BLADE BASE SHAPE | STIPE SURFACE COARSE RIDGE | STIPE SURFACE SMOOTH OR FINE RIDGE | RIBS PROM. | RIBS NOT PROM. | BULLATIONS MANY | BULLATIONS INTER-MEDIATE | BULLATIONS FEW | COMMENTS | SPECIMEN SIMILAR TO *COSTARIA* AT: |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *C. costata* collected and determined by Doty | | | | | | | | | | | | | |
| DUD 307027 (two specimens) | South Bay, Coos Co., Oregon | June 1939 | X | CUN OBT | ✓ | | ✓ | | | ✓ | | Old specimens | Sooke or Point No Point (Fig. 27A) |
| DUD 307316 (two specimens) | Pescadero Pt, Monterey Co., California | June 1945 | X | CUN OBT | ✓ | | ✓ | | ✓ | | | " | " (Fig. 27B) |
| *C. mertensii* collected and determined by Doty | | | | | | | | | | | | | |
| DUD 307028 | Boiler Bay, Lincoln Co., Oregon | July 1941 | ✓ | OBT | ✓ | | ✓ | | ✓ | | | Determined by Doty as *C. costata* and changed to *C. mertensii* for his thesis, May, 1945 | Sooke or Point No Point (Fig. 27C) |
| DUD 307029 (two specimens) | South Bay, Coos Co., Oregon | Jan. 1942 | X | CUN OBT | ✓ | | ✓ | | ✓ | | | " | " (Fig. 27D) |

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# CURRICULUM VITAE

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