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SYSTEMATICS OF POLYSTICHUM
in Western North America
North of Mexico
by
David Wagner

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**Systematics of Polystichum in Western North America
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David H. Wagner



**American Fern Society
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Systematics of *Polystichum* in Western North America North of Mexico

DAVID H. WAGNER*

Ferns of the genus *Polystichum* are well represented in the boreal and temperate flora of Pacific North America. One or more species are often conspicuous elements of the understory in mesic lowland forests, whereas other, usually rupicolous, species are found higher in the mountains. Although *Polystichum* is a genus easily recognized, distinguishing between species has often been difficult. This study began in 1972 as an attempt to develop a modern taxonomic treatment of the genus in western North America, north of Mexico. Dr. Warren Wagner had not yet published his ideas on reticulate relationships in *Polystichum*, but sent me the scheme which appeared in the American Fern Journal the next year (W. Wagner, 1973). Using his study, which was based on cytological investigations carried out over several years, as a starting point, I began gathering additional information from as many sources as possible. Effort was made to integrate lines of evidence using modern methods of biosystematic research along with standard herbarium procedures. Assuming it would be easier to describe boundaries between species after understanding their evolutionary relationships, these data were used to test W. Wagner's hypotheses and expand the scheme to include the probable relationships among all the species occurring in the region. After arriving at conclusions regarding the relationships among the species, I revised the classification of *Polystichum* in the region and reviewed the nomenclature appropriate to this classification.

This project was the basis for my Ph.D. dissertation in Botany at Washington State University, Pullman, Washington in 1976. Respectful acknowledgment is due the late Dr. Marion Francis Ownbey, the original senior advisor to this project. Dr. Warren H. Wagner, Jr., provided counsel and encouragement from the outset and assumed primary advisory responsibility following the death of Dr. Ownbey in December, 1974. Thanks are also due to many people without whose help and support this project would have been severely limited in scope. Many of those who have contributed study materials, stimulating discussions, manuscript criticisms, and exhausting footwork with me in the field have had to depend on personal expressions of gratitude as the list is too long to include here. Readers must appreciate that I did not work in solitude. Completion of this work would have been impossible without the patient indulgence of the curators of the following herbaria who have sent specimens on loan (abbreviations according to Holmgren & Keuken, 1974; asterisks indicate only limited material was requested, otherwise all regional material was annotated): ALA, CAN, CAS, CIC, COLO, DAO, DS, *F, GH, HSC, IDF, IDS, *K, LA, *LE, MICH, MO, MONTU, NO, NY, ORE, OSC, *PH, *PR, *PRC, POM, RM, RSA, SOC, UBC, UC, US, USFS, V, WTU, and YU.

*Herbarium, Department of Biology, University of Oregon, Eugene, OR 97403.

Financial assistance has been received from the Washington State University Graduate Student Travel Fund, University of Oregon Faculty Research Award, and a Grant-in-Aid of Research from Sigma Xi, The Scientific Research Society of North America. The scanning electron microscope pictures of spores are present thanks to the generous support of Dr. A. Cohen, Director of the WSU Electron Microscope Center, and the technical assistance of D. Bentley. This study was done at the Marion Ownbey Herbarium and associated taxonomy laboratory at Washington State University. A curatorial research assistantship during 1974-1976 provided me with the means to complete this project.

Grateful acknowledgment is given for permission to use a photograph of *Polystichum munitum* (Fig. 2) from the book *Muir Woods* by James Morley, Howell-North Books, Berkeley, California. The distribution maps were constructed from maps copyrighted by the University of Chicago, permission granted by Bob Smith, Manager of the Goode Base Maps. The photograph of *Polystichum imbricans* (Fig. 3) was taken by B. O. Mulligan of Seattle, Washington.

MATERIALS AND METHODS

Study material.—Most of the opinions expressed in this treatment are based on the examination of over 5,000 herbarium specimens borrowed from the institutions listed above. In addition to pressed herbarium specimens, living plants or offsets of living plants were collected and grown in Pullman. Some were placed in the botany greenhouse and others in a shady plot outside. Spore collections were made by pressing the terminal, sporulating portion of fronds in plain letter envelopes, these dried without heat. Material for chromatography was placed in brown paper bags and dried rapidly at ca. 38° C. Voucher specimens have been deposited in the Marion Ownbey Herbarium at Washington State University (WS).

Chemistry.—Preparation of two-dimensional chromatograms generally followed standard techniques (Mabry, Markham & Thomas, 1970; Harborne, 1967); 46 cm × 57 cm Whatman 3M chromatography paper was used throughout the study. Three types of extracts were used: crude methanol extracts, methanol extracts of powdered fronds which had been pre-washed with ethyl ether or petroleum ether, and purified extracts prepared by precipitation of phenolics with lead (II) acetate. In all chromatograms, the first (long) direction was run with 4:1:1 n-butanol-acetic acid-water and the second (short) direction with 15 per cent acetic acid.

Cytology.—Meiotic chromosomes were studied using standard squash techniques (Manton, 1950) with modifications suggested by Dr. Florence Wagner (pers. comm.). Whole pinnae were fixed in Newcomer's fixative (Newcomer, 1953) after a 24-hour pretreatment at 4°C in water saturated with paradichlorobenzene. Squashes were made using a 1:1 mixture of Hoyer's solution (Beeks, 1955) and aceto-carmin. Preparations containing good meiocytes were made permanent by ringing the coverslips with clear nailpolish after several days on a warming tray. Observations and photomicrographs were made using phase-contrast optics.

Trichome and sorus preparations.—Micropreparations using cellophane tape have been used extensively in this study, following the method described by Daigobo (1972). Trichomes were obtained by lightly pressing a strip of clear cellophane tape to the undersurface of sterile pinnae. Adhering trichomes are removed intact when the tape is lifted. A portion with the trichomes was mounted in piccolyte under a coverglass, sticky side with scales up. Several rachis scales were customarily included in the same mount. To the slides with the mount of trichomes, under a second coverglass, was added a mount of tape which had been pressed on the sori of the same specimen. This part of the preparation contained indusia, sporangia and spores. Spores in equatorial view were selected for measurement, to obtain the polar diameter of the exospore. Ten spores were measured in each sample. Ten sporangia were used to count the number of annulus cells.

Illustrations.—Macrophotography was done with a Minolta SR-T 303 camera equipped with a 50 mm MC Macro Rokkor lens. Drawings of leaf outlines and clearings, indusia and trichomes were made with the aid of a Bausch and Lomb microprojector. Spores were air-dried (untreated) for electron microscopy. They were affixed to sticky copper tape which, in turn, had been stuck to the SEM stubs with double sticky tape. The spores were coated twice, first with carbon and then with gold. The instrument used in this study was an ETEC Autoscan. Most photographs were taken at 10 kv. Light micrographs were made with a Leitz Orthomat automatic camera mounted on a Leitz Orthoplan microscope.

SEPARATION OF *POLYSTICHUM IMBRICANS* FROM *P. MUNITUM*

Background. — Several infraspecific taxa have been described for *Polystichum munitum*. One of these in particular, var. *imbricans*, has drawn comment. Some suggest that it might be a wholly distinct species from the typical variety (Maxon, 1900; Flett, 1903; W. Wagner, 1963; Kiefer in Munz, 1968; Cronquist in Hitchcock et al., 1969; Taylor, 1970); others dismiss it as an ecological form (Frye, 1934; Ewan, 1942; Howell, 1970). The evolutionary significance of this problem is best understood in light of the genetic relationships among the species of *Polystichum* proposed by W. Wagner (1973). He proposed that *P. munitum*, understood to include var. *imbricans*, had hybridized with two other species resulting in two allopolyploid species. If more than one species has been included under this name, then the parentage of the two polyploid species needs re-examination, and analysis of other relationships will likewise need to reflect this interpretation (*Fig. 1*).

In addition to var. *imbricans*, five other infraspecific taxa of *Polystichum munitum* have been described: var. *nudatum*, var. *incisoserratum*, subsp. *solitarium*, subsp. *curtum*, and forma *flabellatum*. The last is a teratological (forked) form of *P. munitum* var. *munitum*, of horticultural significance only, and will not be discussed further. *Polystichum munitum* subsp. *solitarium* was described from two collections from Guadalupe Island off Baja California. Although the locality is certainly notable, the specimens appear to fall within the normal range of variation found in *P. munitum* var. *munitum*. The fern has not been collected on

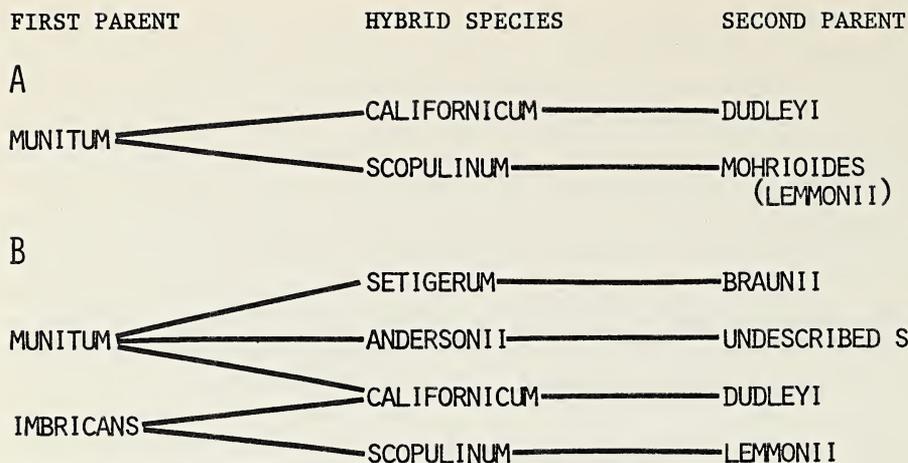


FIG. 1. Amphiploidy in *Polystichum* involving the Western Sword Ferns (*P. munitum*-*imbricans* complex). A. Relationships proposed by W. H. Wagner (1973). B. Relationships proposed in this work (see also Fig. 55).

Guadalupe Island since the type collection in 1896 (R. Moran, pers. comm.). *Polystichum munitum* var. *incisoserratum* is a morphological extreme that is roughly equivalent to *P. acrostichoides* f. *incisum*. I found a plant in Snohomish County, Washington (D. Wagner 468, WS), in which the fronds of the current season all matched the type of var. *incisoserratum* while all the fronds of the previous season had typical morphology. This example illustrates that the form has little taxonomic significance, possibly analogous to the late-maturation phenomenon demonstrated in *P. acrostichoides* f. *incisum* (W. Wagner et. al., 1970).

Two other segregates of *Polystichum munitum*, var. *nudatum* and subsp. *curtum*, are clearly allied with var. *imbricans*. If one adheres strictly to the original description (Eaton, 1878), var. *nudatum* is represented only by the type collection. It is a case in which an individual with unusual morphology has been given a name but subsequently found not to represent distinctive populations of taxonomic or biological significance. The form described by Ewan (1942) as subsp. *curtum* recognizes a more natural series of populations that represent a geographic and ecologic variant. Despite a close superficial resemblance to typical *P. munitum*, subsp. *curtum* shares with var. *imbricans* (and var. *nudatum*) a series of consistent characters that distinguishes them from typical *P. munitum*.

The above interpretation was initially formulated intuitively after becoming familiar with the ferns in the field and herbarium. I have now examined over 2,500 herbarium specimens identified as *Polystichum munitum* and have visited localities from California to Alaska. I have concluded that the ferns formerly included under *P. munitum* represent two distinct species, for the second of which I propose the name *P. imbricans*. (For complete synonymy and nomenclatural adjustments, see taxonomic treatment). Below is a detailed discussion of the characters distinguishing the two. Most of the data reported here were obtained

from a set of specimens selected from herbarium material to represent each species throughout its range. One fertile specimen was selected from each county in which the species has been found, seventy-five specimens of *P. munitum* and fifty-seven of *P. imbricans*.

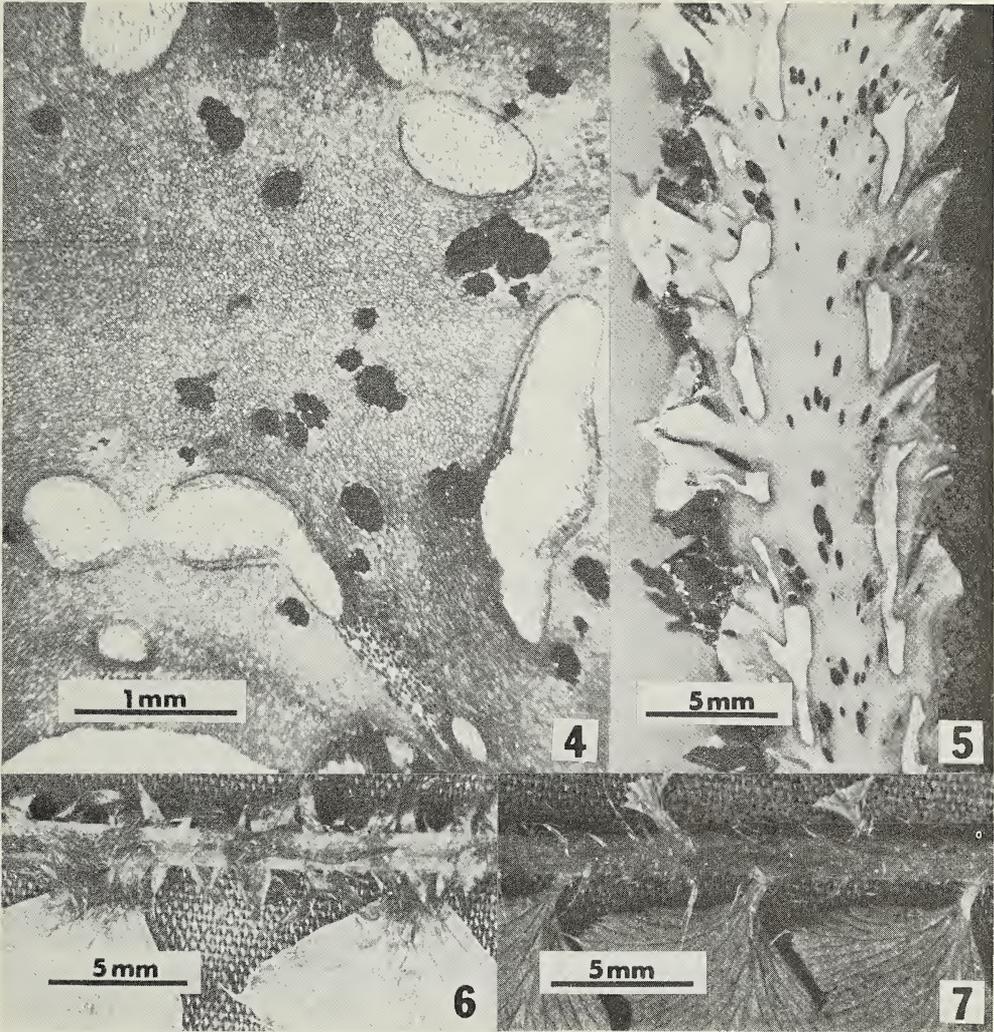
Blade.—*Polystichum imbricans* was originally distinguished from typical *P. munitum* on the basis of smaller size; crowded, lanceolate-oblong, pale, ascending, and imbricate pinnae; sori nearer the margin than the costa; and the stipe and blade nearly naked except for shiny brown scales at the base of the stipe (Eaton, 1878). The imbrication of the pinnae is the most obvious macroscopic character; it is the one which has been most widely used for identification, but which also has been a source of misinterpretation and confusion. *Polystichum imbricans* is typically found in relatively exposed sites in more xeric forest associations than *P. munitum*. Its fronds are usually stiffly erect from a decumbent rhizome, whereas fronds of *P. munitum* are normally arched-ascending on an erect rhizome early in the summer and drooping more and more as the season progresses (Figs. 2, 3). However, as Frye (1934) has observed, when the overstory is cleared and plants of *P. munitum* are subjected to increased insolation, the fronds become dwarfed and more erect, the pinnae crisped and more crowded, ultimately producing an imbricate Sword Fern. This phenomenon may also be seen when *P. munitum* becomes established away from its usual deep forest habitat, as in rocky outcrops at high elevations. When *P. imbricans* was transplanted from Tumwater Canyon, Chelan County, Washington to a shady, well-watered garden in Pullman, however, the imbricate arrangement of the pinnae was retained. Taylor (1970) reported a similar situation with *P. imbricans*, a condition which persisted in 1975 when I saw the plant in his garden. The plant still has imbricate pinnae, although it is not doing nearly so well in the shade as a larger plant from the same clone which has been growing in the sun. *Polystichum imbricans* subsp. *curtum* is found in shadier sites than subsp. *imbricans* (Ewan, 1942) and has flat fronds which are only slightly if at all imbricate.

The imbrication of *Polystichum imbricans* is not the same as the crisping of the pinnae in the sun form of *P. munitum*, and, in the living plant, the pinnae of *P. imbricans* are commonly not imbricate at all. In *P. imbricans* the pinnae remain flat or slightly cupped on the upper side and rotate in two planes: folded towards the center of the blade and twisted along the longest axis (costa) so that the upper surface is in a plane perpendicular to the rachis. Imbrication occurs only in those plants where the pinnae are more or less angled upwards towards the apex of the frond. The impression of imbricate pinnae is usually obtained by pressing specimens that are virtually impossible to spread out flat.

Taylor (1970) characterized *Polystichum imbricans* as having narrower fronds than *P. munitum*. An attempt to quantify this by dividing the blade width by its length (excluding stipe) resulted in the lowest values (signifying the narrowest blades) being obtained from specimens of *P. munitum* greater than one meter in length. Although such specimens are rarely found in the herbarium, plants of this size typify *P. munitum* in regions of its greatest abundance. A similar attempt to quantify the crowdedness of the pinnae by obtaining an (average pinna width)/



FIGS. 2-3. Habitat photographs of *Polystichum*. FIG. 2. *Polystichum munitum* in Marin County, California. Photo by J. Morley. FIG. 3. *Polystichum imbricans* in Chelan County, Washington. Photo by B. O. Mulligan.



FIGS. 4-7. Rhizome and rachis scales of *Polystichum*. FIG. 4. Cross-section of rhizome of *Polystichum munitum*, showing sclereid clusters. FIG. 5. Dried rhizome of *Polystichum munitum*, split and polished to show sclereid clusters. FIG. 6. Rachis scales of *Polystichum munitum*. FIG. 7. Rachis scales of *Polystichum imbricans*.

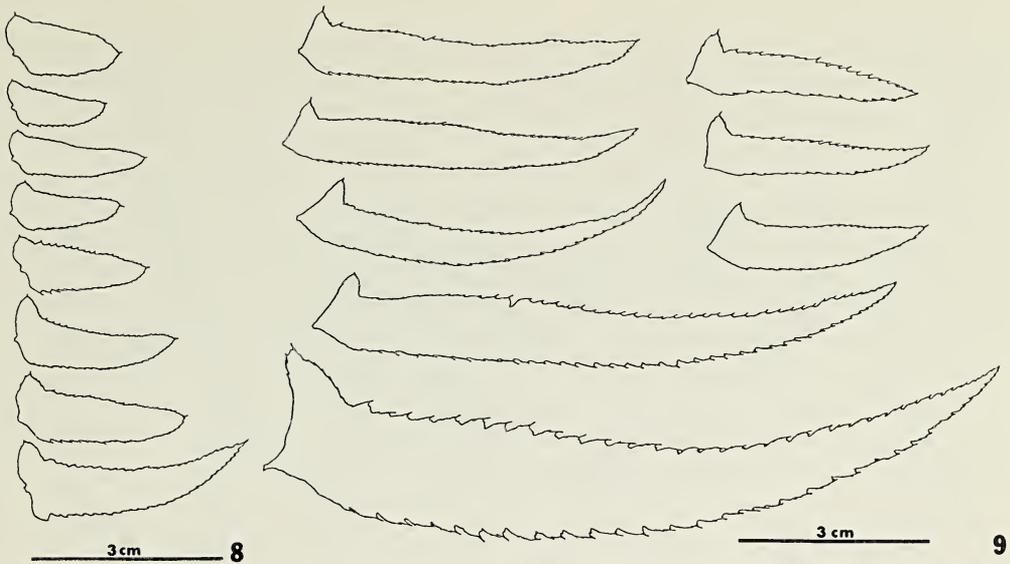
(spacing on the rachis) ratio failed to produce meaningful results. Variability among fronds in a single plant commonly exceeded average differences between each species. These two presumptive distinctions are false impressions generated by the condensation of the frond of *P. imbricans* into its unique conformation.

Rhizome.—An examination of rhizome anatomy has led to the discovery of a character that has proven useful in distinguishing *Polystichum munitum* from *P. imbricans*. Sclereid clusters are found in the pith of *P. munitum* with a high level of constancy. The clusters are dense aggregations of greatly thickened (lignified?) cells with little or no lumen visible in cross-sections (Fig. 4). The clusters are

fusiform, 0.1–0.3 mm thick, and 0.5–1.5 mm long. They are randomly scattered throughout the pith of the rhizome and are found in the central part of the stipe bases. The sclereid clusters are sufficiently numerous that they are readily noticed in sections cut with a pocket knife (*Fig. 5*). Where present, rhizomes on the herbarium specimens from the selected set mentioned above were studied by carefully shaving exposed portions of the pith with a scalpel. Thirty specimens of *P. munitum* were examined: ten from Oregon, six from Washington, five each from Idaho and California, two from British Columbia and one each from Alaska and Montana. Only one specimen, a small plant from Hood River County, Oregon, did not have sclereid clusters visible in the pith of the rhizome. It is likely that lack of sclereid clusters in this specimen reflects its youth. A three-year-old sporophyte grown from spores of a plant (*D. Wagner 244, WS*) known to have typical sclereid clusters had not yet developed sclereid clusters. *Polystichum imbricans* generally lacks sclereid clusters. Out of 24 specimens of the study set examined, only three had sclereid clusters: one each from Lane and Baker Counties, Oregon and one from Tulare County, California. Specimens lacking the clusters included thirteen from California, three each from Oregon and British Columbia and two from Washington. Further checking in the field showed that mature plants of *P. munitum* invariably possess sclereid clusters. Three populations of *P. imbricans*, all in Oregon, had up to ten per cent of the individuals with sclereid clusters. With this character, absence seems to be taxonomically definitive, i.e., lack of sclereid clusters provides a means of positive identification as *P. imbricans*, whereas the presence of sclereid clusters strongly indicates identity as *P. munitum* without excluding the possibility of being *P. imbricans*.

Pinnae.—Width/length ratios of the longest pinna on a frond have proven to be valuable for characterizing *Polystichum imbricans*. Width measurements were made immediately in front of the auricle, from the apex of the first acroscopic serrature to the apices of the serratures on the basiscopic margin of a pinna. With few exceptions, the longest pinna on a frond of *P. imbricans* subsp. *imbricans* is less than five times longer than broad (ratios greater than 0.2), whereas the longest pinnae on fronds of *P. munitum* are much longer (ratios usually much less than 0.2). Exceptions are found in juvenile plants of *P. munitum*, where the pinnae may be relatively short and broad, and in *P. imbricans* subsp. *curtum*, whose slender pinnae are the most obvious morphological feature distinguishing it from the typical form.

The pinnae of *Polystichum imbricans* are distinctive in their outline (*Fig. 8*), both at the base and at the apex. The bases of the pinnae in *P. imbricans* are invariably oblique throughout, whereas the bases of the pinnae in *P. munitum* are nearly always cuneate in the upper part of the frond (*Fig. 9*). Sterile pinnae of *P. munitum* often have an oblique base, especially the lowest two or three pinna-pairs. With corresponding frequency, the tips of the pinnae in *P. imbricans* are cuspidate. In *P. munitum*, the pinnae taper gradually to the apex and lack an apiculum, particularly the pinnae bearing sori. In occasional specimens of *P. imbricans* subsp. *curtum* the terminal spine is obscured because of the slender shape of the pinnae, and rarely the pinnae will be merely acuminate. Juvenile



FIGS. 8-9. Pinna outlines of *Polystichum*. FIG. 8. Pinna outlines from eight different specimens of *Polystichum imbricans*. All are taken from the middle of the frond. The lowest pinna is of subsp. *curtum*, the rest are of subsp. *imbricans*. FIG. 9. Pinna outlines from eight different specimens of *Polystichum munitum*.

plants and specimens of *P. munitum* in exposed sites may occasionally have obtuse and/or apiculate pinnae.

Trichomes.—*Polystichum imbricans* is generally less scaly than *P. munitum* (Maxon, 1900). Various specimens of *P. imbricans* have been described as naked, notably in the description of var. *nudatum* (Eaton, 1878). A close examination of the type revealed previously overlooked scars on the rachis and stipe where scales were formerly attached. Some of these scales still persist on the isotype. In every case of specimens having been described as naked, I found signs of trichomes that have been lost. *Polystichum imbricans* is characterized by readily deciduous scales; their absence on the upper part of the stipe is a good field character. However, old fronds from the previous season must be examined, as young fronds retain their ramentum in the early part of the growing season. The character is fairly good in herbarium specimens but must be used with caution as the scales of both *P. imbricans* and *P. munitum* are often rubbed off by the collector or in later handling.

Whereas presence or absence of scales on the stipe and rachis is strongly suggestive for identification purposes, scale morphology is taxonomically definitive. At the base of the stipe are large scales that are broader than the linear scales on the rhizome. In *Polystichum munitum* these stipe base scales are generally ovate-lanceolate; in *P. imbricans* the stipe base scales are lanceolate to linear-lanceolate. Rhizome and stipe base scales in *P. munitum* are usually coffee brown, occasionally with a dark central stripe. The color of these scales in *P. imbricans* is usually light castaneous, never with a dark central stripe. The size of the scales diminishes gradually up the stipe in *P. munitum*, whereas in *P. imbricans*

cans there is an abrupt diminution in size of the scales. The scales are always persistent on the stipe bases in *P. imbricans*, giving a tufted appearance to specimens detached at the juncture with the rhizome, especially when the upper stipe scales have been lost. In both species, the dorsal surface of the stipe and rachis bears mostly sub-filiform, long (2-4 mm) scales with much smaller scales scattered among them. In *P. munitum* the scales of the ventral side of the rachis and stipe vary greatly in size. Small scales, similar to the infralaminar scales described below, are scattered among numerous larger linear-lanceolate scales with the largest scales being ovate-lanceolate. These ovate-lanceolate scales at the base of the blade in *P. munitum* are the single most useful character visible without magnification for distinguishing it from *P. imbricans* (Figs. 6, 7). *Polystichum imbricans* has both large and small scales on the underside of the rachis. The largest scales are linear to linear-lanceolate and more uniform in size than the larger scales on the ventral side of the rachis in *P. munitum*.

