THE GENUS ISOTHECIUM IN PACIFIC NORTH AMERICA

by

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B.Sc., The University of British Columbia, 1964

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Botany

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

September, 1966

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Date Oct 17, 1966.

ABSTRACT

An analysis was made of the variation in the genus *Isothecium* from Pacific North America. The study consisted of herbarium work and experimental studies, including coldframe cultures, transplant experiments and aseptic spore cultures. Within the designated area *Isothecium* was found to consist of a complex of ecotypes or forms, each distinct in growth-form and leaf morphology. Intermediates were found between the forms. The growth-forms were phenotypically plastic, and resembled each other under uniform culture conditions. Leaf morphology remained constant even under culture and is therefore a useful taxonomic character.

The study is illustrated by twelve plates of photographs, three pages of line drawings and three distribution maps. A hypothesis is given to explain the disjunct distribution of *Isothecium stoloniferum* var. *spiculiferum*, and var. *myurellum*.

As a result of an extensive study of nomenclature *Isothecium spiculiferum* (Mitt.) Ren. & Card. (Crum, Steere & Anderson 1964) was found to be an illegitimate name. An argument is presented to demonstrate that by a strict application of the Rules of Botanical Nomenclature (1961), *Isothecium stoloniferum* Brid. is the first available legitimate name.

Three varieties are recognized under *Isothecium stoloniferum*: var. *stoloniferum*, var. *spiculiferum* and var. *myurellum*. *Isothecium cristatum* (Hampe) Robinson is recognized as a distinct species composed of a complex of ecotypes, which are not recognized here as clearly defined varieties until further experimental work is done.

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ACKNOWLEDGMENTS

The author wishes to thank Dr. W.B. Schofield who directed the research, provided financial support and helped prepare the manuscript; Dr. J.E. Bier who provided culturing facilities and suggested supplementing the media with a moss extract; Dr. T. Bisalputra who provided photographic facilities and assisted in many ways during the photography of the spore cultures; Dr. F.A. Lang who supplied the base map of Pacific North America: Dr. K.I. Beamish and Dr. T.M.C. Taylor who read the manuscript and gave many useful suggestions during its preparation; Dr. V.J. Krajina with whom I had many discussions which helped to consolidate my ideas, and finally my wife who helped to type the manuscript.

INTRODUCTION

Isothecium is probably the most polymorphous moss genus in western North America. This variability impressed early workers such as Lesquereux (1868) who said of Hypnum stoloniferum (i.e. Isothecium stoloniferum):

> This species is particularly polymorphous. In order to elucidate the remarkable disposition of this moss to modify its form under peculiar circumstances, especially under the influence of wind and fog, Mr. Bolander sent me a large specimen, whose branches on one side are elongated in slender filiform stolons, from six inches to one foot long, while on the other side the stem and branches are thick, short, with large leaves. The filamentous part according to Mr. Bolander's remarks, was hanging from a branch exposed to wind and fog, while the other part, presenting a normal development, was, by its extension to the other side of the trunk, preserved against this action. ... I can but therefore consider the multiplication of species from such polymorphous mosses as a hazardous task. I have admitted as a species the more distantly related form of H. Brewerianum* which growing in dense tufts on dry rocks, has a black color, short stems, short obtuse leaves, and in appearance totally different from H. stoloniferum. But even on dry rocks, the part of the caespites which is not directly exposed to the sun's influence passes to a yellowish green color, and bears some more elongated attenuate branches, even stolons, showing more and more an approach to H. stoloniferum or H. myosuroides, for Professor Muller does not separate these species.

Although leaf morphology is variable the great diversity of growth-forms must have impressed early workers even more. It was this variation that led to the description of a rash of new species, especially by Mitten and Kindberg (see chapter 4).

* Isothecium cristatum (Hampe) Robinson

Early workers, for example Grout (1928), have recognized the *Isothecium* in eastern America as a separate species, *myosuroides*, but the more recent interpretation is to consider them one species Robinson (1962). The present author was impressed with the resemblances between eastern and western North American material of *Isothecium*, although the eastern material is much more stable in growth-form and leaf morphology. Hybridization work is needed within the genus to determine whether the forms or ecotypes are intersterile and to determine whether the eastern and western American taxa are "good" species by biosystematic standards.

Experimental methods similar to those used by the present author have been used by others to understand very polymorphic species, for example: P.J. Chamberlain (unpublished manuscript) with *Hypnum cupressiforme*; D. Briggs (1965) with four species of *Dicranum* and Lodge (1959, 1960 I & II) with *Drepanocladus fluitans* and *D. exannulatus*.

The findings of Chamberlain closely parallel those in *Isothecium*. *Hypnum cupressiforme* was found to be composed of "several distinct lines or races which are genetically discrete and probably would breed true amongst themselves. However it also appears probable that these races are not intersterile and that the myriad of intermediate forms are in reality hybrids."