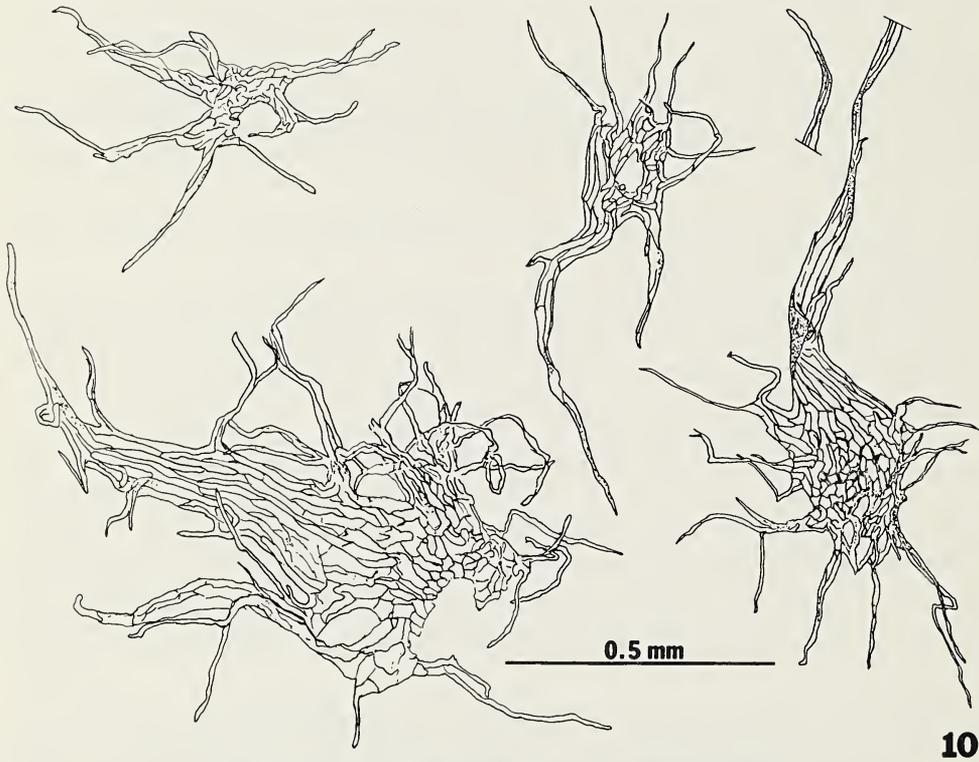


FIG. 10. Infralaminar scales of *Polystichum munitum*.

Easily overlooked, scaly trichomes are also found on the undersurface of the pinnae of these ferns. Daigobo (1972) relates that they occur on all polystichums and uses the morphology of these structures, which he calls microscales, to characterize the sub-sections of *Polystichum* in eastern Asia. I have found them to be very useful for taxonomic purposes, but prefer to call them infralaminar scales in accordance with their location.

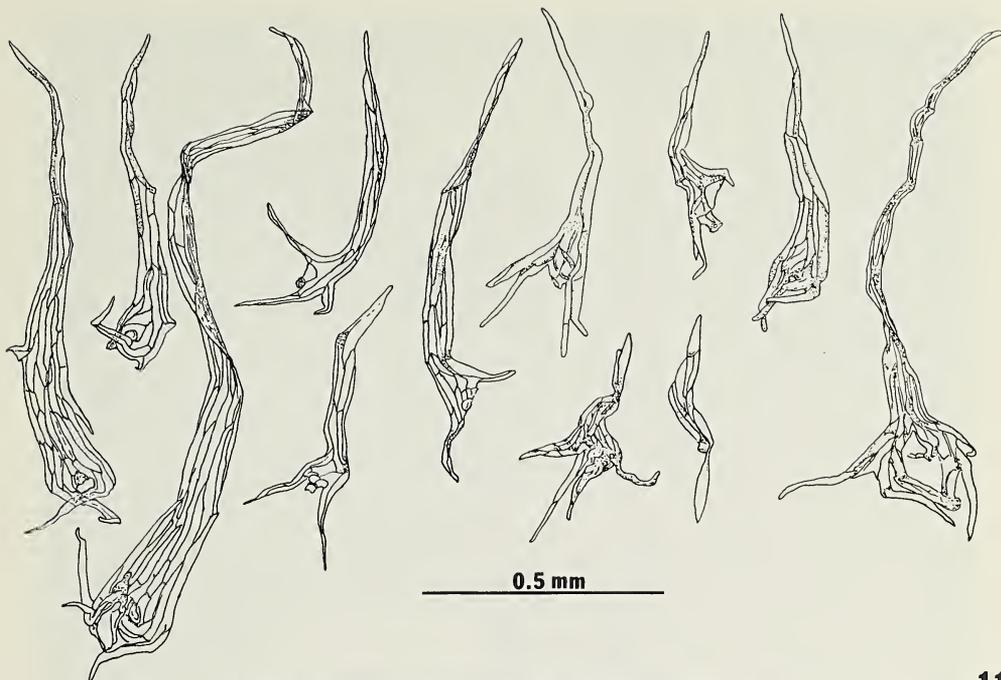


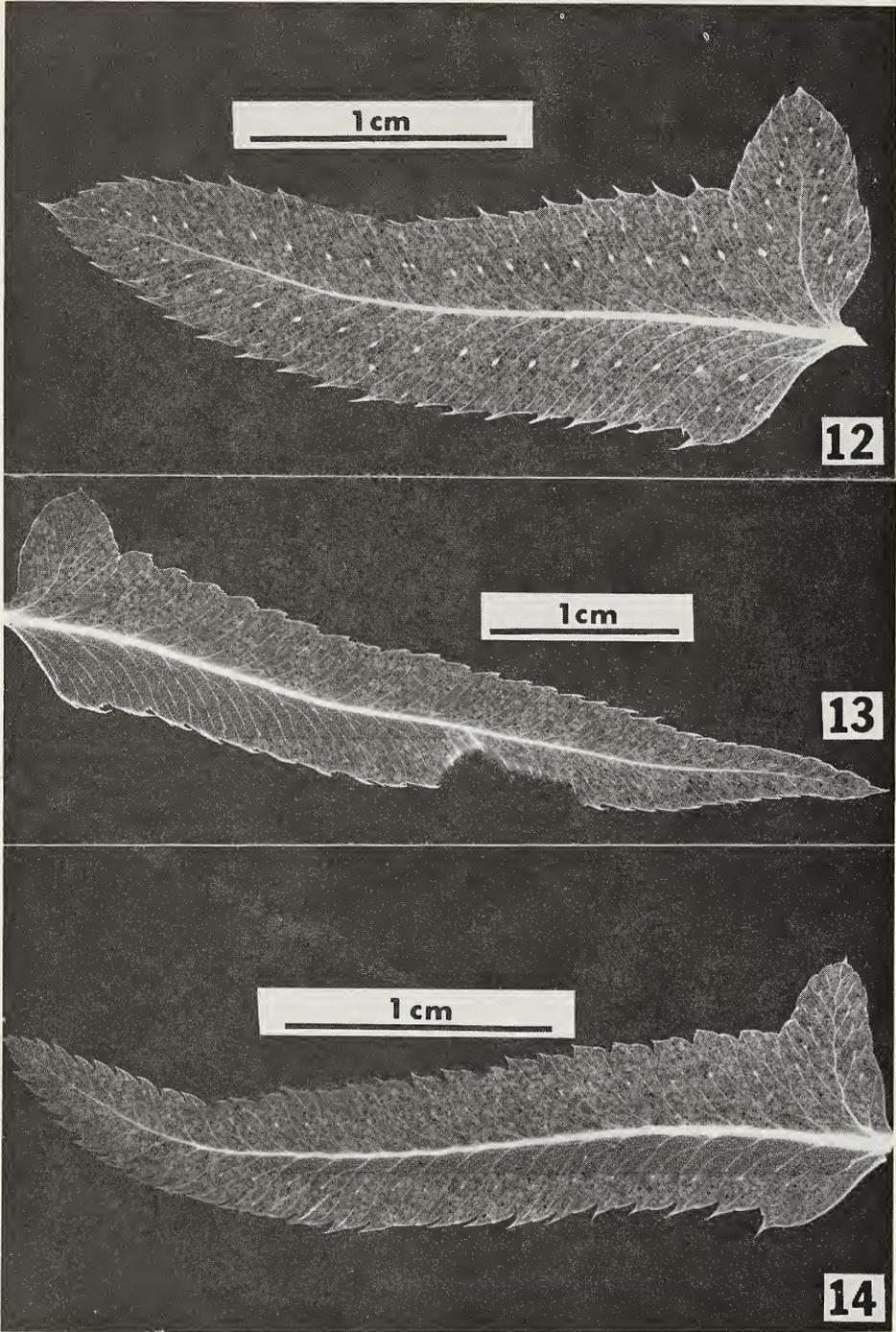
FIG. 11. Infralaminar scales of *Polystichum imbricans*.

11

The infralaminar scales of *Polystichum munitum* are lanceolate or linear-lanceolate above a widened, arachnoid base. The base of these scales have numerous hair-like, contorted projections (Fig. 10). The infralaminar scales are frequently enlarged and crowded along the costa at the base of the pinna in *P. munitum*, where they are conspicuous without magnification as a fuzzy, brown, lanulose vestiture. The scales along the costa may have an elongate, tapering body, often reaching 2 mm. On other areas of the pinna, the scales are usually shorter with the basal projections nearly as long as the main body of the scale.

The pinnae of *Polystichum imbricans* have smaller (averaging ca. 0.5 mm) infralaminar scales than *P. munitum*. The scales appear stouter, with thicker cell walls, and with fewer, straight or angular projections (Fig. 11). The thicker cell walls cause the infralaminar scales of *P. imbricans* to appear darker brown than those of *P. munitum* when viewed in a light microscope. The scales of *P. imbricans* are strongly birefringent whereas the scales of *P. munitum* are scarcely visible with crossed polarizing filters. The thin cell walls of the infralaminar scales of *P. munitum* collapse irregularly when dry (even in fresh specimens) and cause the contorted appearance described above. This contrasts sharply with the rigid angularity of the scales of *P. imbricans*, where the thick cell walls prevent collapse of the cells even when dry.

The infralaminar scales of *Polystichum imbricans* are more evenly distributed over the undersurface of the pinnae than in *P. munitum*, and enlargement or crowding of the scales at the base of the pinnae is rarely noticeable. In *P. imbricans*



FIGS. 12-14. Cleared pinnae of *Polystichum*. FIG. 12. *Polystichum imbricans* subsp. *imbricans*. FIG. 13. *Polystichum imbricans* subsp. *curtum*. FIG. 14. *Polystichum munitum*.

cans subsp. *curtum*, the infralaminar scales are often larger than in subsp. *imbricans*, and are often very dark brown, giving a speckled appearance to the underside of the pinnae when viewed without magnification.

Soral position.—The sori of *Polystichum munitum* are usually midway between the costa and the margin of the pinna. Occasional specimens have the sori slightly nearer to the costa or margin. Medial sori also are usual in *P. imbricans*, but many specimens have the sori clearly nearer the margin than the costa, sometimes strikingly so. The latter cases have caused several authors to cite this character as distinguishing *P. imbricans*, but it is not constant and cannot be readily quantified. The usefulness of such a character is further reduced by the fact that large specimens of both species usually have more than one row of sori between the costa and margin.

Sorus position with regard to the fertile vein varies considerably in both species being considered here. In *Polystichum imbricans*, the soral receptacle characteristically is lateral on the fertile vein, with the vein reaching the margin and somewhat clavate at the end like sterile veins. An extreme is reached in specimens from Tumwater Canyon, Chelan County, Washington (Fig. 12), where the veins anastomose regularly near the ends. This reticulation is remarkable, since it is often considered of generic significance (W. Wagner, 1974). *Polystichum imbricans* subsp. *curtum* has the soral receptacle terminal on the fertile vein, much like the condition most frequently encountered in *P. munitum* (Figs. 13, 14). However, *P. munitum* is not uniform in this respect, since an occasional robust specimen will have both lateral sori and anastomosing veins (Fig. 15).

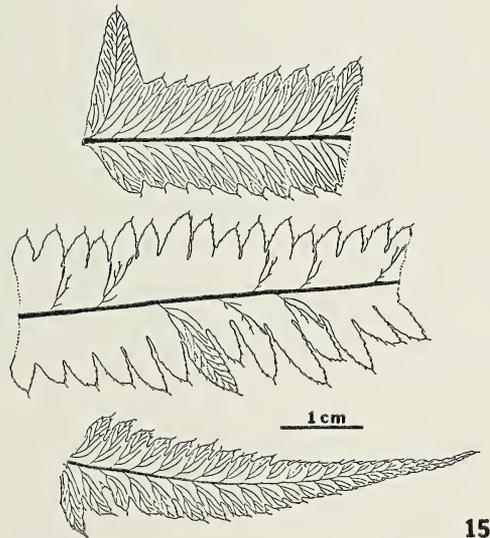
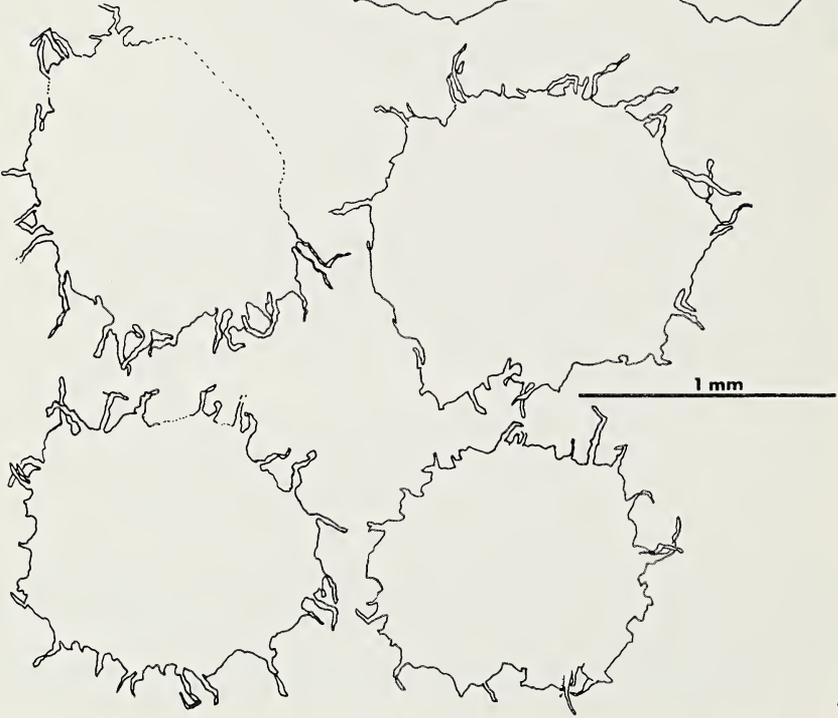
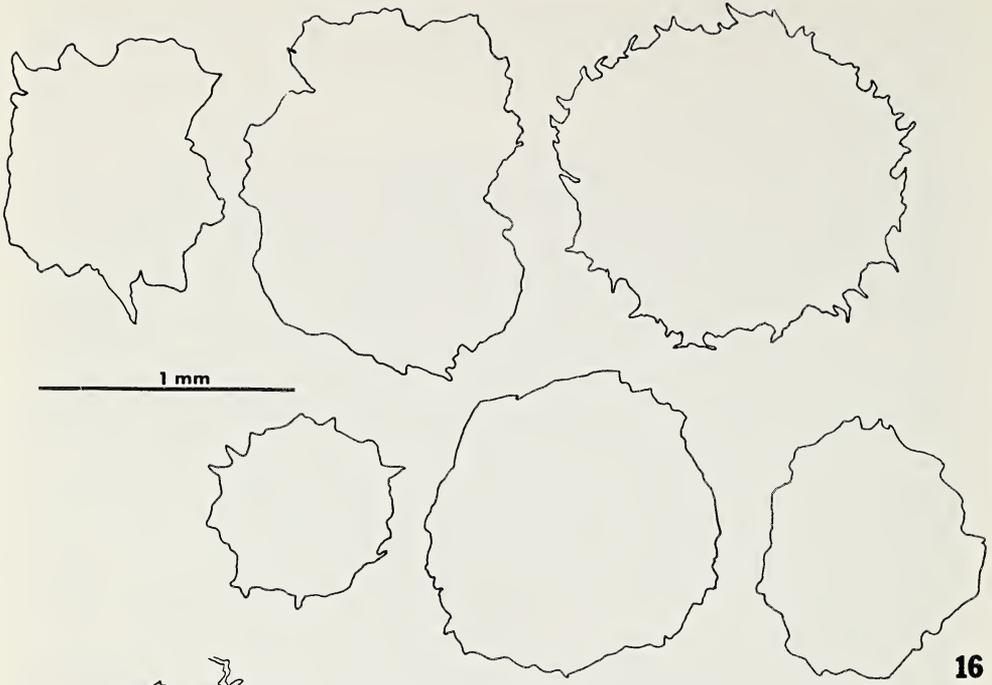


FIG. 15. Middle pinna from an incised frond of *Polystichum munitum*. Only veins with anastomoses and veins of one segment are drawn in middle portion.



FIGS. 16-17. Indusia outlines of *Polystichum*. FIG. 16. *Polystichum imbricans*. FIG. 17. *Polystichum munitum*.

Indusia.—Although I have been unable to locate published material, it is evident from annotations on herbarium specimens that Carlotta Hall conducted an extensive study of indusia in *Polystichum munitum* and *P. imbricans* at the University of California, Berkeley. She considered the indusium to be definitive in separating the two forms (see also Maxon in Abrams, 1923). The indusia of *P. munitum* bear multicellular hairs, cilia, on the margins (Fig. 17). These cilia are contorted when the indusia are dry, many of the cells having collapsed. Here, as in the sublaminar scales, the cell walls seem to be thinner in *P. munitum* than in *P. imbricans*. The indusia of *P. imbricans* are typically entire (Fig. 16) but may be sharply toothed. Long, rigid teeth are common in *P. imbricans* subsp. *curtum*. In the rare specimens in which the cells of these teeth have collapsed, the indusia may be considered ciliate.

The cilia of the indusia may be difficult to see in mature specimens of *Polystichum munitum* because the indusia usually become much folded as the sporangia mature. The indusia remain attached to the sorus, hidden among the sporangia, into the following spring. The indusia of *P. imbricans* usually remain spread out over the ripe, dehisced sporangia and detach like little umbrellas soon after the spores are shed. Out of 75 specimens of *P. munitum* examined, 72 had ciliate indusia, 2 had short projections only, and one had lost all indusia; out of 59 specimens of *P. imbricans*, 51 had entire indusia, 7 had short, straight projections, and 1 had ciliate indusia.

Annulus.—Callan (1972) first noticed that *Polystichum munitum* generally has fewer indurated cells in the annulus than *P. imbricans*. Copeland (1947) stated that in *Polystichum* the sporangia generally have more than 18 cells in the annulus. *Polystichum munitum* has averages of 13 to 14 cells in the annulus, often with very little variation on a single plant. I found several specimens in which all 10 counted sporangia had 13 cells in the annulus, and counted 50 sporangia on each of 2 specimens in which only 2 out of 50 did not have 13 annular cells. *Polystichum imbricans* shows much greater variation, both within a single specimen and among samples of the species as a whole. The averages generally fall between 15 and 19 cells in the annulus. The average rarely falls below 14.5, and so is useful as a diagnostic character (Table 1). The average has been found as high as 26.5 on a specimen from Mt. Tamalpais, Marin County, California.

TABLE 1. QUANTITATIVE DATA FROM STUDY SET OF *POLYSTICHUM MUNITUM*, *P. IMBRICANS* SUBSP. *IMBRICANS*, AND *P. IMBRICANS* SUBSP. *CURTUM*. Pinna width index = width/length of longest pinna on specimen. For number of annulus cells and polar diameter of exospore, an average of ten counts or measurements is used for each specimen. n = number of specimens.

	Pinna Width Index			Annulus Cells			Exospore Diameter		
	<i>mun.</i>	<i>imb.</i>	<i>cur.</i>	<i>mun.</i>	<i>imb.</i>	<i>cur.</i>	<i>mun.</i>	<i>imb.</i>	<i>cur.</i>
n	75	49	10	75	49	10	57	37	10
\bar{x}	0.15	0.27	0.20	13.5	17.4	17.2	34.7	37.2	39.2
min	0.10	0.19	0.13	12.3	13.5	15.1	30.5	32.8	35.0
max	0.31	0.37	0.28	16.9	26.5	20.2	39.4	40.8	42.6
s.d.	0.39	0.05	0.40	0.71	2.51	1.50	2.29	2.13	2.38

Spores.—The spores of *Polystichum munitum* and *P. imbricans* are distinctive in both size and morphology. Measurements from 47 specimens of *P. munitum* and 47 specimens of *P. imbricans* (both subsp. *imbricans* and subsp. *curtum*) show that the spores of *P. imbricans* average 3 μm larger in the longest dimension than *P. munitum*, i.e., 37.7 μm and 34.7 μm respectively (Fig. 18, Table 1). Variation within each species is considerable, and the variation of each overlaps the other, so that spore size is not useful as a taxonomic character by itself. It is remarkable that the range from the smallest spore to the largest spore is a difference which one might associate with a difference in ploidy. However, all specimens examined so far have been diploid. The values for *P. munitum* are somewhat larger than those reported by W. Wagner (1973) for spores mounted in diaphane, possibly due to the difference in mounting media but probably due to his small sample size (only two specimens were measured).

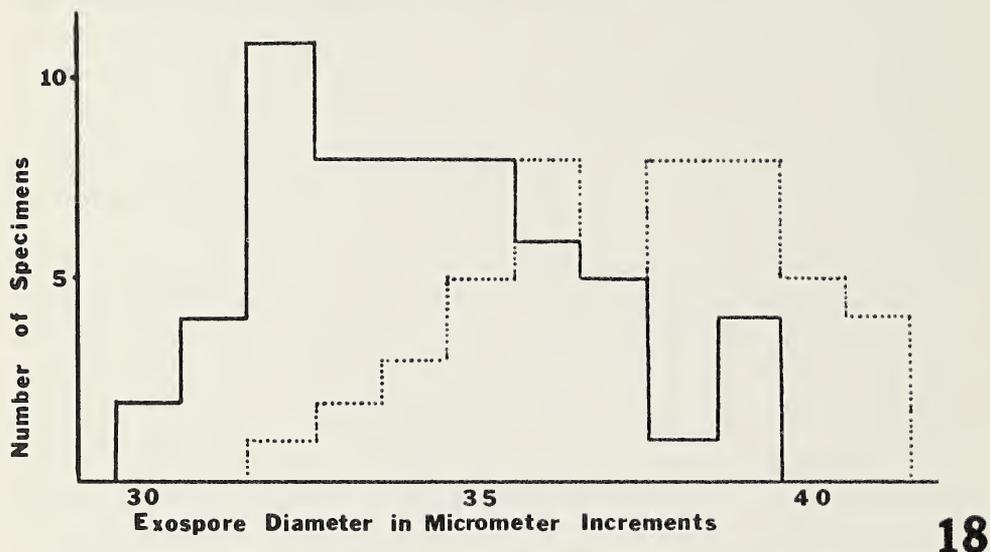
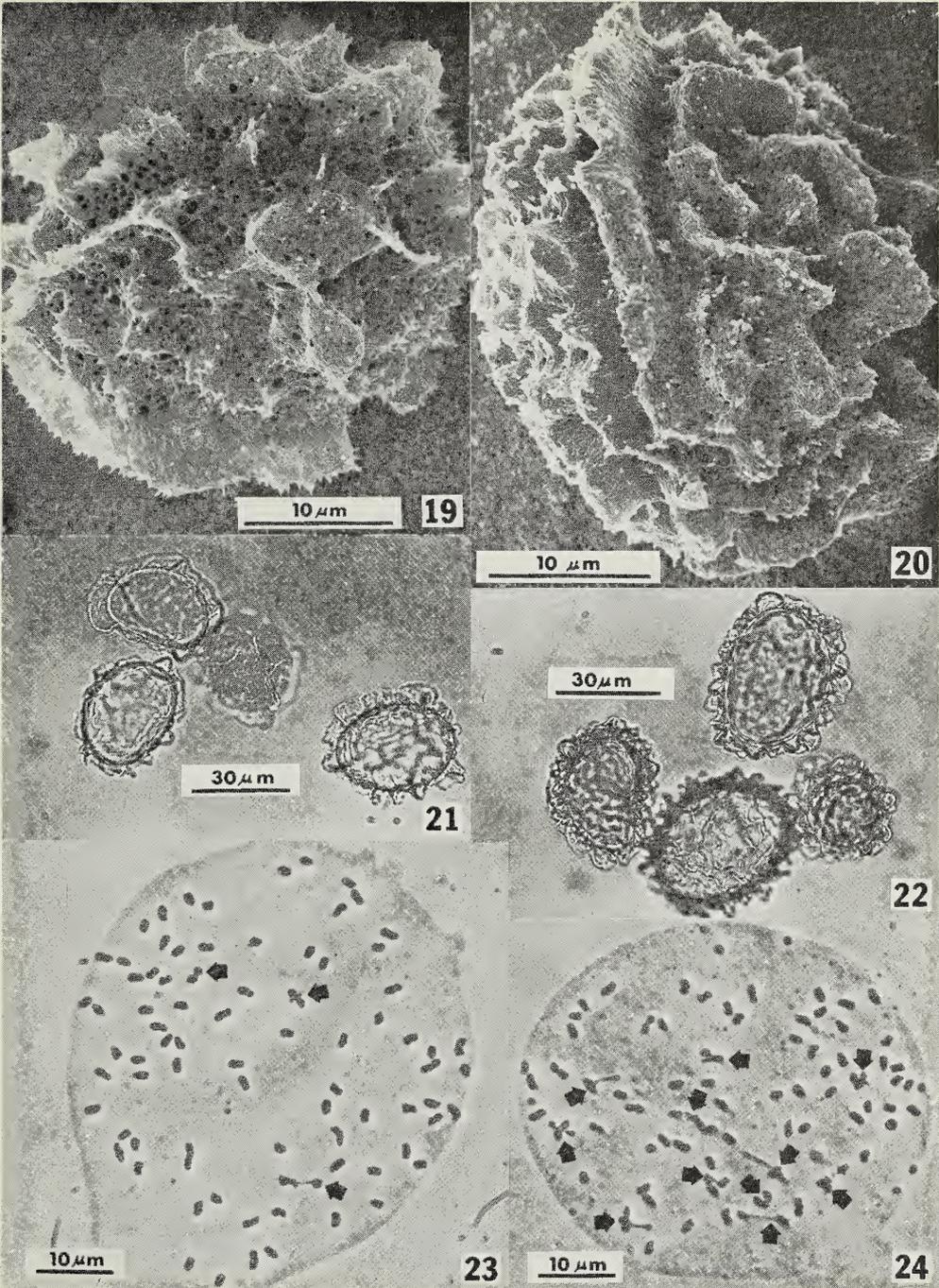


FIG. 18. Histogram of average exospore diameter from 57 specimens of *Polystichum munitum* (solid line) and 48 specimens of *P. imbricans* (dotted line). $n = 10$ for each specimen.

When viewed through light microscope, the perine of *Polystichum imbricans* spores (Fig. 22) appears darker and more tightly appressed than in *P. munitum* (Fig. 21). Spore collections of *P. imbricans*, when observed *en masse* in sample vials, appear dark brown, whereas the spores of *P. munitum* appear light yellow. This color difference can be discerned in single spores when using a strong light source and a 20 \times dissecting microscope. The critical features of spore morphology are revealed in scanning electron micrographs. The folds of the perine in *P. munitum* are high, rounded, often perforated, and are copiously supplied with papillae and toothed crests (Fig. 19). These crests can be detected in the optical microscope as a fine fringe on the folds of the perine. The perine of *P. imbricans* is thrown in numerous tight folds (Fig. 20) that lack crests, although papillae are present. Perforation of the perine is very sparse. Occasional specimens of *P.*



FIGS. 19-24. Spores and meiocytes of *Polystichum*. FIG. 19. Spore of *Polystichum munitum* (D. Wagner 456, WS). FIG. 20. Spore of *Polystichum imbricans* (D. Wagner 459, WS). FIG. 21. Spores of *Polystichum munitum* (D. Wagner 330, WS). FIG. 22. Spores of *Polystichum imbricans* (I. C. Otis 1053, WS). FIG. 23. Meiocyte of *Polystichum munitum* × *imbricans* with 76 univalents and 3 bivalents (indicated by arrows). FIG. 24. Meiocyte of *Polystichum munitum* × *imbricans* with 60 univalents and 11 bivalents (indicated by arrows).

imbricans have folds in the perine that appear as loose and thin as those in *P. munitum*, but lack the crests. The morphology of the spores of *P. imbricans* subsp. *curtum* does not vary to any degree from subsp. *imbricans*.

Chemistry.—Material of *Polystichum munitum* from nine localities (1 in British Columbia, 4 in Washington, and 2 each in Idaho and California) was examined chromatographically. Material of *P. imbricans* from five localities (2 in Washington, 1 in British Columbia, and 2 in California) was examined. Unfortunately, uniform species-specific patterns were not obtained. The variability of phenolic composition within each species is considerable even on a qualitative basis. The greatest variability was found in *P. munitum*, where from 17 to 26 compounds were detected in crude methanol extracts, whereas *P. imbricans* showed greater uniformity in the 21 or 22 compounds usually detected. Despite this variability, distinctive patterns for the two species discussed here were obtained from chromatograms visualized with sprays. The most useful were those sprayed with diazotized p-nitroaniline and oversprayed with 20% sodium carbonate. All of the chromatograms of *P. munitum* have four prominent reddish-brown spots in a row in the middle of the chromatogram, parallel to the long direction. The chromatograms of *P. imbricans* are dominated by a single large brown spot in the center and several light yellow spots in the quadrant closest to the origin. A procedure using lead (II) acetate to precipitate phenolics from crude extracts produced the clearest separation of the compounds. The color of the precipitate forms the basis of a simple chemical test that distinguishes *P. munitum* from *P. imbricans*: the washed precipitates of *P. munitum* are a dull gray-green to grayed greenish-brown, and the precipitates of *P. imbricans* are a bright canary yellow. Although accurate quantitative analyses were not performed, it was observed that leaf extracts of *P. imbricans* contain quantities of phenolics many times greater than the amount found in similar extracts of *P. munitum*. No attempt was made to identify the specific compounds beyond determining that the majority of the taxonomically significant compounds are glucosides of kaempferol and quercetin.

Cytology.—Throughout most of the area where *Polystichum munitum* and *P. imbricans* are found, the two species occur in distinct and geographically isolated plant associations. In a few places, however, I have found the two species in sympatry and have searched for intermediate plants for study. On Mt. Newton, near Victoria, British Columbia, I collected a plant (*D. Wagner 556*, WS) that not only had intermediate morphology, but the sporangia appeared to be aborted. An examination of chromosomes at meiosis showed that most of the chromosomes in this plant, $2n=82$, were unpaired. The number of bivalents varied from three to eleven, most with abnormal pairing (*Figs. 23, 24*). Both species are diploids ($n=41$) (W. Wagner in Fabbri, 1963; W. Wagner, 1973; Taylor & Lang, 1963; Callan, 1972; Smith, 1974; D. Wagner, unpubl.). The level of pairing in this specimen is lower than that found in other sterile diploid hybrids in *Polystichum* (W. Wagner 1973; Sleep & Reichstein, 1967).

Summary.—The results of the comparative study of *Polystichum munitum* and *P. imbricans* support the hypothesis that there is a fundamental biological distinction between the two. The quantitative data obtained from the selected set of

TABLE 2. QUALITATIVE DATA FROM STUDY SET OF *POLYSTICHUM MUNITUM* AND *P. IMBRICANS*. The number of specimens is given for each character state.

	Broad rachis scales		Ciliate indusium		Sclereid clusters in pith		Cuspidate pinna tips		Light, crested spores		Arachnoid infralaminar scales	
	<i>mun.</i>	<i>imb.</i>	<i>mun.</i>	<i>imb.</i>	<i>mun.</i>	<i>imb.</i>	<i>mun.</i>	<i>imb.</i>	<i>mun.</i>	<i>imb.</i>	<i>mun.</i>	<i>imb.</i>
present	74	0	73	0	29	3	3	58	58	3	74	0
intermed.	1	2	2	8	0	0	8	1	2	4	2	3
absent	1	57	0	51	1	21	65	0	0	38	0	56
no data	0	0	1	0	46	35	0	0	16	11	0	0

study specimens are summarized in *Table 1* and the qualitative data in *Table 2*. (The raw data and specimen citations appear in D. Wagner, 1976.) When a pictorialized scatter diagram of six characters is prepared, the correlation of characters is demonstrated graphically (*Fig. 25*). Positive identification of a plant as one species or the other depends more on a correlated series of subtle characters than on a few obvious macro-morphological features. Obviously, some characters are more useful than others. Although no one character should be considered definitive for identification, the following ranking of characters is proposed, beginning with those considered most reliable: width of rachis scales, number of indurated

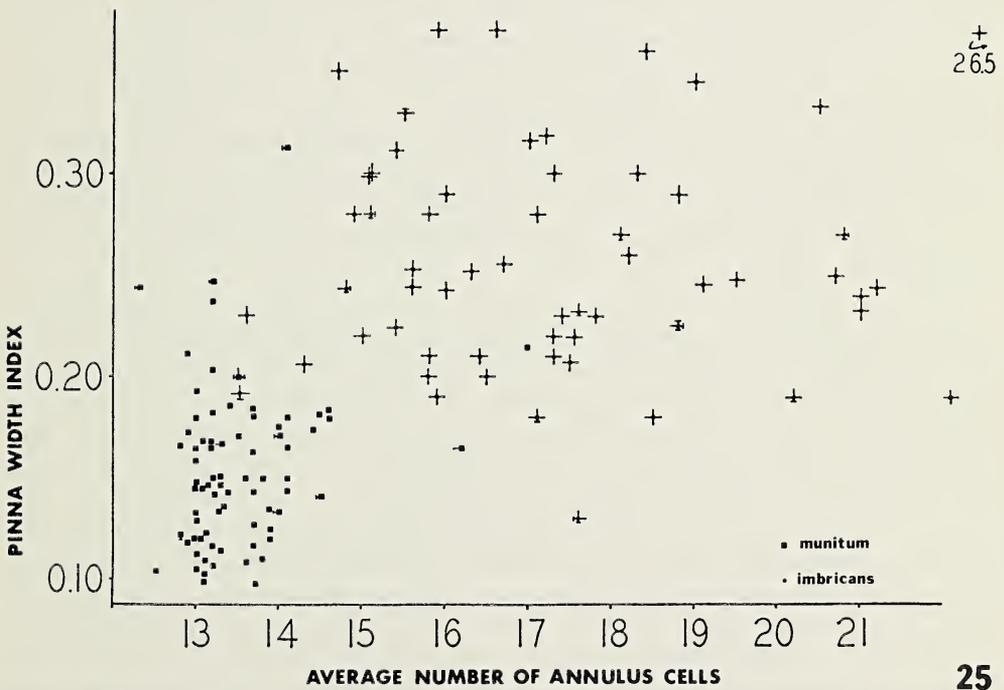


FIG. 25. Pictorialized scatter diagram of six characters in *Polystichum munitum* and *P. imbricans* from study set of specimens representing entire range of both species. Bar to the right indicates presence of stout, non-arachnoid infralaminar scales, down indicates entire indusia, left indicates mucronate fertile pinna tips, and up indicates narrow rachis scales.

cells in the annulus, nature of indusium margin, presence of sclereid clusters, morphology of infralaminar scales, persistence of upper stipe scales, shape of pinna apex, and pinna width index. Not included in this ranking are characters that require special techniques or substantial previous experience with both species.

The general appearance of *Polystichum imbricans* subsp. *curtum* is intermediate between *P. imbricans* subsp. *imbricans* and *P. munitum*. *Polystichum imbricans* subsp. *curtum* differs from subsp. *imbricans* in the arched, non-imbricate fronds with rather long, tapering pinnae, a greater tendency towards having sharp projections on the indusium, darker scales, and the soral receptacle being terminal on the veins. In all other characters, except ecological and geographical habits (see Ecology and Phytogeography), there is agreement between the two subspecies, particularly in the characters which are important in separating *P. imbricans* from *P. munitum*.

THE ORIGIN OF POLYSTICHUM ANDERSONII

One of the most exciting problems encountered in botany is the prediction and subsequent discovery of new species. Such an undescribed species was predicted and identified during my study of *Polystichum andersonii*. This fern is one of the most distinctive in the Pacific Northwest, since it is the only one to bear a prolific bud on the frond. In earlier studies, this fern was found to be tetraploid with $n=82$ (Taylor & Lang, 1963; W. Wagner in Fabbri, 1963). Later, in Snohomish County, Washington, W. H. Wagner and A. Kruckeberg found a natural sterile hybrid between this species and *P. munitum* that had 41 pairs of chromosomes and 41 univalents at meiosis. This caused Wagner some concern, as he did not believe the tetraploid to be an allopolyploid (W. Wagner, 1973). He thought the morphology of *P. andersonii* to be too distinctive to be influenced by the genome of *P. munitum*. However, this situation is very similar to that of the polystichums in Europe.

The relationships of the European polystichums have been well studied genetically (Manton, 1950; Manton & Reichstein, 1961; Sleep & Reichstein, 1967). A summary of their findings is presented in Fig. 26. Of the four sexual taxa of *Polystichum* in Europe, two are diploid (*P. lonchitis* and *P. setiferum*) and two are tetraploid (*P. aculeatum* and *P. braunii*). All six possible hybrid taxa from these four species have been found in nature and described. Chromosomes of five of these have been studied from naturally occurring plants; the sixth, *P. × lonchitiforme*, has been studied cytologically only from artificially synthesized plants (Sleep & Reichstein, 1967). Many of the other hybrids have also been studied from material created experimentally. An analysis of chromosome pairing patterns in spore mother cells of these hybrids provides information about the genetic relationships between their parents. These hybrids were originally detected, and their putative parents proposed, on the basis of morphological intermediacy and sterility (predominantly inviable spores).

Polystichum aculeatum is a fertile sexual species intermediate in morphology between *P. lonchitis* and *P. setiferum*, although it is closer in appearance to *P.*

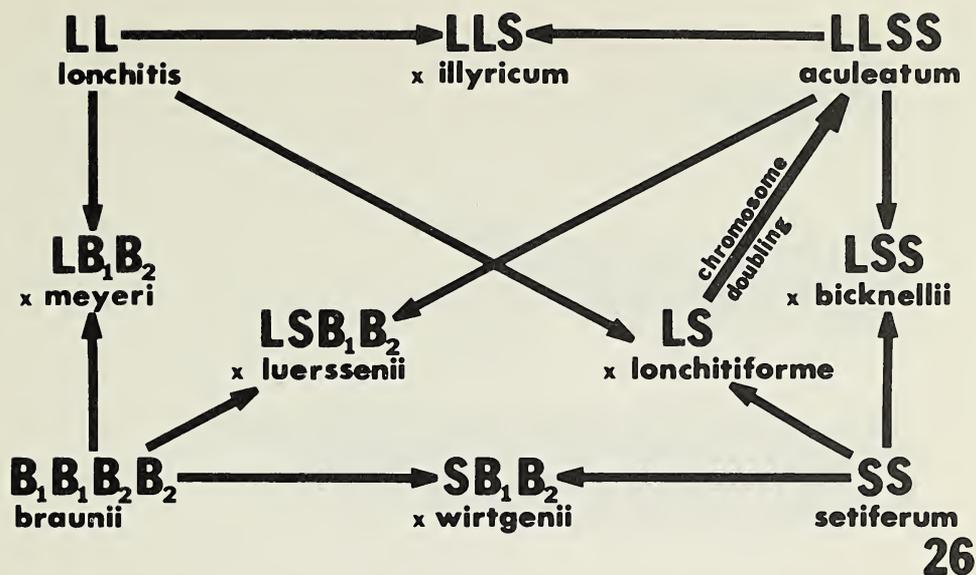


FIG. 26. Genome composition of the species and hybrids of *Polystichum* in Europe, from data in Sleep and Reichstein (1967).

setiferum. The similarity between *P. setiferum* and *P. aculeatum* caused considerable taxonomic confusion (Alston, 1940) until Manton (1950) demonstrated that the former is diploid and the latter is tetraploid. That *P. aculeatum* is an allotetraploid was suggested by Manton (1950), who found *P. × illyricum* to be triploid with approximately 41 univalents and 41 bivalents at meiosis. *P. × illyricum* had been considered to be the cross between *P. lonchitis* and *P. aculeatum* since its description in 1892 (Christensen, 1913). The cytological data led Manton to postulate *P. lonchitis* as one of the diploid parents of *P. aculeatum*. Half of the chromosomes in *P. aculeatum* were homologous (paired) with the chromosomes of *P. lonchitis*.

The morphology of *Polystichum aculeatum* suggested that the second diploid parent was *P. setiferum*, the species with which it had previously been confused. To test this hypothesis, Manton (1950) synthesized the hybrid between *P. aculeatum* and *P. setiferum*. The resulting plant showed the predicted 41 bivalents and 41 univalents at meiosis. Naturally occurring plants of this hybrid, *P. × bicknellii*, were later examined and found to exhibit the same pairing behavior as the synthesized plant (Manton & Reichstein, 1961).

The relationship between *Polystichum andersonii* and *P. munitum* closely parallels that between *P. aculeatum* and *P. lonchitis*, both morphologically (Fig. 27) and cytologically (W. Wagner, 1973). The idea that *P. andersonii* is an allotetraploid is corroborated by the pattern of its chromatograms. When they are sprayed with diazotized p-nitroaniline, the same four reddish-brown spots seen in *P. munitum* are displayed. The sclereid clusters found in the rhizomes of *P. munitum* are present also in *P. andersonii*. Since *P. munitum* is simply pinnate like *P. lonchitis* and *P. andersonii* is bipinnatifid like *P. aculeatum*, I postulated that

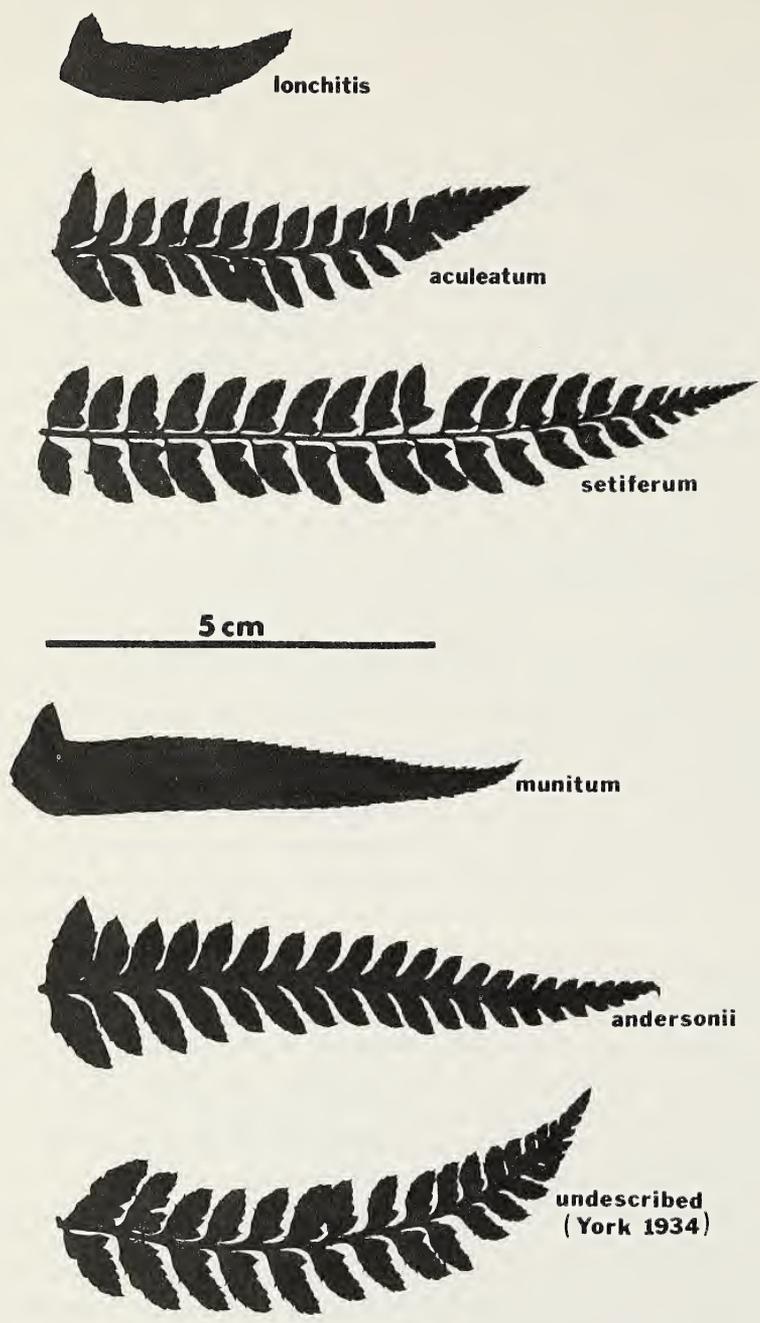


FIG. 27. Typical mid-frond pinnae of *Polystichum lonchitis*, *P. aculeatum*, and *P. setiferum* compared with *P. munitum*, *P. andersonii* and an undescribed plant from the northern coast of British Columbia, Canada.

somewhere one would discover a diploid, bipinnate ancestor to *P. andersonii* that resembled *P. setiferum*. This hypothetical ancestor should bear a proliferous bud on the rachis, lacking in *P. munitum* but present in *P. andersonii*. Considering the range of *P. andersonii* (northern Oregon to Alaska) and the range of *P. munitum* (California to Alaska), I proposed that the most likely area for the unknown diploid to occur would be the coastal forests of northern British Columbia and southeastern Alaska.

TABLE 3. COMPARISON OF *POLYSTICHUM MUNITUM*, *P. ANDERSONII* AND SPECIMEN FROM ALICE ARM, BRITISH COLUMBIA.

<i>Polystichum munitum</i>	<i>Polystichum andersonii</i>	<i>Alice Arm specimen</i>
Lacks vegetative bud	With vegetative bud	With vegetative bud
Once pinnate	Bipinnatifid	Bipinnate
Indusia ciliate	Indusia sparsely ciliate	Indusia entire
Infralaminar trichomes arachnoid	Infralaminar trichomes with contorted projections	Infralaminar trichomes simple
Widespread in West, both coastal and interior	Frequent only along northern coast, occasional in interior	Northern coast

After having formed this hypothesis, I discovered a specimen in the University of British Columbia herbarium that matched the predicted morphology. It was found along the northern British Columbia coast at Alice Arm in 1934 by A. D. York. Although the collection is fragmentary, enough of three fronds is preserved to provide evidence that this is the predicted species (*Fig. 27, Table 3*). A formal description of this species is being postponed until the plant can be rediscovered and its chromosome number determined.

THE DISTINCTION OF *POLYSTICHUM BRAUNII* AND THE ORIGIN OF *P. SETIGERUM*

A clear understanding of the relationships of *Polystichum andersonii* has been confused by the presence of two other large, divided polystichums in the Pacific Northwest. *Polystichum braunii* is the most familiar, being one of the two members of the genus with a circumboreal distribution. It is represented in North America by subsp. *purshii* (Fernald) Calder & Taylor. The only consistent difference between the Eurasian subspecies (subsp. *braunii*) and subsp. *purshii* seems to be the increased proportion of broad to filiform laminar scales of the latter (Calder & Taylor, 1968a). Within the region of this study, recognition of this "weak segregate" (Calder & Taylor, 1968a) serves no useful purpose. *Polystichum braunii* is tetraploid (Manton & Reichstein, 1961; Taylor & Lang, 1963; Calder & Taylor, 1968b) and has been shown to be not derived from other European polystichums. Manton and Reichstein (1961) reported cytological data from *P. × wirtgenii* and *P. × luerssenii*, the *P. braunii* hybrids with *P. setiferum* and *P. aculeatum*, respectively (*Fig. 26*). The hybrid with *P. lonchitis*, *P. × meyeri*, was described and investigated cytologically by Sleep and Reichstein (1967). In each case, few bivalents were found in meiocytes of the hybrids, indicating that there is no chromosome homology between *P. braunii* and the two European diploid species.

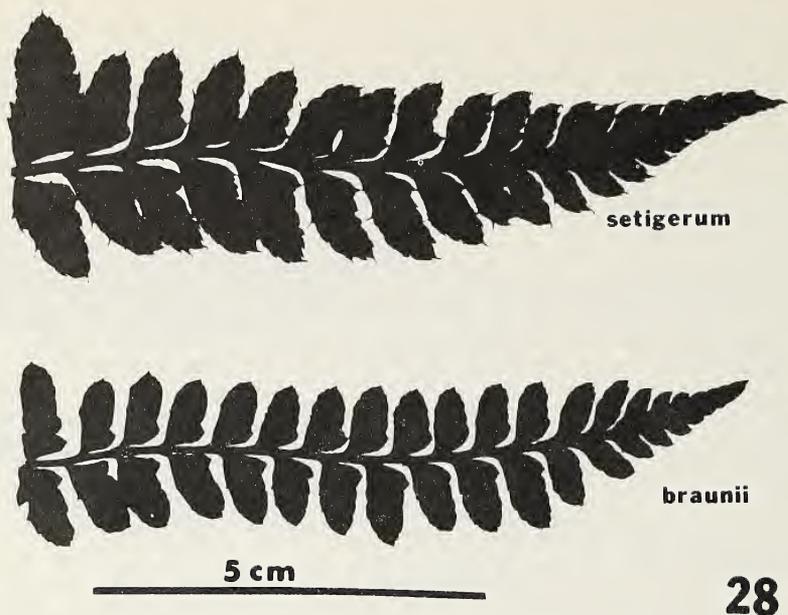
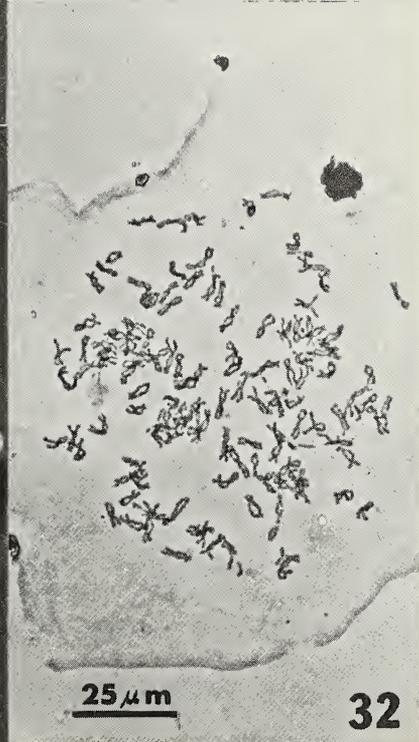
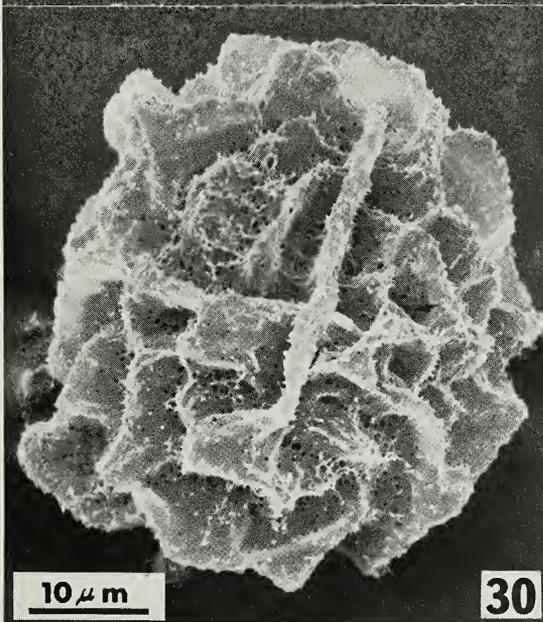
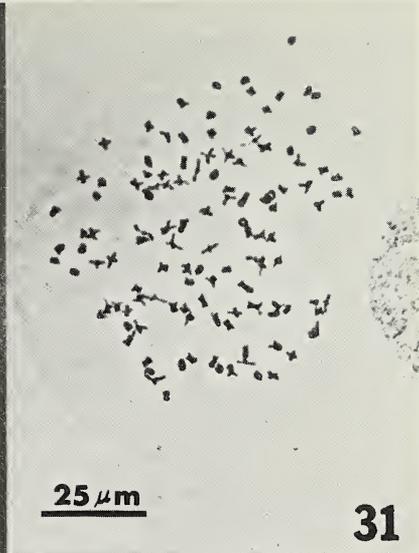
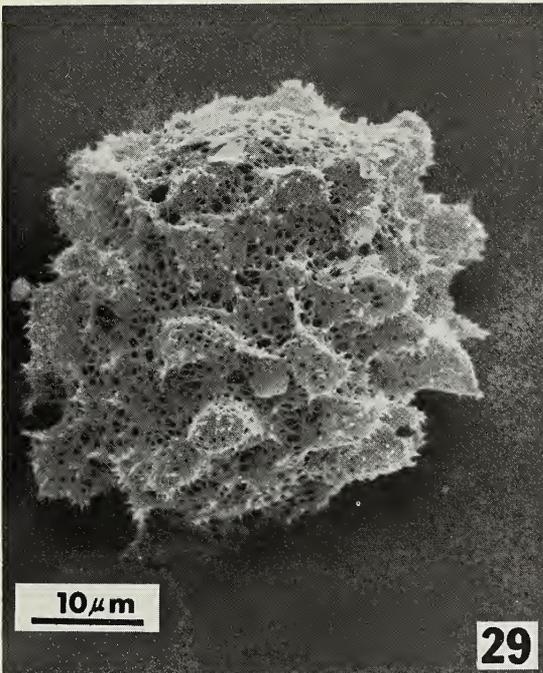


FIG. 28. Typical mid-frond pinnae of *Polystichum setigerum* and *P. braunii*.

The similarity between *Polystichum andersonii* and *P. braunii* has led some authors to regard them as conspecific and to reduce *P. andersonii* to infraspecific status under *P. braunii* (Calder & Taylor, 1965; Hultén, 1968). However, the distinctions between these two species are clear and easy to recognize. *Polystichum braunii* has bipinnate fronds with the pinnae completely dissected into pinnules in the main part of the blade (Fig. 28). Although *P. andersonii* has pinnae that are usually incised to the costa, the segments are adnate to the costa for most, if not all, of their width (Fig. 27). The presence of a proliferous bud on the frond of *P. andersonii* is taxonomically definitive (Maxon, 1918). It is found on all specimens except very young, juvenile plants that are indeterminable unless clearly associated with mature plants in the field. Of over 200 specimens examined, at least one proliferous bud was found on mature specimens. The spores of *P. braunii* are very distinctive and are quite different from the spores of *P. andersonii* (Figs. 29, 30). The morphology of *P. braunii* does not suggest a relationship with *P. munitum*, a condition that should be evident if *P. andersonii* and *P. braunii* were conspecific and the relationships proposed above were accepted. If *P. braunii* is an allotetraploid, as Manton and Reichstein (1961) believed, it is likely that two bipinnate diploids were involved in the original hybridization, and not any one pinnate species.