The opinion of Briggs (1965) concerning the varietal rank coincides with my own. He suggests ...."that varietal names may appropriately be used for morphologically distinct intra-specific populations which are stable in cultivation." The judgement as to what constitutes a morphologically distinct character must be left to the taxonomist. Next the taxomonist must determine which characters are stable and which are not. This, along with an analysis of the variation, has been the primary aim of the present study.

Chapter 1

Growth-forms, Coldframe Cultures and Transplant Experiments

Growth-forms

Until recently growth-form in cryptogams has received little attention. Raunkiaer's life-form system (1907) places the majority of bryophytes under one category, the Chamaephytes (i.e. the perennating buds or shoot apices are borne on shoots very close to the ground). This system does not consider the gross morphology of the colony which appears to be of prime importance for the survival of the moss, thus the term "growth-form" (Du Rietz, 1931) has come into use.

Gimingham and Roberts (1950) proposed a classification of growth-form types modified from the morphological classification of Meusel (1935). This system was later further modified by Gimingham and Birse (1957). Further modifications were proposed by Horikawa and Ando (1958) and Iwatsuki and Hattori (1956). The main categories usually given in such classifications are as follows:

(i) Cushion forms: erect, compacted stems forming a dome-shaped structure.

(ii) Turf forms: erect, compacted stems which are parallel to one another.

(iii) Mat forms: stems (or thallus) interwoven to form a mat lying prostrate over the substratum.

(iv) Weft forms: with loosely intertwined stems and branches, apices usually ascending.

(v) Dendroid forms: tree-like appearance; leafy canopy raised above the ground level.

(vi) Pendulous: stems greatly elongated; overhanging a tree trunk, branch, log or rock. Having a hair-like appearance.

Some have considered the "Feather form" as a major category. I would rather consider it a sub-category, since it describes only the branching pattern.

The growth-form types found in the genus *Isothecium* from Pacific North America, as proposed by the present author, are as follows:

(a) Pendulous (P): See plate 11 fig. 46.

(b) Mat forms:

(i) Large dense mat (DM): stems compacted, with many branches over 1 cm. Commonly on rocks in wet stream valleys. (*Isothecium stoloniferum* var. *myurellum*). See plate 10 fig. 40.

(ii) Small dense mat (dm): stems compacted, with short branches less than 1 cm. On dry rocks or infrequently corticolous in regions characterized by dry summers. (*Isothecium stoloniferum* var. *myurellum* and *Isothecium cristatum*). See plate 9 fig. 34.

(iii) Large loose mat (LM): main stems over 3 cm., loosely interwoven, their apices sometimes turned upward. Predominantly on decaying wood. (*Isothecium stoloniferum* var. *spiculiferum*). See plate 9 fig. 36.

(iv) Large loose mat - pinnately branched (LM-p): branching strongly pinnate; predominantly corticolous. (*Isothecium stoloniferum* var. *stoloniferum*). See plate 11 fig. 44.

The work of Gimingham (1957) and Birse (1957 II; 1958 III & IV) has emphasized the significance of bryophyte growth-form as correlated with the micreoenvironment. Tagawa (1961) pioneered the physio-ecological approach for studying growth-forms. Working with *Ulota crispula* Brid., a small cushion epiphyte, he found that the growth-form had "no great significance as to hold the water in the cushion" but was "effective in decreasing the rate of the evaporation and transpiration." Further, these relationships were shown to be purely physical phenomena. It is to be hoped that a physio-ecological study will be carried out in the future on a single genus such as *Isothecium* which, having a wide spectrum of growth-forms, would lend itself very well to such an investigation.

It is thought that the growth-form is one of the key factors enabling the dry habitat forms to survive under dry conditions. Those forms on dry, semi-exposed to exposed rock have shortened lateral branches while those on rocks in humid stream valleys have well developed lateral branches (compare plate 9 fig. 34 & 9 fig. 35). As a result of having short lateral branches a more compact mat develops. I. cristatum has the most compact mat of the specimens examined. The main stem arches upward and the short branches (less than 5 mm.) are appressed parallel to the stem (see plate 9 fig. 33). The more compact mat would effectively reduce the surface of the mat exposed and create dead air spaces within the mat. It also appears that julaceousness* is a key factor in the survival of the dry habitat forms. The overlapping of the leaves not only reduces the area exposed but also creates dead air spaces between the leaves and stem. It is of interest that a positive correlation exists between julaceousness and dry or exposed habitats in Japanese material of Isothecium subdiversiforme Broth. and Dolichomitriopsis diversiforme (Mitt.) Nog. which the author has examined.

The pendulous or "hairy" form, is always found overhanging rocks, branches or logs or festooning tree trunks (see plate 11 fig. 46). In the literature (W.C. Steere, quoted in Thomson & Ketchledge 1958) the pendulous form is suggested

* overlapping of the leaves when dry, giving the stem a worm-like appearance (see plate 9 fig. 33).

to be the result of a "drip-tip effect." The following explanation for this growth form has been proposed by V.J. Krajina (personal communication).