The other species that has caused confusion among polystichums with divided fronds in the Pacific Northwest is *Polystichum setigerum*. This fern was first collected by Thaddeus Haenke in 1791 at Nootka Sound, Vancouver Island, British Columbia. It was described as a species of *Nephrodium* by Presl in 1825



FIGS. 29–32. Spores and meiocytes of *Polystichum*. FIG. 29. Spore of *Polystichum braunii* (Flory F-254, USFS). FIG. 30. Spore of *Polystichum andersonii* (Macoun, 1914, CAN). FIG. 31. Meta-phase meiocyte of *Polystichum setigerum*, plane of focus showing 121 of the 123 bivalents. FIG. 32. Meiocyte at diakinesis in *Polystichum setigerum* showing normal pairing behavior of chromosomes.

and transferred by him to *Polystichum* in 1836. The name was soon placed in synonymy under *P. aculeatum* (Hooker, 1840) where it has remained unnoticed by North American pteridologists (cf. Christensen, 1906). In 1918 Maxon re-described the species as *P. alaskense*. The species has never been recognized in floristic works, having been variously treated under the epithet *alaskense* as a form, variety, or subspecies of *P. braunii* (C. Christensen in Hultén, 1937; Hultén, 1941; Calder & Taylor, 1965). Excellent illustrations comparing *P. braunii*, *P. andersonii*, and *P. setigerum* (as subspecies of *P. braunii*) are found in Calder and Taylor (1968a).

Polystichum setigerum first came to my attention when a fragment of the type was obtained on loan from the U. S. National Herbarium. When the original material was made available by herbaria in Prague, it was possible to establish that *P. alaskense* was synonymous with *P. setigerum*. Although *P. setigerum* has usually been associated with *P. braunii*, it more closely resembles *P. andersonii*. The most obvious feature distinguishing *P. setigerum* is the lack of a proliferous bud found in *P. andersonii*. *Polystichum setigerum* has the pinnae nearly as deeply divided as in comparably sized specimens of *P. braunii* (Fig. 28), but small specimens of *P. setigerum* are less deeply incised than the largest specimens of *P. andersonii*. It would be difficult to use the degree of incision as a feature for identification without the availability of a complete series of collection of all three species for comparison. The enlarged proximal pinnules on basal pinnae in *P. setigerum*, also found in *P. andersonii*, provide the most useful feature for distinguishing this species from *P. braunii*.

A living plant (*D. Wagner 587*, WS) was obtained from Alice Arm, British Columbia, in 1975. Examination of chromosomes at meiosis showed 123 normal bivalents at metaphase I (Figs. 31, 32). Apogamous triploids showing 123 pairs at meiosis have been reported from the Himalayas, Taiwan, and Japan (Daigobo, 1972, 1973), but no reports of sexually reproducing hexaploids in *Polystichum* have been found. In order to determine the situation in *P. setigerum*, spores were sown on sterilized soil and raised without watering from above, using techniques described by Lovis (1968). When the gametangia were mature (after ca. six weeks), one set of gametophytes was watered from above to promote fertilization while another set was allowed to continue development without free water. After 30 days the gametophytes that had been watered produced numerous sporophytes simultaneously. A year after sowing, the gametophytes raised without free water and were still healthy but showed no signs of apogamous sporophyte production. This evidence indicates that *P. setigerum* is a sexually reproducing hexaploid. The presence of 64 normal spores in each sporangium supports this interpretation.

Although there is no cytological evidence to indicate that *P. setigerum* is of hybrid origin, it seems likely that it has arisen as the result of a cross between *P. munitum* and *P. braunii*, followed by doubling of the chromosome number. Such a process would result in a hexaploid species, and the morphology of *P. setigerum* fits this interpretation. If *P. andersonii* were the tetraploid parent, multivalent formation would be expected and the plant should be less divided than *P. andersonii* rather than more. *Polystichum lonchitis* might be considered as a possibility

for the diploid parent. The hybrid between *P. lonchitis* and *P. braunii*, *P.* × *meyeri*, has been found in Europe (Sleep & Reichstein, 1967). Authentic specimens of this hybrid were provided by Reichstein and are quite different from *P. setigerum*. Sleep (pers. comm.) has synthesized the triploid hybrid *P. braunii* × *munitum*, and had independently reached the conclusion that *P. alaskense* (= *P. setigerum*) originated from such a cross. Additional hybrids among these species will have to be found or synthesized in order to confirm this interpretation. Particular attention to searching for these hybrids should be made in the Queen Charlotte Islands of British Columbia, where *P. braunii*, *P. andersonii*, *P. setigerum*, and *P. munitum* are found in proximity.

THE ORIGIN OF POLYSTICHUM SCOPULINUM

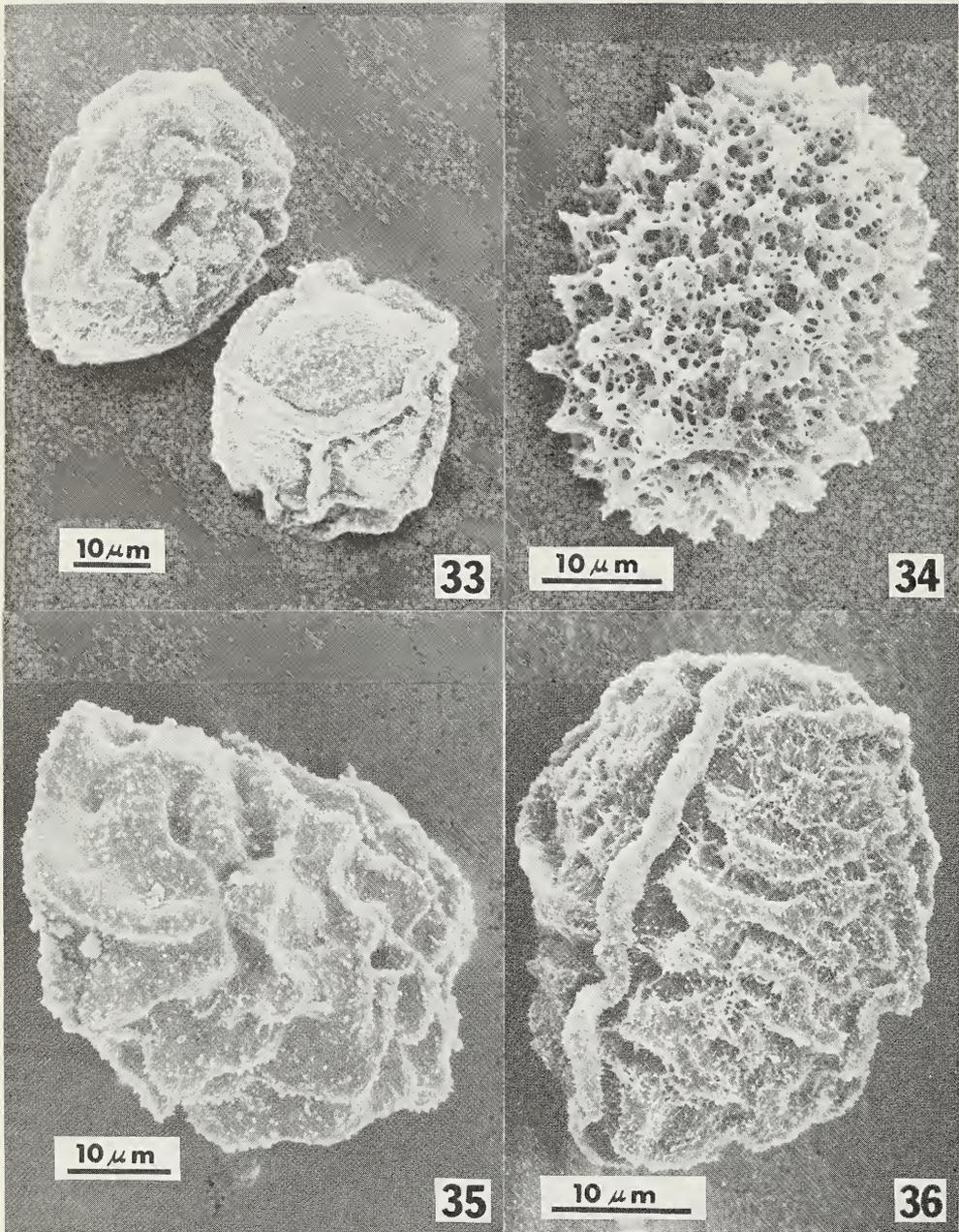
Polystichum scopulinum is one of two amphidiploid polystichums for which *P. munitum sensu lato* had been proposed as a parent (W. Wagner, 1973). The data I have accumulated indicate that *P. imbricans*, and not *P. munitum*, has hybridized with *P. lemmonii* Underw. to produce *P. scopulinum*. This relationship is shown in characters of spore morphology, trichome type, chromatographic pattern, indusium margin, rhizome anatomy, pinna shape, and habitat.

Spores of *Polystichum scopulinum* have very few perforations and vary in perine structure from the appearance of *P. imbricans* spores (Figs. 36, 20), to loose folds or bumps that resemble *P. lemmonii* (Figs. 35, 33). Spores of *P. lemmonii* are very distinctive, having quite smooth or slightly bumpy perines. Under the light microscope, spores of this species appear darker than those of other western polystichums. Scanning electron micrographs confirm the absence of any major ornamentation on the perine. The perine lacks perforations and is not folded into bladders or tight ridges. Variation in spore morphology of *P. scopulinum* is rather remarkable; the significance of the phenomenon is discussed in a later section on *P. kruckebergii*. At this point, the information of interest is that the extreme of variation most unlike *P. lemmonii* resembles *P. imbricans* and not *P. munitum*.

The underside of the pinnae of *Polystichum lemmonii* has very few infralaminar scales, in contrast to the other diploid species in this genus. These scales are largely confined to the costa and are fairly simple in structure, having only short, stout projections at the base of the scale (Fig. 37). The infralaminar scales of *P. scopulinum* are quite similar to those found in *P. imbricans* (Figs. 38, 11). This character is considered to be strong evidence for the relationship between *P. scopulinum* and *P. imbricans*, since in *P. andersonii* the influence of the genome of *P. munitum* in producing arachnoid infralaminar scales is clearly expressed.

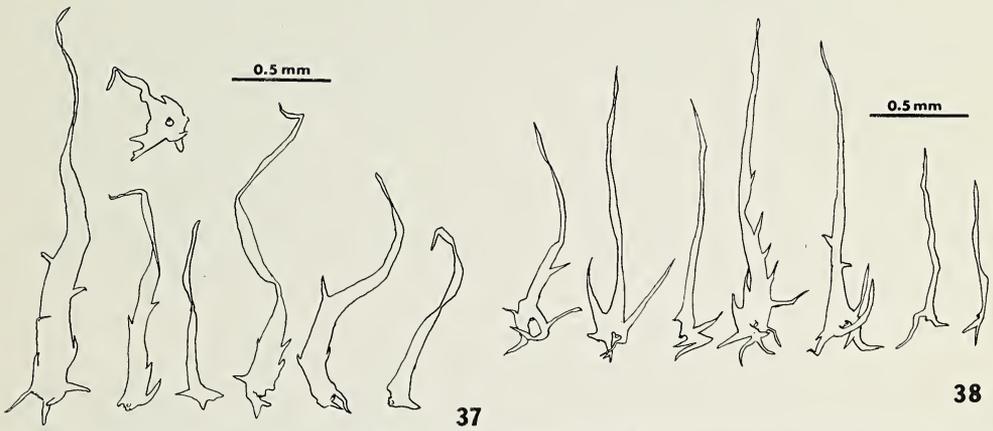
Evidence from features of the margin of the indusium is much like the evidence from infralaminar scales. All three species, *Polystichum lemmonii*, *P. imbricans* and *P. scopulinum*, have entire-margined indusia. If *P. munitum* had a role in the parentage of *P. scopulinum*, one would expect at least short cilia on the edge of the indusia, as in *P. andersonii*.

Corroborative results were obtained from a study of chromatographic patterns of methanolic extracts of the leaves of these ferns. Material from *Polystichum lemmonii* was collected for chromatography at two localities in Washington.



FIGS. 33–36. Spores of *Polystichum*. FIG. 33. *Polystichum lemmonii* from California (Heller 11739, CAS). FIG. 34. *Polystichum mohrioides* var. *elegans* from Chile (von Reutzell in 1939, NO). FIG. 35. *Polystichum scopulinum* from California (Cooke 17611, WS). FIG. 36. *Polystichum scopulinum* from Washington (D. Wagner 458, WS).

Chromatograms were prepared with material of *P. scopulinum* from two localities in Washington and one in southeastern Oregon. The chromatograms of *P. scopulinum* are quite similar to the chromatograms of *P. lemmonii*. Only three spots represent compounds conspicuous in *P. scopulinum* but not detectable in *P. lemmonii*. Unfortunately, these three compounds are detectable in both *P. munitum* and *P. imbricans*. Some quantitative differences can be noted: *P. imbricans* produces much more of these compounds than *P. munitum*. Production of the three compounds in *P. scopulinum* seems to match the levels in *P. imbricans*, but such correspondence is not weighted very heavily in determining relationships.



FIGS. 37-38. Infralaminar scales of *Polystichum*. FIG. 37. *Polystichum lemmonii*. FIG. 38. *Polystichum scopulinum*.

Rhizomes of *Polystichum lemmonii* have sclereid clusters that are not like those found in *P. munitum*. Here, the clusters are very slender and elongate, ca. 0.4×2.0 mm. Although two specimens of *P. scopulinum* were found to have elongated sclereid clusters, eight others lacked them. Since sclereid clusters appear to be universal in the rhizomes of *P. munitum*, any hybrid with another species with sclereid clusters, such as *P. lemmonii*, could be expected to have them also. The situation described here indicates that *P. imbricans* is involved instead, since it is the most likely source of a genome that is characterized by the lack of sclereid clusters in the pith.

The pinna tips provide another feature that indicates *Polystichum imbricans* is related to *P. scopulinum*. *Polystichum lemmonii* is unique among North American polystichums in that its pinnae are entirely non-spinulose. The apices of the pinnae of *P. scopulinum* are occasionally round and entire like *P. lemmonii*, especially in juvenile or dwarf specimens. In most collections, however, the pinna apices of *P. scopulinum* are cuspidate like those in *P. imbricans* subsp. *imbricans* (Fig. 8). The apiculum may be very slender. In all cases, the pinna-tip is obtuse, with small, incurved teeth smaller than the terminal tooth.

The habitats of these ferns provide some support for the relationships proposed here, although such evidence is perhaps better used to explain how the relation-

ship came about. *Polystichum lemmonii* is strictly confined to areas where ultramafic rocks (ferromagnesian rocks called serpentine by most plant ecologists) appear at the surface (Kruckeberg, 1964, 1969). It inhabits crevices in rock outcrops and cavities under boulders of talus slopes in subalpine or occasionally midmontane sites. *Polystichum lemmonii* may be gregarious in these situations and form large clones that spill out from the cracks or from under the host boulder. *Polystichum imbricans* subsp. *imbricans* is mostly encountered on rocky slopes with normal soil chemistry in midmontane areas, below the usual range of *P. lemmonii*.

That *P. imbricans* occasionally is found on serpentine soils in the Siskiyou Mountains of southwestern Oregon and northern California indicates that the hybridization with *P. lemmonii* is in this direction and not with *P. munitum*, which has never been found on serpentine. The habit and habitat of *P. scopulinum* is clearly intermediate between its two putative parents. It occupies more xeric sites than *P. lemmonii* (Thompson, 1931) and has stiffly erect fronds with pinnae oriented as in *P. imbricans*. The rhizome of *P. scopulinum* is frequently more branched than in *P. imbricans*, so that it may form large clones as in *P. lemmonii*. *Polystichum scopulinum* is found both on serpentine soils as well as on normal soils; thus it grows in the two areas characteristic of *P. imbricans* and *P. lemmonii*.

THE ORIGIN OF POLYSTICHUM CALIFORNICUM

Polystichum californicum has been the most problematical species in this study. Warren Wagner presented a preliminary report on its origin in 1963 and a full report in 1973. He concluded that *P. californicum*, a tetraploid, is an amphidiploid derived from a cross between *P. munitum* and *P. dudleyi*. This conclusion was based on cytological studies of all three possible hybrids among these three species, all collected at a single locality. The two triploid backcrosses, showing an equal number of univalents and bivalents at meiosis, suggested a classical case of allopolyploidy, i.e., *P. munitum* and *P. dudleyi* were the obvious choices for diploid parents of the tetraploid *P. californicum*.

Somewhat conflicting results were obtained by Callan (1972), who worked independently on a triploid hybrid between *Polystichum californicum* and *P. imbricans* (treated by Callan as *P. munitum* var. *imbricans*). He found 41 bivalents and 41 univalents at meiosis in the hybrid. Callan was aware of W. Wagner's ideas on the relationships of *P. californicum* (W. Wagner in Hitchcock et al., 1969), but not of the report of a cytological analysis of a *P. californicum* × *munitum* hybrid (W. Wagner in Fabbri, 1963). Assuming *P. imbricans* was merely a variety of *P. munitum*, Callan felt his results corroborated the opinion expressed by W. Wagner in the manual *Vascular Plants of the Pacific Northwest* (Hitchcock et al., 1969). Since my own investigation has demonstrated the distinction between *P. munitum* and *P. imbricans*, Callan's results suggested to me that there were actually two distinct species included under *P. californicum*.

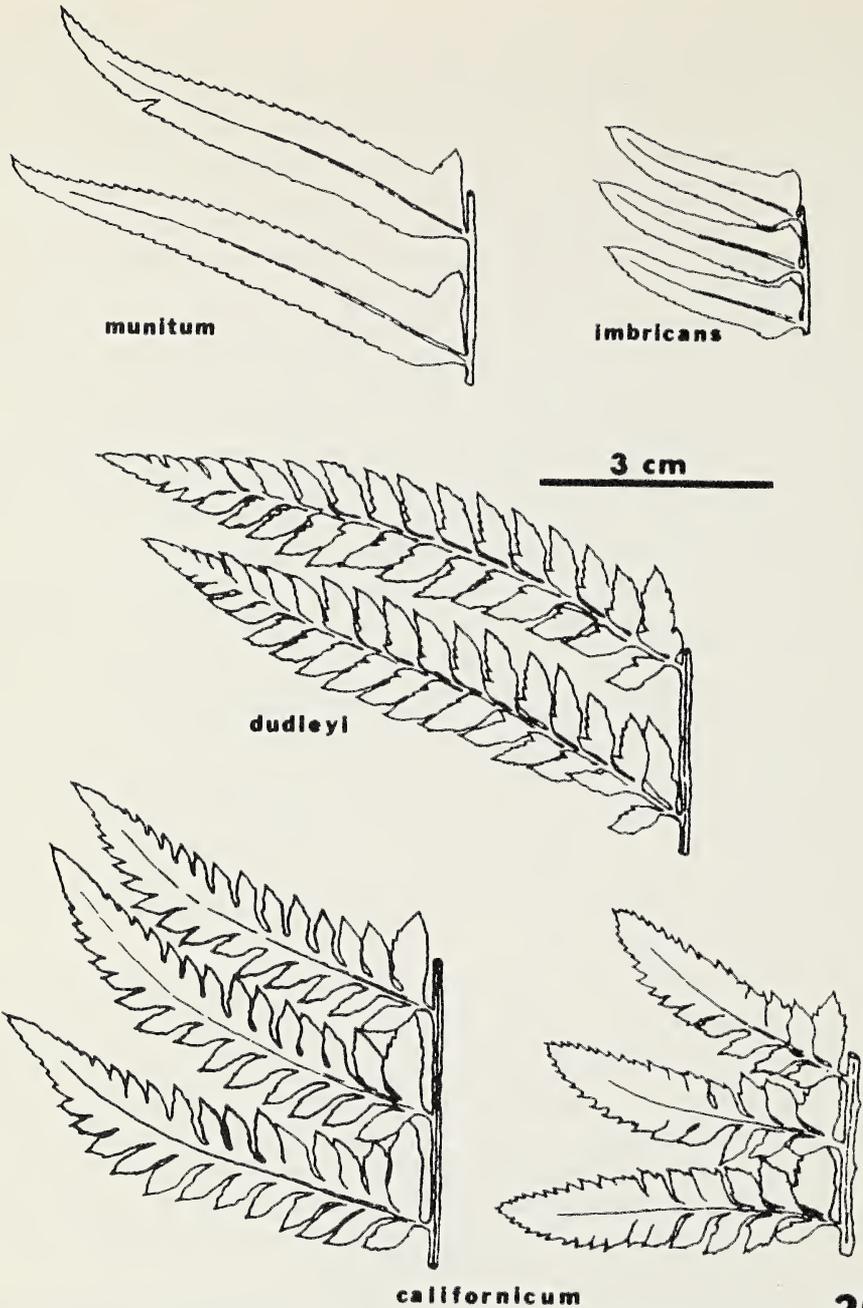
At first it seemed that it would indeed be possible to define distinctions between these hypothetical species. Specimens of *Polystichum californicum* from the

northern part of its range, the northern counties of California through Oregon into Washington, come from more xeric habitats than the material that W. Wagner studied from the redwood zone. Cuspidate pinna tips predominate in these plants, a condition associated with *P. imbricans*, whereas pinnae from specimens originating in the redwood forests have acuminate tips like both *P. dudleyi* and *P. munitum* (Fig. 39). The strikingly different appearance of these plants is demonstrated by recent mis-identifications of these northern populations from British Columbia, Washington, and Del Norte County, California, as *P. scopulinum*. The main characters that distinguish the northern plants from forms of central and southern California are short stature and short, more spinulose pinnae (Fig. 39). Since *P. munitum* and *P. dudleyi* both have relatively long pinnae, the intermediates between these tend to have long pinnae also. The short pinnae in the northern forms might be attributed to influence from the genome of *P. imbricans*. A specimen of *P. californicum* collected in Humboldt County, California, growing with *P. imbricans*, showed a remarkable slenderness in the dwarfed fronds that were produced after the plant had been transplanted into the greenhouse (Fig. 40). These fronds possibly could be mistaken for *P. imbricans*.

As the herbarium study progressed and a full range of specimens was examined, the distinctions between the northern and southern forms proved impossible to maintain. Many collections were encountered that could not be clearly identified with either of the two hypothetical taxa. Size and shape of the pinnae vary imperceptibly from one extreme to the other. Characters that distinguish *Polystichum munitum* from *P. imbricans* are not clearly expressed in *P. californicum*, in which most characters are rather uniform. Surprisingly, the infralaminar scales vary little. All specimens have elongate, filiform scales, much like the hair-like scales of *P. dudleyi* (Fig. 41). However, unlike the simple bases in *P. dudleyi*, these scales have long and angular projections in *P. californicum* (Fig. 42). This condition is unlike either *P. imbricans* or *P. munitum*, although might seem somewhat intermediate between these types.

Chromatograms of specimens of *Polystichum californicum* from Pierce County, Washington, and Humboldt County, California, were compared with those of specimens from a redwood forest near Cazadero, Sonoma County, California. The specimens collected in Humboldt County were from a locality where *P. imbricans* occurred and hybridization was taking place. The Sonoma County locality represented the situation with *P. munitum* and *P. californicum* growing together and hybridizing. Chemical patterns in all specimens of *P. californicum* were quite uniform and generally deviating from *P. dudleyi* in the direction of *P. imbricans*. The significant point is that the patterns are the same: only one chemotype seems to be present in *P. californicum*.

Indusium characteristics are not useful, since *P. dudleyi* has strongly ciliate indusia and this character is expressed in all forms of *P. californicum*. Likewise, the chaffiness of the stipe and rachis shows the influence of *P. dudleyi*, with only certain individuals deviating towards either *P. munitum* in having broad, dark brown scales or towards *P. imbricans* in having narrow, deciduous scales.



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FIG. 39. Representative pinnae from *Polystichum munitum* (D. Wagner 244, WS), *P. imbricans* (D. Wagner 266, WS), *P. dudleyi* (Ashment in 1974, WS), and southern and northern forms of *P. californicum* (left, Sonoma County, California, Skelley in 1973, WS; right, Pierce County, Washington, D. Wagner 328, WS).

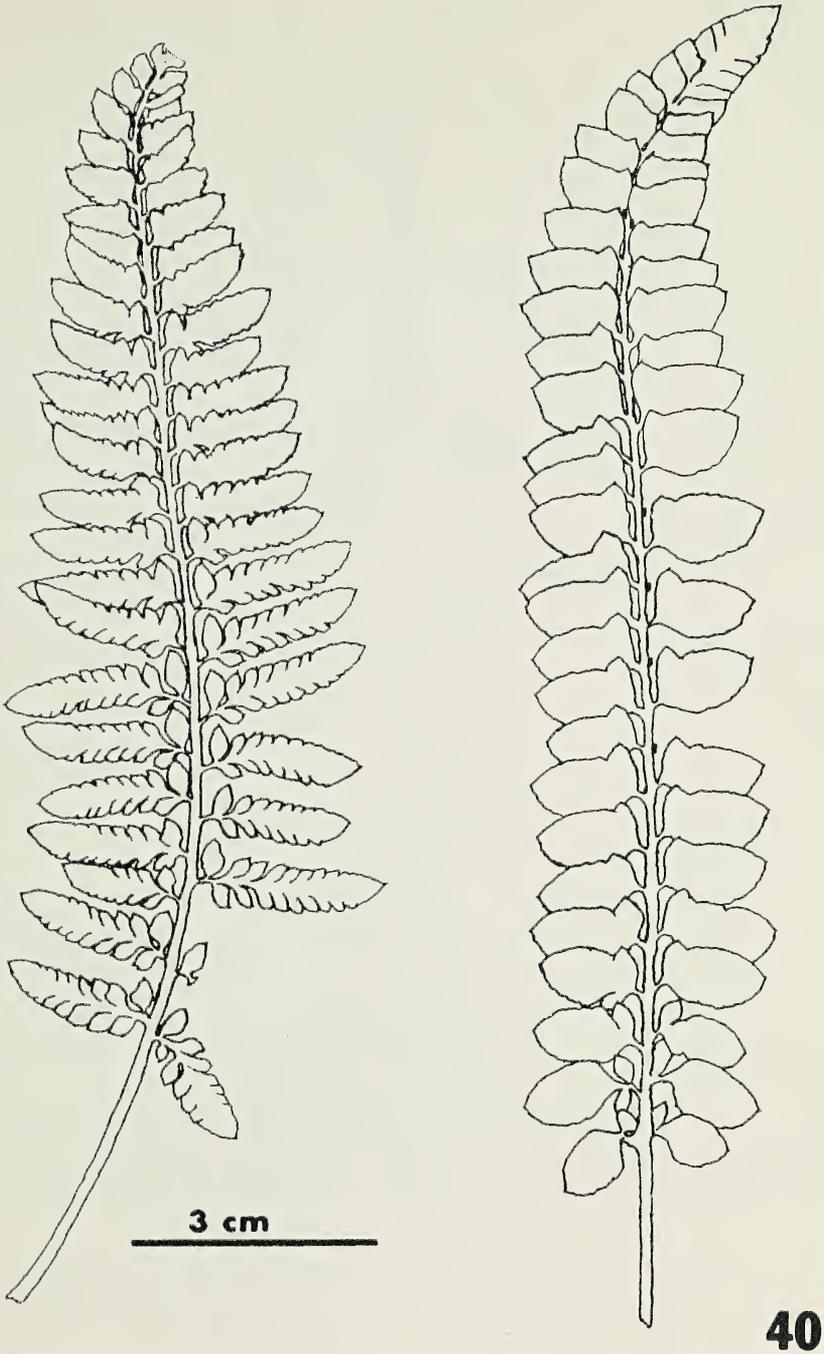
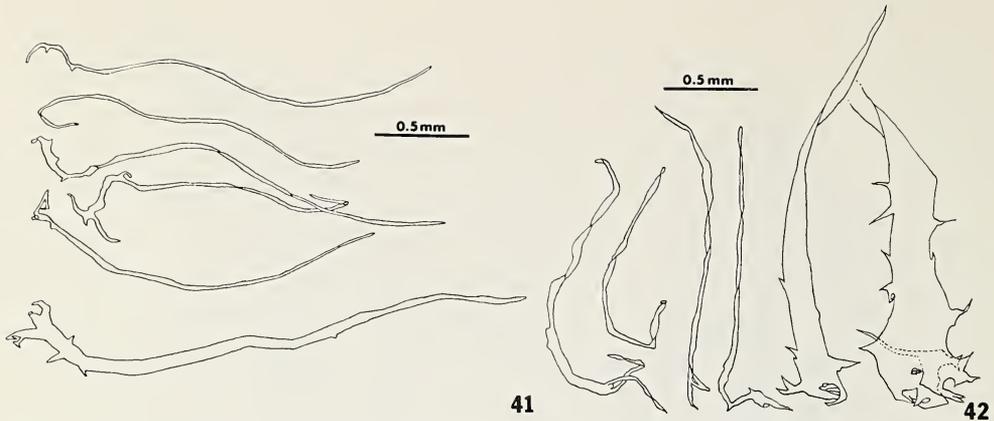


FIG. 40. Fronds of *Polystichum californicum* from Humboldt County, California, grown in a greenhouse. Left, from 1975; right, from 1976 (D. Wagner 697a, WS).



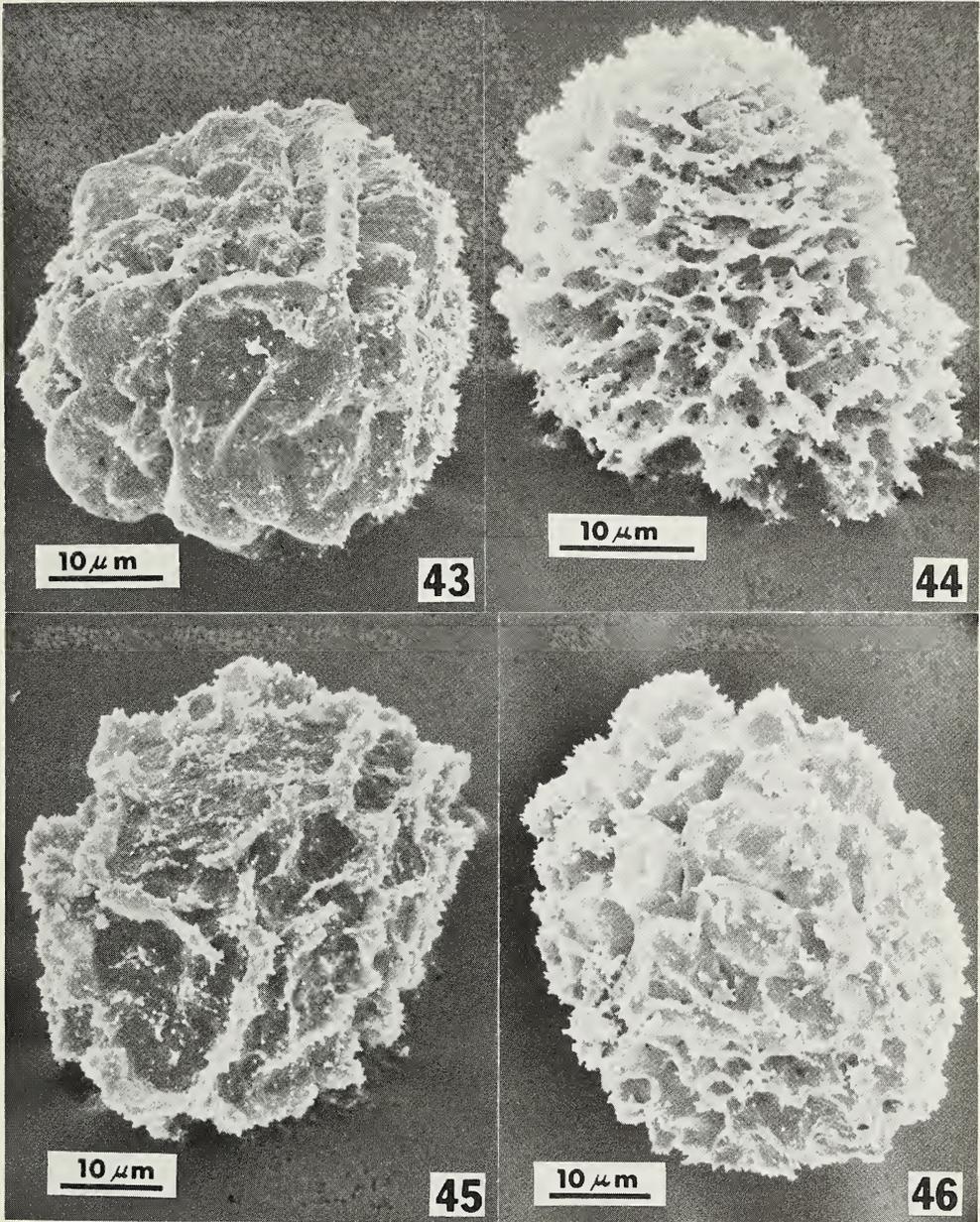
FIGS. 41–42. Infralaminar scales of *Polystichum*. FIG. 41. *Polystichum dudleyi*. FIG. 42. *Polystichum californicum*.

The spore morphology of *P. californicum* shows the influence of two genomes. A specimen (*N. Hall 340*, WS) of *P. californicum* from the redwood region has spores that are unlike any of the possible parents (*Fig. 44*). The toothed, interlocking plates that cover the surface of these spores may possibly be the result of the presence of *P. munitum* genome, the spores of which do have some crests (*Fig. 19*). Spores from a specimen (*D. Wagner 697a*, WS) of *P. californicum* collected in Humboldt County, California, where it was growing with *P. imbricans*, have low, fairly tight folds that are similar to *P. dudleyi* (*Figs. 43, 45*). These are similar to *P. imbricans* also and are compatible with the idea that *P. imbricans* has contributed a genome. A specimen of *P. californicum* from Santa Clara County (*Hesse 2427*, CAS), however, has a morphology intermediate between the two extremes just illustrated (*Fig. 46*).

The results of the study of *Polystichum californicum* are puzzling. Until a more refined analysis of the variation can be performed, the most satisfying interpretation seems to be that both *P. imbricans* and *P. munitum* have hybridized with *P. dudleyi* to produce amphidiploids of great similarity. For the present, in a species-complex where one would expect two tetraploid species, only one polymorphic species can be recognized.

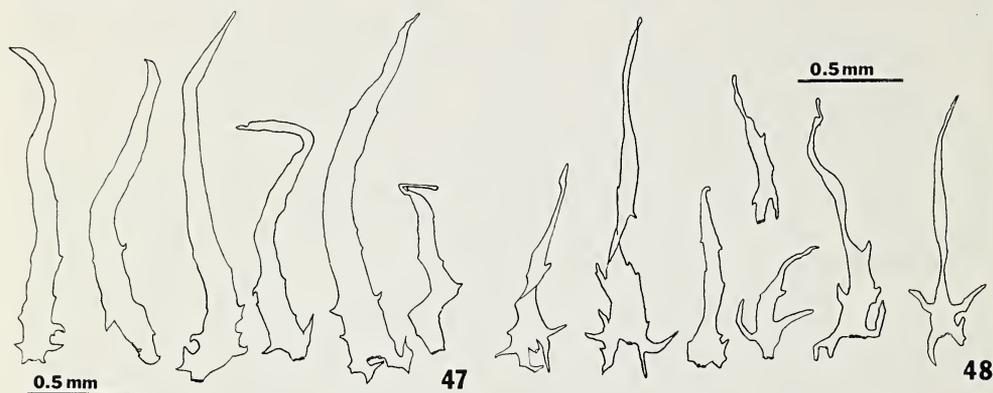
THE ORIGIN OF POLYSTICHUM KRUCKEBERGII

Polystichum kruckebergii is perhaps the most fascinating of the western polystichums, both for its rarity and for its charming habit. Described only recently (*W. Wagner, 1966*), it occupies a position between *P. lonchitis* and *P. lemmonii*. *W. Wagner (1966, 1973)* proposed that *P. kruckebergii* is the amphidiploid between *P. lonchitis* and *P. lemmonii*. None of the sterile hybrids between these three species have been discovered, but the intermediacy of *P. kruckebergii* between *P. lonchitis* and *P. lemmonii* is clear. Morphological characters have been discussed in some detail in previous studies (*W. Wagner, 1966, 1973*).



FIGS. 43-46. Spores of *Polystichum*. FIG. 43. *Polystichum dudleyi* (Leschke, 1946, OSC). FIG. 44. *Polystichum californicum* from Redwood region of California, grown in a garden in Seattle, Washington (Hall 340, WS). FIG. 45. *Polystichum californicum* from Humboldt County, California (D. Wagner 697a, WS). FIG. 46. *Polystichum californicum* from Santa Clara County, California (Hesse 2427, CAS).

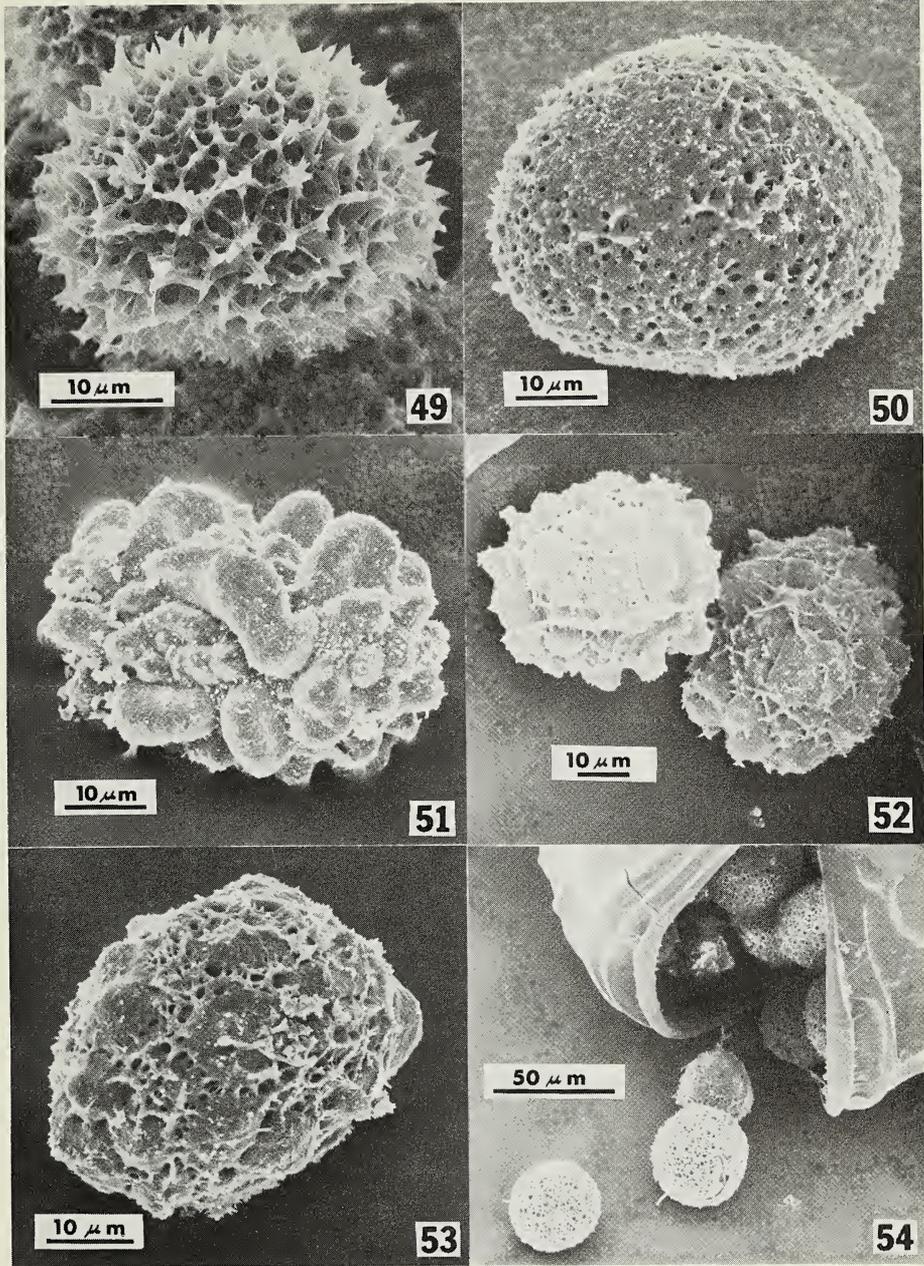
The infralaminar scales of *Polystichum lemmonii*, as described previously, are sparse, confined mainly to the costa, and have a few short, stout basal projections (Fig. 37). *Polystichum lonchitis* normally has a dense indumentum of lanceolate to linear-lanceolate infralaminar scales. In *P. lonchitis* these scales rarely have basal projections and so are often widest above the base (Fig. 47). The infralaminar scales of *P. kruckebergii* show an intermediate condition between *P. lonchitis* and *P. lemmonii*: lanceolate to linear-lanceolate with occasional short, stout, basal projections (Fig. 48), these sparsely scattered along the costa.



FIGS. 47–48. Infralaminar scales of *Polystichum*. FIG. 47. *Polystichum lonchitis*. FIG. 48. *Polystichum kruckebergii*.

The habitat preference of *Polystichum kruckebergii* also shows the influence of the genomes of both *P. lonchitis* and *P. lemmonii*. As mentioned earlier, *P. lemmonii* is a strict serpentiphile in montane forest zones (Kruckeberg, 1969). *Polystichum lonchitis* is found in normal to basic (limestone) areas of temperate subalpine (and boreal) forest zones. *Polystichum kruckebergii* is able to thrive on serpentine soils, but is not confined to them. It is widespread in subalpine forest regions throughout the mountainous western United States and is as frequent in non-serpentine areas as it is on serpentine.

The principle that hybrid forms show intermediate characters does not always help when evidence is sought from spore morphology. *Polystichum lonchitis* is the only species of North American polystichum with a spiny perine (Fig. 49). This is very different from the spore morphology of *P. lemmonii* (Fig. 33). One might expect the spores of a hybrid species combining the genomes of these two species would have easily recognized intermediate morphology. This is indeed the case with many specimens of *P. kruckebergii* (Fig. 50), but occasional specimens are clearly unlike either parent (Fig. 51). I have examined spores from two different plants from Devil's Thumb, Snohomish County, Washington (*D. Wagner* 337, 338, WS), which have different spore types. The most remarkable specimen, however, is the collection by J. W. Thompson from Custer County, Idaho. Here, three distinct spore types were found on a single plant (Figs. 52, 53, 54), apparently only one type found in any given sporangium. It is notable that in this



FIGS. 49–54. Spores of *Polystichum*. FIG. 49. *Polystichum lonchitis* (D. Wagner 331, WS). FIG. 50. *Polystichum kruckebergii* from Snohomish County, Washington (D. Wagner 337, WS). FIG. 51. *Polystichum kruckebergii* from Clallam County, Washington (Thompson 14178, WS). FIG. 52. *Polystichum kruckebergii* from Custer County, Idaho (Thompson 14039, UC). FIG. 53. *Polystichum kruckebergii*, from same specimen as in Fig. 52. FIG. 54. Spores and sporangium of *Polystichum kruckebergii*, from same specimen as in Fig. 52. Note all spores in sporangium are nearly identical.

specimen the three spore types range in similarity from one parent to the other parent. In the previous examples of *P. scopulinum* and *P. californicum* similar patterns of spore morphology have been described. Variation ranging between two parental types is common, and novel types can be found. Spore morphology seems to be an exception to the principle that intermediate characters are found in hybrids.

COMPARISON OF POLYSTICHUM LEMMONII AND P. MOHRIOIDES

Polystichum lemmonii has often been considered conspecific with the South American *P. mohrioides* (Bory) Presl. Fernald (1924), W. Wagner (1973), and Raven (1963) cited *P. mohrioides* as an example of an amphitropical disjunct; Moore (1972) mentioned that this species is also amphi-antarctic. The conspecificity has been in doubt since the Shasta Fern (*P. lemmonii*) was discovered. Daniel C. Eaton, the first pteridologist to see the Shasta Fern, believed it to be distinct (Wheeler, 1937), then immediately retracted his first statement (Eaton, 1879). Both Underwood (1900) and Maxon (1901) believed it was distinct, and Underwood named it after its discoverer, J. G. Lemmon. The common name derives from the fact that on labels of the type collection, Mt. Shasta was listed as the collecting locality. St. John (1942) suggested that this fern was not collected there, but instead across the valley on Mt. Scott or Mt. Eddy. The recent work by Kruckeberg (1964, 1969) demonstrated that *P. lemmonii* is a strict serpentinophile and is unlikely to occur on Mt. Shasta. It has not been collected there since Lemmon's reputed first collection.

In an effort to settle this question of amphitropical conspecificity, I have borrowed specimens identified as *Polystichum mohrioides* from three herbaria: Kew, the Field Museum, and Tulane. I received ferns of three forms identified as *P. mohrioides*. None of these can be conspecific with *P. lemmonii*, although all were considered as such by Fernald (1924), who even included *P. scopulinum* as a variety of *P. mohrioides*. The closest fern is the one identified as *P. mohrioides* var. *elegans* (Remy) C. Chr., type from Chile. Although robust specimens of *P. lemmonii* are similar to this variety in gross morphology, they have three important characters not found in the South American ferns.

Most spectacular is the difference in spore morphology. The spores of *Polystichum lemmonii* have been described (Fig. 33) as having no sculpturing. A scanning electron micrograph of spores from a specimen of *P. mohrioides* var. *elegans* from Río Simpson in Chile (von Reutzell in 1939, NO) shows an elaborately sculptured perine (Fig. 34). These spores do not resemble spores of *P. lemmonii* in any respect.

A second character by which *P. lemmonii* is distinct from *P. mohrioides* is in the nature of the lower stipe and rhizome scales. All forms of *P. mohrioides* examined have black or black-centered scales on the stipe and rhizome. The corresponding scales on *P. lemmonii* are concolorous and pale reddish-brown. Fernald (1924) noted this character but dismissed its significance.

A third character involves the substrate preferences of these ferns. *Polystichum lemmonii* is restricted to ultramafic outcrops, one of the two ferns that have been

described as “faithful indicators” of serpentine-type areas (Kruckeberg, 1964, 1969). *Polystichum mohrioides* var. *elegans* is found on feldspathic granite in Argentina (Eyerdam 23862, F), and andesite and dacitic volcanics in Chile (Gajardo-Michell, pers. comm.).

These three bits of information are sufficiently substantive that the name *Polystichum lemmonii* is recommended for the Shasta Fern of North America. The true extent of the relationships between the North and South American ferns needs further study. Chromosome counts on *P. mohrioides* could provide additional evidence.

SUMMARY OF PHYLOGENETIC CONSIDERATIONS

The previous sections discuss several places where relationships among the polystichums of the western United States have been unclear. All of these results are presented graphically in Fig. 55. Basic species are shown as branches entering from the bottom without specific origins defined. The reticulate nature of evolution in *Polystichum* is depicted by offshoots of these basic species anastomosing

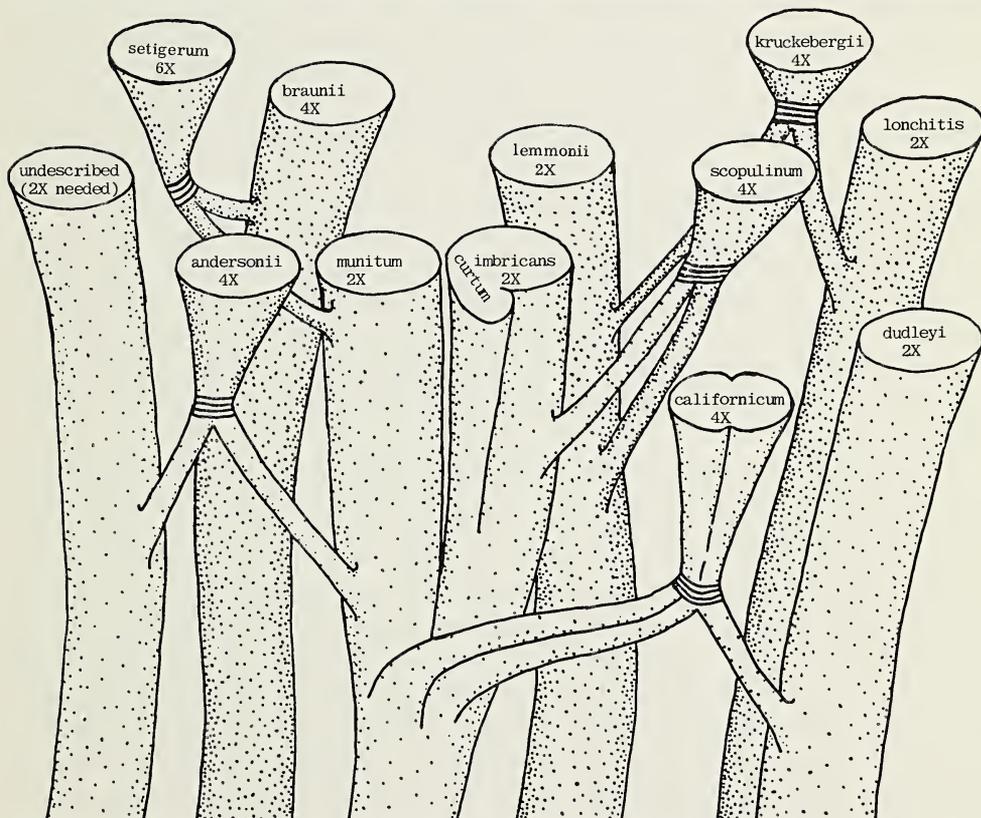


FIG. 55. Hypothetical evolutionary relationships among 12 species of *Polystichum* found in western North America. Undescrbed species predicted diploid. Although depicted as originating from single offshoots, hybridization and doubling of chromosome number presumably occurred repetitively in the past for each of the allopolyploid species.

(hybridizing) and forming independent lines through amphiploidy. Five such amphiploids are represented. Cross-bands immediately above the juncture of the offshoots indicate that a doubling of chromosome number has taken place.

Polystichum munitum and *P. imbricans* are depicted as coming from an immediate common ancestor. Although subsp. *curtum* is shown as a lobe of *P. imbricans*, its morphology indicates that it may be closer to the ancestor than either subsp. *imbricans* or *P. munitum*. *Polystichum imbricans* subsp. *curtum* is intermediate between subsp. *imbricans* and *P. munitum* in habit, pinna shape, size and location of the sorus receptacle on the fertile vein. The clear separation between *P. munitum* and *P. imbricans* indicated at the tips of the branches in Fig. 55 may not be a truly accurate representation of the situation in nature. Despite the cytological evidence from the sterile hybrid found on Mt. Newton, Vancouver Island, there is also some evidence of hybridization without loss of fertility in other areas. I have seen two localities where hybrid swarms seem to occur, one on Vancouver Island in natural vegetation and one in the Columbia River Gorge on a disturbed site. These have not yet been analyzed to see if hybrid segregation is indeed occurring.

The offshoot going to *Polystichum californicum* from the *P. munitum*-*P. imbricans* branch is drawn departing below the divergence of these two species. This interpretation helps to explain why *P. californicum* seems to be a single, polymorphic taxon. The actual situation is undoubtedly more complex than what is drawn, for it is clear that sterile diploid hybrids, such as *P. dudleyi* × *munitum* (W. Wagner, 1973), are still being formed in nature and probably are still undergoing doubling of chromosome number. This means that tetraploids that are fertile continue to be created *de novo* in nature and are capable of contributing to the gene pool of the already established tetraploid species. This phenomenon should be expected wherever two diploid parents of an amphidiploid are found sympatrically. Such a process has not been properly documented, and further study needs to be done to determine if this introgression-like phenomenon indeed takes place in nature.

The notion of dividing the genus *Polystichum* into sections or subgenera (Tagawa, 1940) is attractive because of the convenience of such treatment when dealing with such a large, worldwide genus. If one were to consider western North American species only (excluding Mexico), it seems that three or four sections could be defined. One section would include the once-pinnate species *P. imbricans*, *P. lonchitis*, and *P. munitum*. A second section would contain the twice pinnate, aculeate species *P. braunii* and *P. dudleyi*. *Polystichum lemmonii* would belong in a section of its own on the basis of its unique morphology and substrate preferences. Other members of this section might be found in South America. *Polystichum aleuticum* C. Chr., an endemic on a single island in the Aleutian Archipelago, is in another section, probably with other species from Asia (sect. *Lasiopolystichum* of Daigobo, 1972).

These divisions of *Polystichum* probably represent fairly natural groups, but the validity of such an arrangement breaks down when one attempts to place the amphidiploid species into the scheme. All of the proven hybrid species have

originated from crosses of species in different groups. The system of describing sections of a genus assumes a cladistic evolutionary pattern, but the actual processes are reticulate. Introducing subgeneric categories would probably result in many monotypic sections containing a single amphidiploid, such as seems to occur in the classification of Daigobo (1972).

ECOLOGY AND PHYTOGEOGRAPHY

The distribution of *P. munitum* (Fig. 56) coincides with the boundaries of a vegetation province characterized by *Tsuga heterophylla* or an ecological equivalent as the climax dominant. This *Tsuga heterophylla* province extends, in lower to middle elevations, from southeastern Alaska to central California, where *Sequoia sempervirens* becomes conspicuous in the forest associations (Daubenmire, 1969, 1978). It also occurs on the western slopes of the major mountain ranges of northern Idaho, western Montana and southeastern British Columbia. In the terminology of Krajina (1965) this province includes all of the Coastal Western Hemlock and Interior Western Hemlock Biogeoclimatic Zones and the wetter portion of the Coastal Douglas-Fir Biogeoclimatic Zone. The province encompasses the *Picea sitchensis* Forest Zone and the *Tsuga heterophylla* Forest Zone of Franklin and Dyrness (1973). In California, the communities which may be included in the *Tsuga heterophylla* province are the North Coastal Coniferous Forest, the Redwood Forest, and probably part of the Douglas-Fir Forest (Munz & Keck, 1949, 1950).

Pseudotsuga menziesii, the most valuable timber species of the Pacific Northwest, is an important seral tree in the *Tsuga heterophylla* province and reaches its maximum growth rate in this province. Because of its ubiquitous occurrence in well-drained, moist habitats, the Sword Fern is recognized as an indicator of sites good for timber production throughout much of the Pacific Northwest. In a study of the *Pseudotsuga*-producing areas of western Washington and Oregon, Becking (1954) mentioned that the Sword Fern-Douglas Fir type group distinguished by a dominance of *Polystichum munitum* in the understory "in general . . . includes all the better sites of the Douglas Fir forests." A report on a similar study on Vancouver Island contains the statement, "The largest trees and highest volumes per acre of any stand were recorded in the *Pseudotsuga*-*Polystichum* plots" (McMinn, 1960). In the poorer sites, the *Polystichum* was replaced by *Gaultheria shallon*. High timber productivity is again associated with *Polystichum munitum* in the subalpine forests of the *Abies amabilis* Zone in the Cascade Mountains of southwestern Washington. The poorer (drier) sites here have *Xerophyllum tenax* becoming conspicuous in the understory (Franklin, 1966).

The *Pseudotsuga menziesii* province lies along the drier, inland margins of the *Tsuga heterophylla* province. In these areas, which are too dry for *Tsuga heterophylla*, *Pseudotsuga menziesii*, or an ecological equivalent, is climatic climax (Daubenmire, 1978). *Polystichum imbricans* is widespread throughout this province and largely is confined to outcrops and rock mulch soils. Particularly notable in the northern part of this province, in British Columbia, Washington and Oregon, is the presence of *Quercus garryana* as a seral species. *Polystichum*

imbricans is found with *Quercus garryana* on Vancouver Island, in the Columbia River Gorge, and in the Willamette and other interior valleys of Oregon. On the eastern slopes of the Cascade Mountains in Washington, *Polystichum imbricans* is found with *Pinus ponderosa*, another seral species in this province. However, *Pseudotsuga* is always present in these forests and will ultimately assume dominance (Daubenmire, 1978). *Polystichum imbricans* is listed as occurring in the Mixed Evergreen Forest of southwestern Oregon (Franklin & Dyrness, 1973). Label data indicate that *P. imbricans* occurs in the following communities in California: Mixed Evergreen Forest, Northern Oak Woodland, Yellow Pine Forest, Red Fir Forest, and Subalpine Forest (Munz & Keck, 1949, 1950). The ability of *P. imbricans* to grow in serpentine areas has been mentioned; it has been collected from such areas in southwestern Oregon and northwestern California. The distribution and habitat of *P. imbricans* (Figs. 57, 58) and especially of *P. californicum* (Fig. 59) suggest that they are members of a Californian floristic element that occupies Mediterranean climatic areas west of the Cascade Mountains (Schofield, 1969). One interpretation of the disjunct populations of the northern form of *P. californicum* in Washington and British Columbia is that they migrated into the area during the Hypsithermal Interval and are now relicts barely surviving a cooler period.

Polystichum lonchitis is a montane-boreal species found throughout the northern parts of the northern hemisphere. It is found near sea level in southeastern Alaska, but is mostly confined to subalpine forest zones south of Canada. *Polystichum lonchitis* is found much further south in the Rocky Mountains than in the Sierra Nevada (Fig. 63). *Polystichum lonchitis*, unlike *P. munitum*, is rarely mentioned in vegetation studies since it is a rupicolous fern. This means that, like many ferns, it occurs in special microhabitats that represent discontinuities in the surrounding vegetation on normal soils, and thus is ignored by forest ecologists.

The importance of *Polystichum lemmonii* in serpentine vegetation has been documented by a relevé technique (Kruckeberg, 1969). It is notable that this serpentinophile occurs both in the mesic subalpine forest zone of the western Cascade Range of Washington and also in the drier and certainly much hotter valleys of the Wenatchee and Siskiyou Mountains (Fig. 60). *Polystichum scopulinum* and *P. kruckebergii*, both amphidiploid species possessing a genome of *P. lemmonii*, are capable of growing in serpentine areas. Each seems to be just as likely to occur in nonserpentine areas, and so these two species, like *P. imbricans*, may be called *bodenvag* plants (Kruckeberg, 1951). The ranges of these two amphidiploid species (Figs. 61, 62) are far more extensive than that of *P. lemmonii* itself. *Polystichum scopulinum* and *P. kruckebergii* occur throughout the Cascade, Sierra, and Rocky Mountains, and both have sporadic, if not disjunct, distributions. *Polystichum kruckebergii* seems to be rare everywhere, whereas *P. scopulinum* is quite abundant in the serpentine areas where *P. lemmonii* is found. *Polystichum scopulinum* is well known for its occurrence on Mt. Albert on the Gaspé Peninsula, Quebec (Scoggan, 1950). Here, 2,400 miles from the nearest part of its western range, it seems to represent an example of west to east long-distance spore transport (W. Wagner, 1972). The occurrence of *P. munitum* in

South Dakota is a similar, though less dramatic, example of the same phenomenon. Remarkably, on Mt. Albert *P. scopulinum* again grows on serpentine (Scoggan, 1950).

Three of the polystichums occur primarily in regions covered by ice during the most recent glaciation of the Pleistocene: *P. andersonii*, *P. braunii* and *P. setigerum* (Figs. 64, 65, 66). The undescribed species parental to *P. andersonii* belongs in this phytogeographic group and is presumed to occur in similar habitats. All occupy mesic, shady habitats in lowland and lower to middle montane forests. They are frequently found in crevices of stabilized boulder-talus or rocky areas under deciduous hardwoods such as *Acer macrophyllum*, *A. circinatum* or *Alnus rubra*. Although *P. andersonii* is presently found south of the greatest extent of the continental ice-sheet, all of these southern localities are in or near drainages occupied by extensive valley glaciers during the Pleistocene. Calder and Taylor (1968a) suggested that *P. jenningsii* Hopkins (type from Mount Rainier, Washington) may represent a distinct race of *P. andersonii* endemic to the Cascades, but, as noted by Maxon (1920) its distinctness was shown to be unfounded as additional collections of *P. andersonii* became known.

The remaining three species of *Polystichum* have restricted ranges in western North America. *Polystichum aleuticum* is known only from the type collection from Atka Island in the Aleutian Archipelago. *Polystichum microchlamys* has been collected several times on Attu, the westernmost island of the Aleutian Archipelago, but has mainly a northeast Asian distribution (Sleep, 1971). *Polystichum dudleyi* is restricted to coastal central California (Fig. 67), where it grows in moist, shady canyons.

TAXONOMY

Polystichum Roth, Tent. Fl. Germ. 3:31, 69. 1799.

Rhizomes stout, erect to decumbent, usually much branched in older plants, densely clothed in old stipe bases that are mostly living and modified for storage. Stipes shorter than the blades, and, with the rhizomes, bearing large, chaffy, dark brown (black) to light reddish brown scales. Blades usually dark green, evergreen, pinnate, bipinnatifid, bipinnate to tripinnatifid (rarely more divided), in most species spinulose toothed and furnished to a greater or lesser extent with reddish-brown to pale brown scales. Pinnae mostly linear-lanceolate, falcate, auricled at the base. Sori circular, indusium peltate. Spores bilateral, invested with a perine that is usually elaborately ornamented. $x=41$.

KEY TO THE TAXA OF POLYSTICHUM IN WESTERN NORTH AMERICA

1. Fronds pinnate, the pinnae entire, denticulate, or serrate, spinulose . . . 2.
1. Fronds bipinnatifid to bipinnate, the pinnae lobed, incised, or pinnate, spinulose or not . . . 5.
2. Lowest pinnae subtriangular to broadly trowel-shaped, symmetrical; all pinnae spreading spinulose; stipe length less than one-tenth of the frond; spores spiny; boreal and subalpine.
 9. *P. lonchitis*
2. Lowest pinnae ovate to lanceolate-falcate, auriculate, asymmetrical; pinnae incurved spinulose; stipe length more than one-tenth of the frond; spore perine folded to bumpy, lacking spines . . . 3
3. Stipe and rachis persistently chaffy; scales on abaxial side of rachis ovate-lanceolate, greater than 1 mm wide; indusium ciliate; pinnae acuminate, lacking an apiculum at the apex, cuneate at the base.
 11. *P. munitum*
3. Stipe and rachis often naked; scales on abaxial side of rachis linear to linear-lanceolate, less than 1 mm wide; indusium entire to sharply toothed; pinnae cuspidate or apiculate at the apex, oblique at the base . . . 4.
4. Pinnae short, less than 5 times longer than wide; fronds usually stiffly erect; pinnae folded inwards and horizontally oriented; under boulders in semi-exposed, drier sites of mesic montane forests.
 - 6a. *P. imbricans* subsp. *imbricans*
4. Pinnae long, more than 5 times longer than wide; fronds plane and arching; on shady woodland floor of mixed-evergreen forests in the Pacific Southwest.
 - 6b. *P. imbricans* subsp. *curtum*
5. Pinnae not at all spinulose, endemic to serpentine areas of the Pacific Northwest.
 8. *P. lemmonii*
5. Pinnae apiculate to spinulose . . . 6.
6. Fronds clearly bipinnate, the pinnules distinct, sessile or petiolate . . . 7.
6. Fronds bipinnatifid, the pinnules adnate to the costa for at least 2 mm, usually connate . . . 9.
7. Fronds with a proliferous bud on the rachis; expected along northern coast of British Columbia . . . (undescribed Alice Arm diploid)
7. Fronds lacking a proliferous bud on the rachis . . . 8.
8. Fronds dark green, narrowed at the base, the basal pinnae ca. one-third the length of the middle pinnae; boreal.
 3. *P. braunii*
8. Fronds light green, not conspicuously narrowed at the base, the basal pinnae ca. one-half the length of the middle pinnae; endemic to central and southern California.
 5. *P. dudleyi*
9. Pinnae lacking filiform scales on either surface . . . 10.
9. Pinnae with filiform scales, conspicuous on the lower surface . . . 12.
10. Scales prominent on both upper and lower surface of the fronds, endemic to Atka Island.
 1. *P. aleuticum*
10. Scales prominent on lower surface of the fronds, if at all . . . 11.
11. Pinnae acute at the apex, especially at the base of the blade, and armed with coarse (visible without magnification), spreading teeth.
 7. *P. kruckebergii*
11. Pinnae obtuse at the apex, occasionally cuspidate, and armed with fine, incurved teeth.
 12. *P. scopulinum*
12. Fronds with a proliferous bud on the rachis usually one-third of the way down from the tip; occasional in the Pacific Northwest as far south as Oregon.
 2. *P. andersonii*
12. Fronds lacking a proliferous bud . . . 13.
13. Pinnae not incised to the costa, the pinnules (except the auricle) connate for at least one-fourth their length; mostly Californian, but extending sporadically into Oregon, Washington, and British Columbia.
 4. *P. californicum*
13. Pinnae incised to the costa, the pinnules scarcely connate . . . 14.

14. Pinnules deeply incised; disjunct on Attu Island, mainly a species of northeastern Asia.

10. *P. microchlamys*

14. Pinnules slightly toothed but not incised; rare along the northern Pacific coast.

13. *P. setigerum*

1. *Polystichum aleuticum*

Polystichum aleuticum C. Chr. in Hultén, Svensk. Bot. Tidskr. 30:515, f. 1a. 1936.—TYPE: Aleutian Islands, Atka, 5 Jul 1932, W. J. Eyerdam 1086 (S, not seen; isotypes CAS, DS, US).

Rhizomes apparently erect; fronds 10–15 cm, linear-lanceolate; stipe one-third of the frond; pinnae ovate, 4–8 mm, relatively symmetrical, slightly overlapping, gradually reduced below; the largest pinnae incised one-half or less; pinna-apex and pinna-teeth rounded, short bristle-tipped; all parts abundantly provided with linear, broad-based, pale brown scales. Known only from the type collection.

ILLUSTRATION: Hultén (1968, p. 53).

2. *Polystichum andersonii*

Polystichum andersonii Hopkins, Amer. Fern J. 3:116, pl. 9. 1913.—*Polystichum braunii* (Spencer) Fée var. *andersonii* (Hopkins) Hultén, Ark. Bot., n.s. 7:5. 1968.—*Polystichum braunii* subsp. *andersonii* (Hopkins) Calder & Taylor, Canad. J. Bot. 43:1388. 1965.—TYPE: Canada, British Columbia, Vancouver Island, Strathcona Park, Elk River, 2 Aug 1912, J. M. Macoun (CAN).

Polystichum jenningsii Hopkins, Ann. Carnegie Mus. 11:362, pl. 37. 1917.—TYPE: Washington, Mount Ranier National Park, 18 Aug 1915, O. E. & G. K. Jennings 9960 (CM, not seen).

Rhizomes erect on forest floor; mature fronds ca. 50–100 cm long, lanceolate or narrowly lanceolate, often narrowed at the base with subtriangular lowermost pinnae, these usually at right angles to the rachis; stipe of medium length, persistently chaffy; pinnae cut to the costa but the segments rarely undercut; pinna segments spinulose toothed, scaly on both surfaces with filiform scales, scales on the costae and rachis broader; proximal acroscopic pinnule enlarged throughout, both proximal pinnules enlarged on lowest pinnae; one or more proliferous buds on the rachis in all but juvenile specimens; $n=82$.

ILLUSTRATIONS: Abrams (1923, p. 12) Hitchcock et al. (1969 p. 88.)

DISTRIBUTION: Lowland coastal forests from the Alaska panhandle to Mount Jefferson in Oregon; interior moist forests of southeastern British Columbia, northern Idaho and western Montana (Fig. 64).

3. *Polystichum braunii*

Polystichum braunii (Spencer) Fée, Mém. Fam. Foug. 5:278. 1852.—*Aspidium braunii* Spenser, Fl. Friburg. 1:9. 1825.—*Dryopteris aculeata* var. *braunii* (Spencer) Underw. Our Native Ferns, ed. 4. 112. 1893.—*Dryopteris braunii* (Spencer) Underw. in Britton & Brown, Ill. Fl. North. U. S. 1:15. 1896.—*Aetopteron braunii* (Spencer) House, Amer. Fern J. 10:88. 1920.—TYPE LOCALITY: Europe (FB, not seen).

Polystichum braunii var. *purshii* Fernald, Rhodora 30:30, pl. 159. 1928.—*Polystichum braunii* subsp. *purshii* (Fernald) Calder & Taylor, Canad. J. Bot. 43:1388. 1965.—TYPE: Vermont, Smuggler's Notch, 9 Aug 1877, C. E. Faxon (GH, not seen).

Rhizomes erect on forest floor; mature fronds ca. 50–100 cm long, broadly lanceolate, narrowed at the base; stipe of medium length, persistently chaffy; pinnae slenderly lanceolate; middle and upper pinnae gradually tapering, falcate; lower pinnae straight sided, abruptly tapering to the apex; pinnae generally 1-pinnate, the pinnules petiolate or rarely slightly decurrent, basal pinnules not enlarged (at least on lowest three or four pairs of pinnae); pinnules short falcate to oblique-rhombic, toothed with slender bristle-tips on the teeth; laminar scales all filiform or (in var. *purshii*) some broad-based and linear, broader scales on the costae and rachis; $n=82$.

ILLUSTRATIONS: Hultén (1968 p. 54, as var. *alaskense*); Taylor (1970, p. 176).

DISTRIBUTION: Circumboreal, south along the coast of western North America as far as the Squamish River, British Columbia, and in the interior forests of southeastern British Columbia and northernmost Idaho (*Fig. 65*).

4. *Polystichum californicum*

Polystichum californicum (D. C. Eaton) Diels, Nat. Pflanzenf. 1(4):191. 1899.—*Aspidium californicum* D. C. Eaton, Proc. Amer. Acad. Arts 6:555. 1865.—*Aspidium aculeatum* var. *californicum* (D. C. Eaton) D. C. Eaton in Wheeler, Rep. U. S. Geogr. Surv. 100th Merid. 6:336. 1878.—*Dryopteris aculeata* var. *californica* (D. C. Eaton) Underw., Our Native Ferns, 4th ed. 112. 1893.—*Aetopteron californicum* (D. C. Eaton) House, Amer. Fern J. 10:88. 1920.—*Polystichum aculeatum* var. *californicum* (D. C. Eaton) Jepson, Man. Fl. Pl. Calif. 36. 1923.—TYPE: "Deep gulch on the west descent of the Mts. near Santa Cruz (Bean's Ranch)," Jun 1864, H. N. Bolander (YU; isotype GH).

Rhizomes erect on forest floor or in rocky crevices; fronds 40–75 cm long, linear-lanceolate to lanceolate, hardly narrowed at the base in typical forms; stipes often rather long, more than one-third of the frond, with a deciduous ramentum above; pinnae deeply cut, the segments often slightly undercut and overlapping, with sparse to thick, filiform hairs below and along the costa above; indusia ciliate; $n=82$.

ILLUSTRATIONS: Abrams (1923, p. 11); Hitchcock et al. (1969, p. 88)

DISTRIBUTION: Lowland forests near the coast from central California (sporadically from Mendocino County) to southern British Columbia (*Fig. 59*).

5. *Polystichum dudleyi*

Polystichum dudleyi Maxon, J. Wash. Acad. Sci. 8:620. 1918.—*Polystichum aculeatum* var. *dudleyi* (Maxon) Jepson, Man. Fl. Pl. Calif. 36. 1923.—TYPE: "Near bridge, Peter's Creek, Santa Cruz Mts.," 2 May 1903, W. R. Dudley (US; isotypes DS, MO).

Rhizomes erect on forest floor; fronds 50–100 cm long, broadly lanceolate, scarcely narrowed at the base; stipes of medium length to fairly long, one-third of the frond, persistently chaffy; pinnae 1-pinnate, the segments petiolate, spinulose-toothed, often with the proximal pinnules enlarged and incised, densely clothed with filiform scales on both surfaces; indusia ciliate; $n=41$.

ILLUSTRATION: Abrams (1923, p. 12).

DISTRIBUTION: Confined to coastal central California, from San Luis Obispo County to Marin and Napa Counties (*Fig. 67*).

6a. *Polystichum imbricans* subsp. *imbricans*

Polystichum imbricans (D. C. Eaton) D. H. Wagner, *comb. et stat. nov.*, subsp. *imbricans*.—Based on *Aspidium munitum* var. *imbricans* D. C. Eaton in Wheeler, Rep. U. S. Geogr. Surv. 100th Merid. 6:335. 1878.—*Polystichum munitum* var. *imbricans* (D. C. Eaton) Maxon, Fern Bull. 8:30. 1900.—*Polystichum munitum* f. *imbricans* (D. C. Eaton) Broun, Index No. Amer. Ferns. 149. 1938. (Broun incorrectly ascribed this combination to Clute. It is clear from the context that Clute (1907) used the word "form" in a nontaxonomic sense).—*Polystichum munitum* subsp. *imbricans* (D. C. Eaton) Munz, Fl. So. California 21. 1974.—LECTOTYPE (chosen here): California, Plumas Co., Mill Creek, 1877, Mrs. R. M. Austin (YU).

Aspidium munitum var. *nudatum* D. C. Eaton in Wheeler, Rep. U. S. Geogr. Surv. 100th Merid. 6:335. 1878.—*Polystichum munitum* var. *nudatum* (D. C. Eaton) Gilbert, List No. Amer. Pterid. 20. 1901.—*Polystichum munitum* f. *nudatum* (D. C. Eaton) Broun, Index No. Amer. Ferns. 148. 1938.—*Polystichum munitum* subsp. *nudatum* (D. C. Eaton) Ewan, Amer. Fern J. 32:100. 1942.—TYPE: California, Yosemite, Nevada Falls, Sep 1866, A. Wood (YU; isotype MO).

Medium sized ferns in rocky areas with decumbent rhizomes under boulders or crevices in outcrops; fronds 25–50 cm long, linear-lanceolate, narrowed by the pinnae folded inwards and twisted horizontally, the fronds non-planar; stipes of medium length, one-fourth to one-third of the frond, with narrow, deciduous scales above; pinnae short-lanceolate, scarcely falcate, entire, often pungently spinulose, the apex mucronate, the base oblique; sori medial or slightly closer to the margin; indusia entire; $n=41$.

ILLUSTRATIONS: Abrams (1923, p. 10); Hitchcock et al. (1969, p. 92).

DISTRIBUTION: Southern California to southern British Columbia, mostly along the Sierra-Cascade axis, with a single record from the Willowa Mountains of Oregon (*Fig. 57*).

6b. *Polystichum imbricans* subsp. *curtum*

Polystichum imbricans subsp. *curtum* (Ewan) D. H. Wagner, *comb. nov.*—Based on *Polystichum munitum* subsp. *curtum* Ewan, *Amer. Fern J.* 32:99. 1942.—TYPE: California, San Bernardino Co., San Bernardino Mts., Sawpit Canyon, 7 Sep 1931, *J. Ewan 5159* (NO; isotypes CAS, DS, RM).

Like subsp. *imbricans*, except larger, the fronds to ca. 80 cm, more nearly planar; pinnae slender, lanceolate, and falcate; sori conspicuously submarginal; indusia often toothed but not ciliate; $n=41$.

DISTRIBUTION: Central to southern California, from the Santa Lucia Mountains to San Diego County, mostly inland from the coast, to fairly high elevations in the mountains, occasionally in the central Sierra Nevada (*Fig. 58*).

7. *Polystichum kruckebergii*

Polystichum kruckebergii W. H. Wagner, *Amer. Fern J.* 56:4. 1966.—TYPE: Canada, British Columbia, trail to Mt. McLean at Lillooet, 5100 ft, 6 Sep 1954, *J. A. Calder 15550*, with D. B. O. Savile and J. M. Ferguson (WTU; isotypes DAO, NY, RM, UC, US, WS).

Small ferns, the fronds 10–25 cm long, linear-lanceolate; stipes stramineous, usually very short, one-tenth of the frond, sparsely chaffy with pale tan scales; pinnae (entire to) incised, conspicuously spreading toothed, occasionally spinulose, the apex acute, the terminal tooth hardly larger than the subadjacent teeth; pinnae reduced below; indusia entire; $n=82$.

ILLUSTRATION: Hitchcock et al. (1969, p. 90)

DISTRIBUTION: From south-central British Columbia sporadically to San Diego County, California, west to the Steens Mountains of Oregon and the Rocky Mountains in Montana, Idaho and Utah (*Fig. 62*).

8. *Polystichum lemmonii*

Polystichum lemmonii Underw. *Our Native Ferns*, 6th ed. 116. 1900, as “lemmoni.”—*Aetopteron lemmonii* (Underw.) House, *Amer. Fern J.* 10:88. 1920. *Polystichum mohrioides* (Bory) C. Presl var. *lemmonii* (Underw.) Fernald, *Rhodora* 26:92. 1924.—LECTOTYPE (Wheeler, 1937): California, near Mount Shasta, Jul 1879, *J. G. Lemmon* (NY).

Polystichum mohrioides auctt. *amer. non* (Bory) C. Presl, *Tent. Pterid.* 83. 1836.

Small to medium sized ferns, the fronds 15–35 cm long, only slightly narrowed at the base; stipes medium length, ca. one-fifth of the blade, stramineous, sparsely chaffy with pale tan scales; pinnae divided into rounded or denticulate pinnules, never spinulose; indusia entire; $n=41$.

ILLUSTRATIONS: Abrams (1923, p. 10); Hitchcock et al. (1969, p. 90).

DISTRIBUTION: On serpentine soils from the northern Cascades in Washington to Placer County, California. Apparently absent from the Rocky Mountains; isolated in the southern Blue Mountains of eastern Oregon (*Fig. 60*).

9. *Polystichum lonchitis*

Polystichum lonchitis (L.) Roth, Tent. Fl. Germ. 3:71. 1799.—*Polypodium lonchitis* L. Sp. Pl. 2:1088. 1753.—*Aspidium lonchitis* (L.) Swartz, J. Bot. (Schrader) 1800(2): 37. 1802.—*Dryopteris lonchitis* (L.) O. Kuntze, Rev. Gen. Pl. 2:813. 1891.—*Aetopteron lonchitis* (L.) House, Amer. Fern J. 10:88. 1920.—TYPE: Europe, with "Lonchitis" in the hand of Linnaeus (LINN 1251.14, not seen).

Medium sized ferns, mature plants often with dwarfed fronds; the fronds 10–60 cm long, slender; stipes very short, one-tenth of the frond, persistently chaffy with light brown scales; pinnae entire, falcate in the upper part of the frond (except trowel-shaped in dwarfed specimens in exposed places), these the fertile pinnae; lower pinnae reduced, trowel-shaped to subtriangular; pinnae spreading spinulose throughout, with abundant pale scales below; indusia entire; $n=41$.

ILLUSTRATIONS: Abrams (1923, p. 9); Hitchcock et al. (1969, p. 90); Hultén (1968, p. 53).

DISTRIBUTION: Circumboreal, south along the mountain chains in western North America to Alpine County, California, and Graham County, Arizona; abundant only in the northern part of the range (Fig. 63).

10. *Polystichum microchlamys*

Polystichum microchlamys (Christ) Matsumura, Index Pl. Jap. Enum. Pl. Omn. 1:343. 1904.—*Aspidium microchlamys* Christ, Bull. Herb. Boissier 7:820. 1899.—TYPE: Japan, Tidesan, *Faurie 1508* (P, not seen).

Aspidium aculeatum Sw. var. *lobatum* Yabe & Yendo, Bot. Mag. (Tokyo) 18:167. 1904 (*non* Kunze, 1848).—TYPE: apparently lost (Sleep, 1971).

Polystichum braunii (Spencer) Fée var. *kamtschaticum* C. Chr. in Hultén, Fl. Kamtchatka. 38, t. 2. 1927.—*Polystichum kamtschaticum* (C. Chr. in Hultén) Fomin, Fl. Sibir. Orient. Ext. 5:94. 1930.—*Polystichum braunii* subsp. *kamtschaticum* (C. Chr. & Hultén) Löve & Löve, Taxon 26:326. 1977.—TYPE: Kamtchatka, *Hultén 4451* (S, not seen).

Polystichum braunii var. *subsessile* Komarov, Fl. Penin. Kamtchat. 64. 1927.—TYPE: Kamtchatka, Kholzanskii (Shalsan Pass), 10 Sep 1908, *Komarov* (LE?, not seen).

Rhizomes erect on forest floor; stipe of medium length, persistently chaffy; fronds broadly lanceolate, to 80 cm or larger; pinnae pinnatifid; the segments undercut and decurrent, lanceolate, coarsely and sharply spinulose-toothed, with slender reddish scales below; basal acroscopic pinnule of pinnae enlarged.

DISTRIBUTION: Northern Japan, Sakhalin (?), and Kamtchatka; disjunct on Attu Island at the westernmost tip of the Aleutian Archipelago. See Sleep (1971) for further details on diagnosis and distribution.

11. *Polystichum munitum*

Polystichum munitum (Kaulf.) C. Presl, Tent. Pterid. 83. 1836.—*Aspidium munitum* Kaulf. Enum. Fil. 236. 1824.—*Dryopteris munita* (Kaulf.) O. Kuntze, Rev. Gen. Pl. 2:813. 1891.—*Aetopteron munitum* (Kaulf.) House, Amer. Fern J. 10:89. 1920.—TYPE: California, *Chamisso* (Probably collected in vicinity of the Presidio, San Francisco, in 1816, *fide* Ewan, 1942; holotype not positively located, possibly the specimen at LE, or at LZ and destroyed; isotype B, not seen).

Aspidium munitum var. *incisoserratum* D. C. Eaton, Ferns No. Amer. 1:188. 1878.—*Polystichum munitum* var. *incisoserratum* (D. C. Eaton) Underw. Our Native Ferns, 6th ed. 116. 1900.—*Polystichum munitum* f. *incisoserratum* (D. C. Eaton) St. John, Proc. Biol. Soc. Wash. 41:191. 1928.—TYPE: 49° N. Lat. (Canada-U.S.A. border), *Lyall* (YU).

Nephrodium plumula C. Presl, Rel. Haenk. 1:33. 1825.—*Polystichum plumula* (C. Presl) C. Presl, Tent. Pterid. 83. 1836.—TYPE: Canada, British Columbia, Vancouver Island, Nootka, 1791, *T. Haenke* (PR, not seen, photo GH).

Polystichum munitum subsp. *solitarium* Maxon, Fern Bull. 11:39. 1903.—*Polystichum solitarium* (Maxon) Underw. ex Maxon, Contr. U.S. Natl. Herb. 10:493. 1908.—TYPE: Guadalupe Island off Lower California, Jul-Oct 1896, *A. W. Anthony* (GH, not located despite search; isotypes DS, NY).

Large forest floor fern; the fronds 60–180 cm long, linear-lanceolate, rarely narrowed at the base, planar; stipes of medium length, ca. one-fifth the length of the blade, persistently chaffy with broad, ovate-lanceolate scales; pinnae finely to coarsely serrate, or biserrate, short-spinulose, slender, straight to falcate, apex acuminate and lacking an apiculum except in juvenile forms, base cuneate; indusia ciliate; $n = 41$.

ILLUSTRATIONS: Abrams (1923, p. 10); Hitchcock et al. (1969, p. 92); Hultén (1968, p. 54).

DISTRIBUTION: Lowland, moist coniferous forests from southeastern Alaska to Santa Barbara County, California; interior moist forests of southeastern British Columbia, western Montana, and northern Idaho. Disjunct stations in South Dakota and Guadalupe Island off Lower California (*Fig. 56*).

12. *Polystichum scopulinum*

Polystichum scopulinum (D. C. Eaton) Maxon, Fern Bull. 8:29. 1900.—*Aspidium aculeatum* var. *scopulinum* D. C. Eaton, Ferns No. Amer. 2:125. 1880.—*Polystichum aculeatum* var. *scopulinum* (D. C. Eaton) Gilbert, List No. Amer. Pterid. 20. 1901.—*Polystichum lonchitis* var. *scopulinum* (D. C. Eaton) M. E. Jones, Bull. Montana State Univ., Biol. Ser. 15:7. 1910.—*Aetopteron scopulinum* (D. C. Eaton) House, Amer. Fern J. 10:89. 1920.—*Polystichum mohrioides* var. *scopulinum* (D. C. Eaton) Fernald, Rhodora 25: 89. 1924.—TYPE: Wyoming, Upper Teton Canyon, 28 Jul 1872, Hayden (YU).

Small to medium sized rupicolous ferns; fronds 15–40 cm long, slenderly lanceolate, hardly narrowed below; stipes medium to long, ca. one-fifth to one-third the length of the blade, provided with light tan to brown scales, these sparse and deciduous above; pinnae deeply incised (only the auricle incised in alpine forms), mucronate to rarely spinulose, the teeth at the apex small, incurved, the terminal tooth or apiculum larger than the subterminal teeth, apex obtuse; pinnae usually folded inwards and horizontally oriented as in *P. imbricans*; indusia entire; $n = 82$.

ILLUSTRATIONS: Abrams (1923, p. 11); Hitchcock et al. (1969, p. 92).

DISTRIBUTION: Throughout western United States in the mountainous regions. Sporadic except in the serpentine areas from the Wenatchee Mountains of Washington to the Trinity Mountains of northern California. Disjunct on the Gaspé Peninsula, Quebec. (*Fig. 61*).

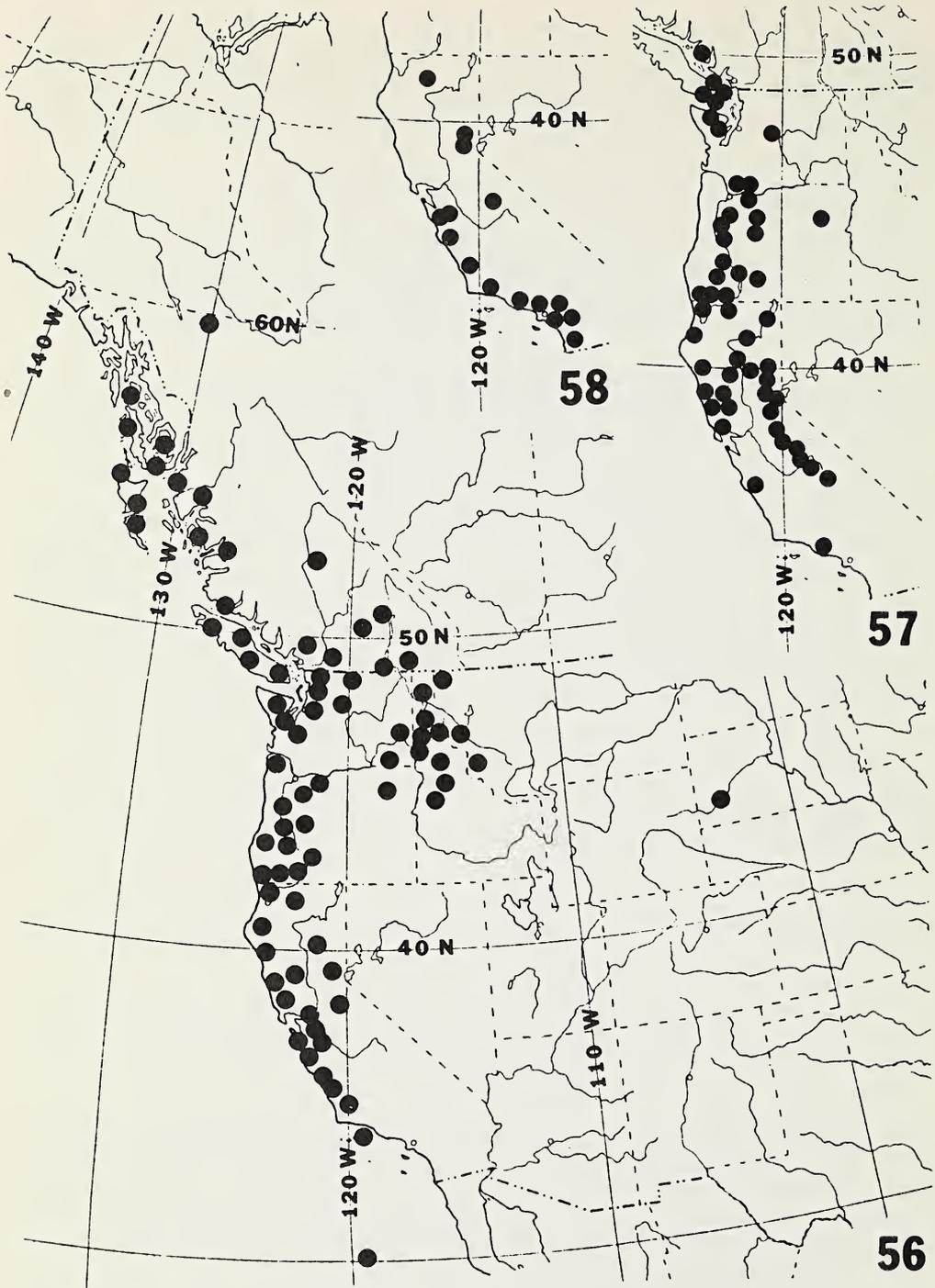
13. *Polystichum setigerum*

Polystichum setigerum (C. Presl) C. Presl, Tent. Pterid. 83. 1836.—*Nephrodium setigerum* C. Presl, Rel. Haenk. 1:37. 1825.—TYPE: Canada, British Columbia, Vancouver Island, Nootka Sound, 1791, T. Haenke (PR, PRC, fragment US).

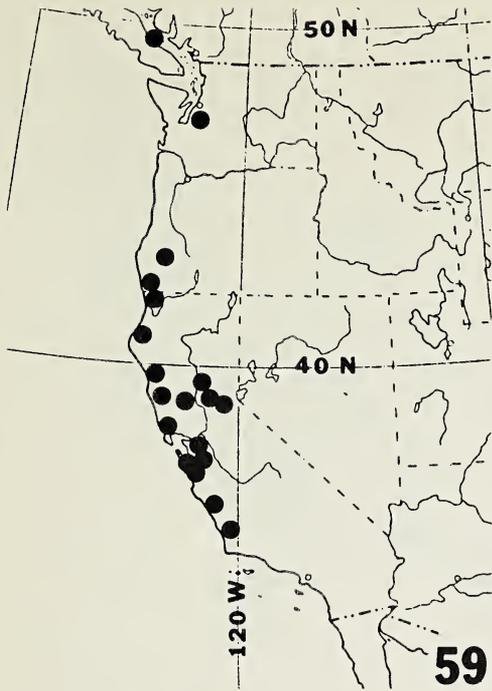
Polystichum alaskense Maxon, Amer. Fern J. 8:35. 1918.—*Polystichum braunii* f. *alaskense* (Maxon) C. Chr. in Hultén, Fl. Aleutian Isls. 49. 1937.—*Polystichum braunii* var. *alaskense* (Maxon) Hultén, Fl. Alaska and Yukon. 31. 1941.—*Polystichum braunii* subsp. *alaskense* (Maxon) Calder & Taylor, Canad. J. Bot. 43:1388. 1965.—TYPE: Alaska, Cleveland Peninsula, Helm Bay, 19 Aug 1901, J. B. Flett 1917 (US; isotypes GH, NY, US, WTU).

Large forest floor fern; mature fronds ca. 50–100 cm long, lanceolate, narrowed at the base, the lower pinnae usually deflexed; stipe of medium length, ca. one-fifth of the frond, persistently chaffy; pinnae cut to the costa, the segments undercut and petiolulate in the middle part of the frond, scaly on both surfaces with filiform scales, broader scales on the costae and rachis; basal acroscopic pinnules enlarged throughout, the basisopic pinnules also enlarged in the lowest several pinnae; indusia ciliate; $n = 123$.

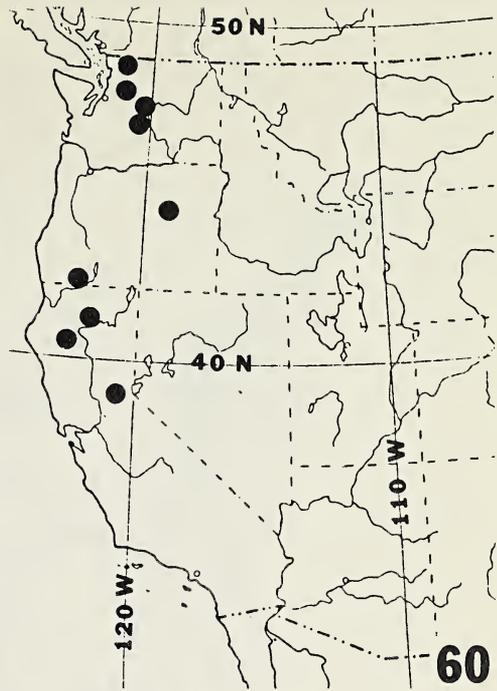
DISTRIBUTION: Lowland coastal forests from the Alaska panhandle to Cheekeye, 50 miles north of Vancouver, British Columbia. Disjunct on Attu Island at the westernmost end of the Aleutian Archipelago (*Fig. 66*).



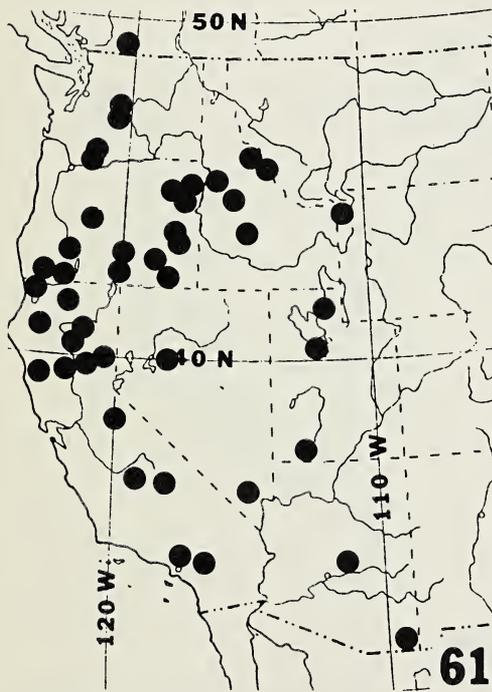
FIGS. 56–58. Distributions of *Polystichum*. FIG. 56. *Polystichum munitum*. FIG. 57. *Polystichum imbricans* subsp. *imbricans*. FIG. 58. *Polystichum imbricans* subsp. *curtum*.



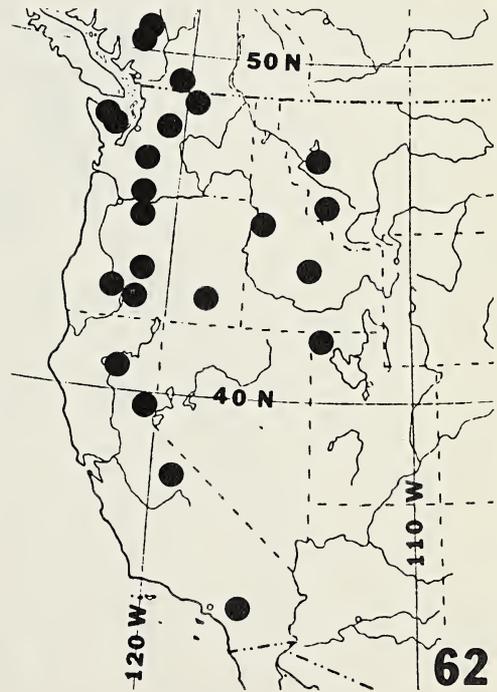
59



60



61



62

FIGS. 59–62. Distributions of *Polystichum*. FIG. 59. *Polystichum californicum*. FIG. 60. *Polystichum lemmonii*. FIG. 61. *Polystichum scopulinum* (not shown is the locality on Mt. Albert, Gaspé Peninsula, Quebec, Canada). FIG. 62. *Polystichum kruckebergii*.

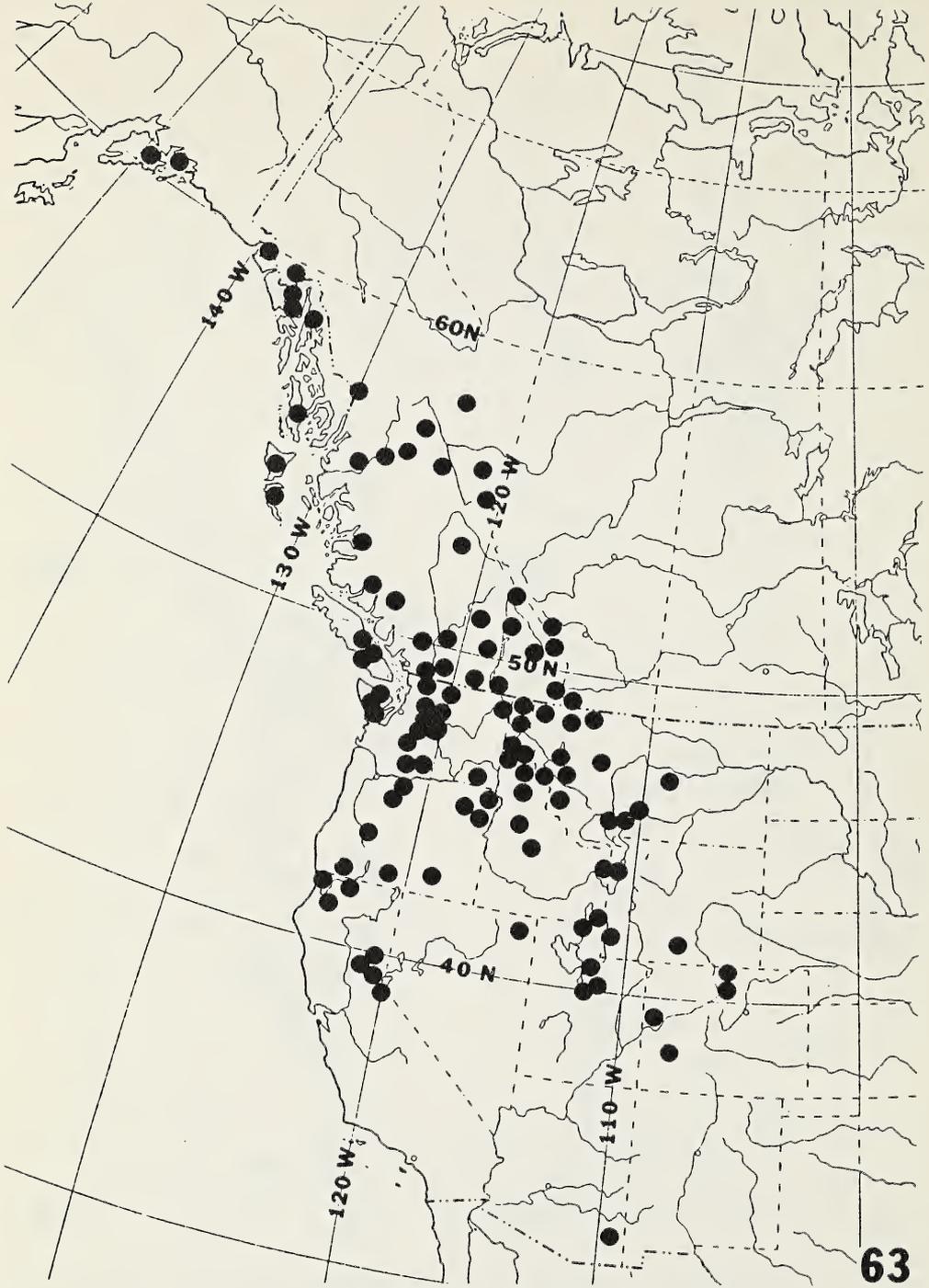
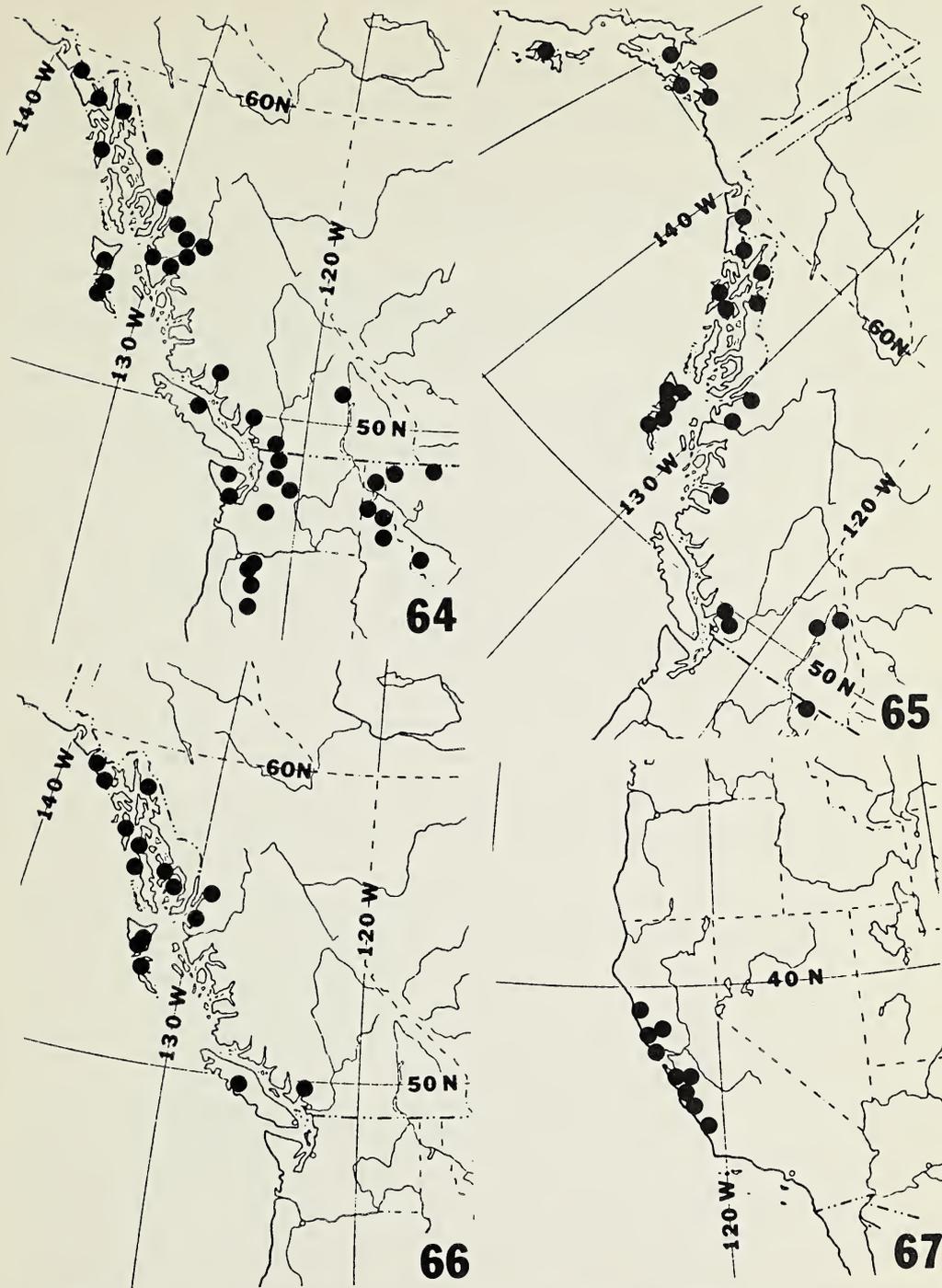


FIG. 63. Distribution of *Polystichum lonchitis* in western North America.



FIGS. 64-67. Distributions of *Polystichum*. FIG. 64. *Polystichum andersonii*. FIG. 65. *Polystichum braunii* in western North America (not shown is the locality on Attu, the westernmost island of the Aleutian Archipelago). FIG. 66. *Polystichum setigerum* (not shown is the locality on Attu). FIG. 67. *Polystichum dudleyi*.

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REPRESENTATIVE SPECIMENS

Polystichum andersonii

ALASKA: Baranof Isl., Red Bluff Bay, *Stephens 160* (UC). Disenchantment Bay, *Trelease 2730* (MO). Hyder, moraine of Salmon River Glacier, *Whited 1404* (US). Juneau, left side of Mendenhall Glacier, *Williams 2103* (OSC, WTU). Sum Dum Bay, Tracy Arm, *Cooper 50* (US). Yakutat Bay, *Trelease & Saunders 2731* (MO). Glacier Bay, Gaeke Inlet, *Anderson 757* (CAN).

BRITISH COLUMBIA: Alice Arm, 1.5 mi up Kitsault River, *Wagner 566* (ORE, WS). Aiyansh, Terrace lava fields, below 500 ft, *Beamish, Wade & Pojar 730013* (UBC). Graham Isl., Blackwater Creek 3.5 mi from Juskatla, *Taylor 39A* (DAO, UC). Moersby Isl., below N face of Mt. Moersby, *Calder & Taylor 36397* (DAO, OSC, UC, WTU). Kitimat, Hirsch Creek Trail, 300 ft, *Bates 72/71* (V). Franklin Valley, Mt. Waddington, *Munday* (V). Pitt Lake, N slope of Mt. Blanshard, 5500 ft, *Henson* (DAO). Port Edward, *Calder, Savile & Ferguson 13147* (DAO, UC). Revelstoke, N fork of Illecillawaet River, 3500 ft, *Shaw* (CAN, GH, MO, NY, US). Smithers, Hudson Bay Mt., 3000 ft, *Szczawinski* (CAN, DAO, UBC, V). Stikine River, Great Glacier, *Anderson 658* (NY). Strathcona Park, Elk River Valley, 2300 ft, *Calder & MacKay 31656* (DAO). Cheekye, 0 m, *Taylor 6540* (UBC).

WASHINGTON: Chelan Co.: Horse Shoe Basin, *Elmer 707* (MO, NY, POM, US, WS). Grays Harbor Co.: Col. Bob Lookout, 4000 ft, *Thompson 7276* (DS, MO, NO, NY, ORE, POM, WTU). Jefferson Co.: Elwha Canyon, 4000 ft, *Flett 252*. (LA, WTU). Pierce Co.: Old moraines on Mt. Rainier, 4000 ft, *Flett 2020* (NY, US, WTU). Snohomish Co.: Perry Creek Trail, 3000 ft, *Thompson 14745* (CAN, CAS, COLO, DS, GH, MICH, MO, NY, RSA, UC, US, WS). Whatcom Co.: Mt. Baker Nat. For., 3800 ft, *Hardin 240* (WS).

IDAHO: Bonner Co.: Upper Lightning Creek, Clarks Fork, *Christ 883* (NY). Kootenai Co.: Sandberg (MO). Shoshone Co.: 6 mi SW of Magee Ranger Sta., *Daubenmire 59186* (WS).

MONTANA: Glacier Co.: Vic of Grinnell Lake, 1500–1650 ft, *Standley 16107* (NY, US). Lincoln Co.: Leigh Creek Canyon, below Leigh Lake, *Preece 3283* (MONTU). Ravalli Co.: Kootenai Creek Trail, 5200 ft, *Lackschewitz 3258* (MONTU).

OREGON: Hood River Co.: Lost Lake, Mt. Hood, 3000 ft, *Thompson 11192* (DS, MO, NY, RM, UC, US, WTU). Linn Co.: Pamela Lake on S side of Mt. Jefferson, *Yerke* (WS).

Polystichum braunii

ALASKA: Aittu Isl., Engineer Canyon, 150 ft, *Hardy 52* (WTU). Cold Bay, Frosty Ck., *Schofield 2459* (DAO). Copper River, *Diehl* (CAS). Glacier Bay, *Cooper 137* (US). Harrisburg, *Meehan* (NY). Juneau, Nugget Creek Trail, *Williams 1937* (OSC). Base of Mt. Marathon, Seward, *Calder 6630* (DAO, NY, US, WTU). Kodiak, Buskin Lake, *Lepage 25221* (DAO). Knight Isl., Thum Bay, *Eyerdam 3578* (US). Kuiu Isl., Washington Bay, *Eyerdam 5451* (WTU). Lowe River, 5 mi E of Valdez, *Smith 2313* (UC). Lynn Canal, Endicott River, *Flory F-254* (USFS). Sitka, *Bischoff* (GH, US). Yakutat, 2 mi S of Tanis Lake, *Argus & Chunys 6278* (CAN). Yes Bay, 1000 ft, *Gorman 178* (US).

BRITISH COLUMBIA: 1 mi E of Bella Coola, *Calder, Parmalee & Taylor 18434* (DAO). Graham Isl., Yakoun River ca. 12 mi S of Juskatla, *Calder & Taylor 35500* (COLO, DAO, OSC, UC, WS, WTU). Moersby Isl., below N face of Mt. Moersby, *Calder & Taylor 36503* (DAO). Prince Rupert, 2.5 mi NE of Salvus, *Calder, Savile & Ferguson 13266* (DAO, US). Alice Arm, 2 mi up Kitsault

River, *Wagner 566* (ORE, WS). Squamish, 0 m, *Taylor & Lang 3229* (NY). Cheekye, 7 mi N off river road, *Taylor 6557* (UBC). Kootenai Dist., 4 mi S of Boat Encampment, *Daubenmire 6177* (WS).

IDAHO: Boundary Co.: Lime Creek, *Warren 316* (WS). Hughes Fork, *Warren 317* (LA, WS).

Polystichum californicum

BRITISH COLUMBIA: Texada Isl., *Anderson 666* (V).

WASHINGTON: Pierce Co.: Rocky ledges nr Eatonville, *Flett 1701* (GH, NY, WTU).

OREGON: Curry Co.: Pistol River, 3 mi from ocean, *Schroeder* (OSC). **Douglas Co.:** Panther Leap, 5 mi E of Steamboat Ranger Sta., *Callan* (SOC).

CALIFORNIA: Alameda Co.: Oakland Hills, *Lemmon* (POM, UC, US). **Butte Co.:** Little Chico Canyon, *Austin* (UC). **Del Norte Co.:** Big Flat, *Shockley* (YU). **El Dorado Co.:** S side of Rubicon River Canyon, 2700 ft, *Stebbins 6694* (CAS). **Humboldt Co.:** Humboldt Redwood Park, 300 ft, *Constance 824* (WS). **Marin Co.:** Mt. Tamalpais, *Heller 5720* (MO, NY, US). **Mendocino Co.:** S of Willits, *Branscomb* (UC). **Monterey Co.:** Big Sur, *Follett* (CAS). **Napa Co.:** Swartz Creek, ca. 2 mi SW of Aetna Springs, *Heckard 1363* (UC). **San Luis Obispo Co.:** *Summers* (UC). **San Mateo Co.:** San Gregorio, *Brannan & Kellog* (MO). **Santa Clara Co.:** W of Los Gatos, *Heller 7225* (GH, MO, NY, RM, UC, US, WTU). **Santa Cruz Co.:** *Anderson* (GH). **Sonoma Co.:** Sobre Vista, *Raven 1885* (CAS, NY, RM, WS). **Yuba Co.:** *Knox* (GH).

Polystichum dudleyi

CALIFORNIA: Marin Co.: Camp Tucker, Mt. Tamalpais, *Howell 24308* (CAS). **Mendocino Co.:** Middle Creek, nr Ukiah, *Branscomb* (MICH). **Monterey Co.:** Julia Pfeiffer Burns St. Park, *Smith 552* (UC). **Napa Co.:** 3 mi N of St. Helena, *Lipman* (UC). **San Luis Obispo Co.:** Upper Lopez Canyon, *Hoover 8807* (UC). **Santa Clara Co.:** W of Los Gatos, *Heller 7226* (GH, MICH, MO, NY, RM, UC, US, WS, WTU, YU). **Santa Cruz Co.:** Nr mouth of Jamison Ck., 825 ft, *Hesse 2426* (CAS). **Sonoma Co.:** Cazadero, *Davy 1660* (NY).

Polystichum imbricans subsp. imbricans (study set, except as noted by *)

BRITISH COLUMBIA: Powell River, *Szy* (UBC). Fraser Valley, betw Britton and Yale, *Scoggan 15488* (V). Nanoose Hill, Nanoose Bay betw Parksville and Nanaimo, *Calder & MacKay 29007* (UC). Shawnigan Lake, *Newcombe* (V). Kitimat, *Mendel 381* (UBC). Bald Mt., Cowichan Lake, 1500–1800 ft, *Rosendahl 1861* (UC). Victoria, *Pavlick* (WS).

WASHINGTON: Chelan Co.: Tumwater Canyon, *Wagner 268* (WS). **Clallam Co.:** Lake Crescent, *Flett* (WS). **Jefferson Co.:** Hood's Canal, *Beattie 3116* (UC). **Klickitat Co.:** Columbia River, *Suksdorf 454* (WS). **Skamania Co.:** Wind River, *Flett* (WTU).

OREGON: Baker Co.: Crater Lake, 7200 ft, *Head 1694* (CAS). **Clackamas Co.:** Clackamas River, 5 mi above Estacada, *Thompson 2646* (ORE). **Curry Co.:** Rogue River, *Baker 4201* (OSC). **Deschutes Co.:** Pine Butte, McKenzie Pass Area, *Ireland 2078½* (ORE). **Douglas Co.:** Roman Nose Mt., *Detling 7531* (ORE). **Hood River Co.:** Viento, *Thompson 4041* (GH). **Jackson Co.:** Upper Applegate River, 488 m, *Detling 9120* (ORE). **Jefferson Co.:** Blue Lake, Santiam Pass, *Chambers 2090* (OSC). **Josephine Co.:** Wimer Rd., 2200 ft, *Whittaker SS313S* (WS). **Klamath Co.:** Crater Lake, *Austin 1639* (POM). **Lake Co.:** Grant Mt., *Peck 15565a* (WTU). **Lane Co.:** Bohemia Mt., *Henderson & Patterson* (ORE). **Marion Co.:** Mehama Rd., 2 mi E of Stayton, *Thompson 5152* (WTU).

CALIFORNIA: Amador Co.: Tiger Ck., 4300 ft, *Hansen 647* (US). **Butte Co.:** North Willow Ck., 1650 m, *Copeland* (UC). **Calaveras Co.:** Devil's Nose, 4700 ft, *Howden 186* (UC). **Del Norte Co.:** Whickey Lake, 5160 ft, *Denton 2911* (WTU). **El Dorado Co.:** Camp Ck., nr Baltic Peak, 3300 ft, *Robbins 1993* (UC). **Fresno Co.:** Nr Fresno, *Jones* (MICH). **Glenn Co.:** Slap Jack Camp W of Alder Springs, *Heller 12805* (WTU). **Humboldt Co.:** Along stage road, *Lemmon* (UC). **Lake Co.:** Allen Springs, *Cleveland* (UC). **Madera Co.:** Shuteye Mt., 7000 ft, *Murdoch 2566* (GH). **Marin Co.:** Mt. Tamalpais, *Howe* (UC). **Mariposa Co.:** Yosemite Valley, *Rodin 6429* (UC). **Mendocino Co.:** Mt. Sanhedrin, *Hall 9507* (UC). **Modoc Co.:** Forestdale, 4500 ft, *Baker & Nutting* (NY)*. **Monterey Co.:** Tassajara Hot Springs, 1700 ft, *St. John 51* (UC)*. **Napa Co.:** 6.4 mi S of Middletown, *Johnson 664* (CAS). **Nevada Co.:** Bear Valley, 5400 ft, *True 1058* (CAS). **Placer Co.:** American River, 1250 ft, *Bacigalupi 3854* (UC). **Plumas Co.:** Injun Jim Campground at confluence of Granite Ck. and N fork of Feather River, 2000 ft, *Howell 42004* (CAS). **Shasta Co.:** Oak Run, *Baker & Nutting* (UC). **Sierra Co.:**

Rock Ck., 5000 ft, *S. A. C[ook?]* (GH). **Siskiyou Co.:** Mt. Shasta, MacBride Springs, *Cooke 17732* (WS). **Sonoma Co.:** Geysers Valley, *Redfield 398* (NY)*. **Tehama Co.:** Divide betw Dry Lake and Mineral, 1821 m, *Eggleston 7212* (GH). **Trinity Co.:** Canyon Ck., 5500 ft, *Alexander & Kellogg 5478* (UC). **Tulare Co.:** Mule Peak, 8100 ft, *Kruckeberg 3377* (WTU). **Tuolumne Co.:** Gorge below dam, Twain Harte, *Wiggins 14355* (WS). **Ventura Co.:** White Ledge Peak Rd., *Pollard* (CAS)*.

Polystichum imbricans subsp. curtum (study set, except as noted by *)

CALIFORNIA: **Los Angeles Co.:** San Antonio Canyon, *Baker 3674* (UC). **Mariposa Co.:** Mirror Lake, Yosemite Valley, *Smith 3* (US)*. **Monterey Co.:** Nacimiento Ck., 1375 ft, *Twisselmann 10403* (CAS). **Nevada Co.:** 2 mi S of Washington, 3600 ft, *True 449* (CAS)*. **Orange Co.:** Santa Ana Mts., 4500 ft, *Munz 7754* (CAS). **Placer Co.:** *Herbrand* (JEPS)*. **Riverside Co.:** Mt. San Jacinto, 4500 ft, *Howell 2932* (CAS). **San Bernardino Co.:** Deer Canyon, San Gabriel Mts., 3200 ft, *Wheeler 1444* (NO). **San Diego Co.:** North Peak Cuyamaca, *unknown coll. 60* (UC). **San Luis Obispo Co.:** Rocky Butte, *Hoover 9050* (UC). **Santa Barbara Co.:** La Cumbre Peak, 3800 ft, *Pollard* (CAS). **Santa Cruz Co.:** Alba, 2000 ft, *Thomas 1335* (MICH). **Santa Clara Co.:** N side of Mt Isabel, 2400 ft, *Lundh 21* (UC)*. **Ventura Co.:** Murietta–Santa Ynez Divide, 4600 ft, *Pollard* (CAS).

Polystichum kruckebergii

BRITISH COLUMBIA: Coquahacca Pass, Ladner Ck., *Harrison* (UBC). Lillooet District, 10 mi S and above Bralome, 5200 ft, *Kruckeberg 5738* (RM, UC, WTU). Mt. Chism, 7000 ft, *Underhill* (V). Shulaps Range, head of Blue Ck., 7100 ft, *Holland* (V). Tulameen River, *Kemp* (NY).

WASHINGTON: **Clallam Co.:** Obstruction Point, 6200 ft, *Meyer 1240* (GH, MO, US, WS). **Okano-gan Co.:** Chopaka Mt., 7400 ft, *Wagner 500* (WS). **Pierce Co.:** Mt. Rainier, Owyhigh, 6000 ft, *Flett 3272* (WS). **Snohomish Co.:** Devil's Thumb, 5000 ft, *Wagner 337* (WS). **Yakima Co.:** Mt. Adams, 6000–7000 ft, *Suksdorf* (CAN, GH, UC, US, WS).

IDAHO: **Custer Co.:** Stanley Lake, 8500 ft, *Thompson 14039* (GH, MO, NY, UC). **Idaho Co.:** Sheep Creek Lakes #2, Dry Diggins area, 7500 ft, *Kruckeberg 3192* (CAN, COLO, DAO, NY, OSC, RSA, UC, WS).

MONTANA: **Lake or Missoula Co.:** Lambert Valley, Mission Mts., 8000 ft, *Jones* (POM). **Deerlodge Co.:** SE slope of Mt. Tiny, 9275 ft, *Lackschewitz 4111* (MONTU, WTU).

OREGON: **Deschutes Co.:** N side of Paulina Peak, *Deiling 274* (ORE). **Douglas Co.:** Old Bailey Mts., *Coville & Applegate 470* (US). **Harney Co.:** Steens Mt., cirque above Wildhorse Lake, *Old* (ORE). **Hood River Co.:** N side of Mt. Hood, *Hansen* (WS). **Klamath Co.:** Nr Klamath Lakes, *Evermann* (US). **Wallowa Co.:** Pete's Point, Wallowa Mts., 2700 m, *Peck 18059* (WTU).

CALIFORNIA: **Plumas Co.:** Wade Lake, 7100 ft, *Stevenson 370* (DAV, WS). **San Bernardino Co.:** Mt. San Bernardino, *Parish & Parish* (MO, YU). **Shasta Co.:** Dersch Meadows, *Menzies & Howell 45880* (CAS). **Sierra Co.:** Sierra Buttes, 8000 ft, *Lloyd 4007* (MICH, UC). **Tuolumne Co.:** S slope of Twin Peaks, head of Virginia Canyon, 10,500 ft, *Butts 192* (UC).

NEVADA: **Lincoln Co.:** S end of Pahroc Range, 15 mi E of Crystal Springs, 4950 ft, *Ripley & Barneby 4973* (GH).

UTAH: **Box Elder Co.:** Head of middle fork of Drum Canyon, 9500 ft, *Maguire & Holmgren 22205* (MO, UC, WTU).

Polystichum lemmonii

WASHINGTON: **Chelan Co.:** Base of Three Brothers, 4000 ft, *Thompson 10753* (GH, MO, NY, RM, WTU). **Kittitas Co.:** Below Teanaway–Turnpike trail, 6500 ft, *Kruckeberg 2600* (CAN, COLO, DAO, GH, IDS, MO, NY, RM, RSA, UC, WS, WTU). **Snohomish Co.:** Double Eagle Lakes, *Kruckeberg 5327* (UC, WTU). **Whatcom Co.:** Yellow Aster Butte, *Muenschner 7559* (MO, NY, UC, US, WS, WTU).

OREGON: **Grant Co.:** Baldy Mt., *Kruckeberg 5484* (CAS, RM, UC, WTU). **Jackson Co.:** Red Mt., *Thompson 12376* (CAS, GH, MO, NY, POM).

CALIFORNIA: **Siskiyou Co.:** Mt. Eddy, 7700 ft, *Heller 11739* (CAS, GH, MO, NY, OSC, UC, US). **Trinity Co.:** Mosquito Lake, 6600 ft, *Sharsmith 4830* (CAN, DAO, NY, ORE, RM, RSA, UC, US, WS, WTU). **Placer Co.:** 3 mi S of Yuba Gap, 6750 ft, *Stebbins 6942* (CAS, WS). **Plumas Co.:** Grizzly Hills, 5800 ft, *Leiberg 5112* (ORE).

Polystichum microchlamys (all specimens seen are cited below)

ALASKA: All from Attu Isl.: Massacre Bay, 200 ft, *Van Schaak 732* (MO, NO, US). Jarmin Pass, *Van Schaak 669* (GH, MO). Peaceful Valley, Hill 37, 200 ft, *Soule 534* (GH, MO). Lookout Mt., ca. 0 m, *Soule 276* (MO). Engineer Canyon, Sidden's Valley, 250 ft, *Hardy 316* (CAS, MO, WTU).

Polystichum munitum (study set, except as noted by *)

ALASKA: Anette Isl., woods nr FAA houses, *Tengesdal* (ORE). Heceta Isl., *Walker 743* (WS). Ketchikan, rocky seashore, *Flett 1912* (WTU). Kuiu Isl., Washington Bay, *Eyerdam 8151* (DAO). Milepost 581, Alaska Hwy., 1500 ft, *Bolinger* (OSC).

BRITISH COLUMBIA: Bella Coola, 1 mi E, *Calder, Parmelee & Taylor 18444* (DAO). Butte Lake, N end on E side, 700 ft, *Calder & MacKay 30543* (UBC). About 0.75 mi N of Cascade just S of Kettle River, *Calder & Savile 9513* (DAO). Garibaldi, *McTavish* (UBC). Kyuquot, Spring Isl., 5 m, *Taylor & Szczawinski 409* (DAO). Langara Isl., nr Henslung Bay, *Calder, Savile & Taylor 22584* (UC). Lowe Inlet, *Coville & Kearney 350* (US). Malcolm Isl., *Zarelli* (UBC). Moresby Isl., below N face of Mt. Moresby, 600 ft, *Calder & Taylor 36504* (UC). Pt. Edward, 7 mi S of Prince Rupert, *Calder, Savile & Ferguson 13148* (DAO). Kay Falls, 16 mi W of Revelstoke, *Calder & Savile 10801* (DAO). Salmo Dist., Kootenay Belle Mine, *MacFadden 14035* (CAS). Betw Queen Charlotte City and Skidegate, *Calder, Savile & Taylor 23262* (DAO). Kennedy River area nr Ucluelet, 600 ft, *Young & Hubbard 65* (UBC). E of N arm of Okanogan Lake, nr Vernon, 1900 ft, *Grant* (DAO). Seymour Hill, Victoria, *Pavlick* (WS). N of Williams Lake, 2650 ft, *Geil 67-06-20-01* (UBC). 50 yards S of Yale History Marker, *Standt & Taylor 4190* (DAO).

WASHINGTON: Grays Harbor Co.: Montesano, 200 ft, *Heller & Heller 4035* (WS). Jefferson Co.: Along Quinalt River, nr Graves Ck. Campgr., *Rogers 818* (WS). King Co.: Vashon Isl., *Beattie 3651* (WS). Okanogan Co.: Head of Twisp River, *Whited 38* (WS). San Juan Co.: Mt. Constitution, Orcas Isl., *Beattie 3411* (WS). Snohomish Co.: Granite Falls, *Wagner 456* (WS). Thurston Co.: Percival's Ck., nr Olympia, *Otis* (WS). Walla Walla Co.: Blue Mts., *Piper* (WS). Whatcom Co.: Baker Hot Springs, *Muenschner 7560* (WS). Whitman Co.: Upper Almota Canyon, *Wagner 465* (WS).

IDAHO: Benewah Co.: Santa, 3000 ft, *Epling 8185* (LA). Bonner Co.: Priest River drainage, 3000–4000 ft, *Epling 6573* (LA). Clearwater Co.: Little North Fork Clearwater River, *Pickett 1128* (WS). Idaho Co.: 15 mi E of Kooskia, *Horn 293* (WS). Kootenai Co.: *Sandberg 8* (WS). Latah Co.: Boone's Mill, Harvard, *Ellison* (LA). Shoshone Co.: Nr Wallace, *Palmer 37805* (GH). Valley Co.: Nr McCall, *Teape* (NY).

MONTANA: Mineral Co.: North Fork of Little Joe Rd., *Jermyn 6637, 6638* (MONTU). Ravalli Co.: N slope above hot springs "Spa." Sleeping Child, *Lackschewitz 1029* (MONTU).

OREGON: Benton Co.: Nr Corvallis, *Cole 32* (GH). Clackamas Co.: Tualatin River, *Sheldon 13007* (ORE). Clatsop Co.: Seaside, *Demaree 13447* (GH). Coos Co.: Valley 1.5 mi S of Charleston, *Henderson* (ORE). Crook Co.: Blue Lake, 3500 ft, *Sproat 15* (USFS). Curry Co.: Along bluffs of Chetco River nr Brookings, *Henderson 7305* (ORE). Deschutes Co.: Green Lakes, 7000 ft, *Henderson 14175* (OSC). Douglas Co.: Cow Ck. 1 mi N of Nichols Sta., *Ward 28* (US). Hood River Co.: N base of Mt. Hood on Hood River, *Hall* (UC). Jackson Co.: Nr foot of Mill Creek Falls, Prospect, *Alexander* (UC). Josephine Co.: About halfway to summit of W face of Siskiyou Mts. above Takilma, *Ownbey & Ownbey 1771* (WS). Klamath Co.: Nr Klamath Lakes, *Evermann* (US). Lane Co.: Big Fall Ck., *Henderson 18737* (ORE). Umatilla Co.: Umatilla River, Bingham Springs, 760 m, *Cusick 3285* (WS).

CALIFORNIA: Alameda Co.: Strawberry Canyon, just above Cherry Patch, *Jepson 16548* (JEPS). Butte Co.: Near confluence of Fraich and Peavine Cks., 2000 ft, *Peñalosa 2446* (CAS). Calaveras Co.: Mokelumne Hill, 1500 ft, *Blaisdell* (CAS). Contra Costa Co.: Wild Cat Ck., Berkeley Hills, *Ewan 8628* (NO). Del Norte Co.: S fork of Smith River, 400 ft, *Cooke 25549* (WS). Humboldt Co.: North Dyerville Flat Grove, Humboldt Redwood Park, *Constance 850* (WS). Marin Co.: Pt. Reyes Peninsula, *Ewan 8050* (UC). Mendocino Co.: Navarro River, *Ewan 9339* (NO). Monterey Co.: Carmel highlands above Yankee Pt., 600 ft, *Balls 23607* (UC). Napa Co.: Johannesburg, *Cannon* (CAS). Placer Co.: Dutch Flat on American River, 4016 ft, *Flint* (NO). San Mateo Co.: King's Mt., *Baker 321* (WS). San Luis Obispo Co.: Caan Ck., *Hoover 6589* (CAS). Santa Barbara Co.: Santa Cruz Isl., *Greene* (UC); Del Coco, 1600 ft, *Blakley 3533* (RSA). Santa Cruz Co.: California Redwood Park, *Schockly* (WS). Siskiyou Co.: Canyon Ck., 2500 ft, *Alexander & Kellogg 5622* (UC). Sonoma Co.: Stewarts Pt., *Wolf 5798* (WS).

SOUTH DAKOTA: Pennington Co.: 3 mi SW of Rochford, *Brooks 427* (KANU)*.

MEXICO: Guadalupe Island, *Palmer 102* (GH)*.

Polystichum scopulinum

BRITISH COLUMBIA: Yale Dist., above Tulameen River at Britton Ck., *Kruckeberg 5728* (UC, WTU).

WASHINGTON: Chelan Co.: Hatchery Creek Rd., *Kruckeberg 2804* (CAN, COLO, DAO, ORE, RM, RSA, UC, WTU). Kittitas Co.: Along Beverly Ck., 5000 ft, *Thompson 8560* (GH, NY, POM, UC, US, WTU). Klickitat Co.: On cliffs nr Columbia River nr Bingen, *Suksdorf 2084* (GH, MO, UC, WS). Yakima Co.: Mt. Adams, Wodan's Vale (Hell-Roaring Canyon), *Suksdorf 2799* (GH, WS).

IDAHO: Butte Co.: Great Rift, just N of Watchman, Craters of the Moon Nat. Monument, *Baker 14131* (NY). Elmore Co.: Trinity Lakes, *Davis 2871* (UC, NY, IDS). Idaho Co.: Walton Lakes Trail, 6400 ft, *Lackschewitz 3899* (MONTU); above Sheep Lakes #2, Dry Diggins Area, 7500 ft, *Kruckeberg 3192* (CAS, LA). Valley Co.: Gold Fork Lookout, 8000 ft, *Thompson 13797* (GH, NY, WTU).

MONTANA: Ravalli Co.: St. Joseph Peak, 7200 ft, *Lackschewitz & Fageraas 2963* (MONTU, NY).

OREGON: Baker Co.: Anthony Lakes Region, 7100 ft, *Thompson 13452* (MO, NY, US, WS). Deschutes Co.: Mountain N of Tumalo Ranger Sta., *Whited* (WS, WTU). Harney Co.: Trout Creek Mts., 9000 ft, *Cronquist 8664* (WS, WTU); Steens Mt., above S tributary to Alvord Ck., 7500 ft, *Cronquist 8256* (DAO, NY, WS, WTU). Jackson Co.: Red Mt., *Thompson 12376* (MONTU, RSA, UC, WS). Josephine Co.: S of Oregon Caves, *Applegate* (UC). Klamath Co.: Wizard Isl., Crater Lake, *Baker 6357* (OSC, WTU). Malheur Co.: Jordan Craters, 4600 ft, *Ertter 185/4* (CIC). Union Co.: China Cap Peak, 2894 m, *Cusick 3050* (GH, MO, ORE, RM, UC, WS, WTU). Wallowa Co.: Ice Lake, 8000 ft, *Jones 6591* (GH).

WYOMING: Teton Co.: Bechler Meadows, *Doutt* (RM—photo of specimen in YELLO).

CALIFORNIA: Butte Co.: *Isaman & Knox* (GH). Del Norte Co.: Little Grayback Peak, 6100 ft, *MacNeill* (CAS). Fresno Co.: Silver Lake, Sierra Nevada, 10,500 ft, *Pierson 1508* (RSA). Glenn Co.: Black Butte, *Howell 19251* (CAS, GH, RSA). Inyo Co.: Mt. Tom W of Bishop, 11,500 ft, *Stebbins 6497* (CAS). Los Angeles Co.: Divide betw Little Rock tributary and Bear Ck., *Pierson 2464* (RSA, US). Placer Co.: Devil's Peak SW of Soda Springs, *Stebbins 6856* (WS). Plumas Co.: Summit ridge of Mt. Hough, 7200 ft, *Howell & True 43349* (CAS). San Bernardino Co.: Above Bluff Lake, 7600 ft, *Johnston* (GH, NY, POM). Shasta Co.: Mt. Lassen area, betw Bumpas Hell and Cold Boiling Lake, 7900 ft, *Leschke 1636* (CAS). Siskiyou Co.: Rock Gulch off Jaynes Canyon, 6000 ft, *Wheeler 3059* (CAS, LA, RSA, US); Mt. Shasta, Panther Creek Meadows, 9000 ft, *Cooke 13744* (CAS, OSC, UC, US). Tehama Co.: Lassen Loop S of Diamond Peak, 7200 ft, *Howell 36463* (CAS). Trinity Co.: N slope of N Yolla Bolly Peak, 6500 ft, *Munz 16686* (CAS, RSA). Tuolumne Co.: S slope of Twin Peaks, head of Virginia Canyon, 10,600 ft, *Butts 193* (GH, US).

NEVADA: Clark Co.: Pine Ck., Charleston Mts., *Jaeger* (POM). Pershing Co.: East Humboldt Mts., *Jones* (GH, US).

UTAH: Salt Lake Co.: Little Cottonwood Canyon, 1750–2000 m, *Jones & Eggleston 14734* (GH). Washington Co.: Zion Park, up side canyon from Mt. Carmel Hwy., 6000 ft, *Cottam 5658* (UC). Weber Co.: Nr Ogden, *Jones* (POM).

ARIZONA: Cochise Co.: Chiricahua Mts., *Ferris* (MO). Gila Co.: Parker Canyon, 4500 ft, *Pase 1740* (USFS).

Polystichum setigerum

ALASKA: Attu Isl., Engineer Canyon, Sidden's Valley, *Hardy 404* (MO, WTU). Cenotaph Isl., *Bates 1* (GH). Coronation Isl., Egg Harbor, *Walker 1084* (DS, GH, MICH, MO, NY, RM, RSA, UC, WS, WTU). Ketchikan, Deer Peak, 800 ft, *McCabe 8653* (UC). Kuiu Isl., Washington Bay, *Eyerdam 8138* (DAO, MO). Lituya Bay, *Dall* (GH, US). Mendenhall Glacier nr Juneau, *R. L. L.* (DAO). Russell Fjord, *Coville & Kearney 942* (US). Yakutat, *Chaney* (MO). Yes Bay, *Gorman 242* (US).

BRITISH COLUMBIA: Alice Arm, 1.5 mi up Kitsault River, *Wagner 587* (WS). Graham Isl., N end of Dawson Inlet, *Calder, Taylor & Sherk 35125* (DAO). Graham Isl., Blackwater Ck., 3.5 mi from Juskatla, *Taylor 39B* (DAO, UC). Moresby Isl., below N face of Mt. Moresby, *Calder & Taylor 36505* (DAO). Portland Inlet, Port (Fort) Simpson, *Anderson* (YU). Squamish, 6 mi N of Chickye (Cheekye), *Orloci 3221* (NY). Strathcona Park, Elk River Valley, *Calder & MacKay 31646* (DAO).

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