Rain water picks up minerals from the dust and debris as it washes down tree trunks and over rocks and tree branches. This washing with mineral-rich water promotes the growth of the main stem and thus a hair-like growth-form results. The growing tips also receive more moisture because of dew. In the early morning one can see glistening drops of dew collected on the growing tips. Those dew drops which form above the growing tips are pulled by means of gravity towards the growing tips and collect around them. Thus, two factors, a rich supply of mineral water and a wetter growing point, are thought to be responsible for the extreme elongation of the stem giving the moss a "hairy" appearance.

Coldframe Cultures

MATERIALS AND METHODS

Fresh material was divided into two parts. One was retained as a voucher specimen and the other was cultured in a coldframe. The voucher specimens are shown in plates 9 fig. 36; 10 fig. 38, 40 & 42; 11 fig. 44. The live specimens were cultured in 8 inch clay dishes filled with crushed silica. The pots were placed in an enclosed coldframe with a lined glass roof (to diffuse the sunlight) and a floor covered with 3 inches of dampened vermiculite. Tap water was added when necessary to keep the coldframe and the specimens well moistened. The specimens were sprayed once a month with the mineral solution used in the aseptic spore cultures.

The cultures were maintained from June 1965 to June 1966. Samples of the new growth were examined three times during the year.

RESULTS

Growth occurred throughout the year. Each specimen grew into an extensive mat (see plate 9 fig. 37; 10 fig. 39, 41 & 43; 11 fig. 45). It was remarkable that the new growths of all populations strongly resembled one another. Generally the new growth produced short stems which arched upward and branched irregularly. It was the combination of these two growth phenomena which gave a loose mat appearance to the new growth.

In general the leaves of the new growth closely resembled those of the respective voucher specimens. *Isothecium stoloniferum* var. *stoloniferum* was a notable exception. Compared to its uncultured voucher specimen, leaves of this variety from the coldframe specimen were considerably shorter, the cells at the leaf apex more diamond-shaped, and the pits less conspicuous in all but the alar region. For a characteristic leaf see drawing II fig. 1-7.

Most of the coldframe specimens produced sporophytes in the autumn coincident with sporophyte production in natural populations. This suggests that photoperiod may be an important factor in the fruiting of Isothecium. One notable exception occurred in a specimen of the decayed wood form brought into the coldframe in the early spring of 1966. This specimen had 1/8-1/2 inch sporophytes in late June at which time in nature one finds only remnants of the winter's production of sporophytes. Thus humidity and plentiful supply of liquid water may also be important factors in determining sporophyte production. This point is worthy of further experimentation under controlled conditions.

Transplant Experiments

MATERIALS AND METHODS

Reciprocal transplants were made of the pendulous, semi-exposed rock and the decayed wood forms. The mats were cut into 6 cm^2 portions and transplanted to the various substrates in the late summer of 1964. The moss on each substratum was cut out and the transplant put in its place. As a rule no method of attachment was used. Many transplants were lost because of being poorly attached. In the future it would be wise to use thread or some other means of attachment.

The transplants were examined after 1½ years. In plate 11 fig. 46 to 49 is shown the pendulous form,pendulous form transplanted to semi-exposed rock, semi-exposed rock form and semi-exposed rock form transplanted to decayed wood.

RESULTS

The transplants made in the late summer of 1964 fruited in the normal fashion in the early autumn. Growth during the winter-spring growing season was less than 1 cm. Growth of a similar magnitude was observed during the 1965-66 growing season.

No change was observed either in the growth-form or the leaf shape of the transplants. From the results of the coldframe cultures one would expect the growth-forms of the transplants to change. However, it should be noted that little growth occurred in the transplants while much occurred in the coldframe cultures since these were growing all the year round. The problem could be explored further by maintaining the transplants over a period of years.

Conclusions

(1) The hypothesis is advanced that a combination of shortened lateral branches, which give a dense mat growth-form, and julaceousness may account for the survival of *Isothecium* in dry habitats.

(2) The pendulous form may be the result of what is called the drip-tip effect.

(3) The new growth of the various forms of *Isothecium* under humid coldframe conditions shows that growth-form is not a genetically based characteristic but leaf morphology probably is. The growth-forms changed, each resembling the other, but leaf morphology did not change from that found in nature.

(4) High humidity, a plentiful supply of liquid water and photoperiod appear to play a role in sporophyte production in *Isothecium*.

(5) Reciprocal transplants grow true to their original growth-form and leaf shape.

Chapter 2

Aseptic Spore Cultures

The first objective was to trace the germination of the spore and the stages leading to the mature gametophyte, the second to determine whether leaf morphology was genetically determined in the various forms of *Isothecium stoloniferum*. Spore cultures of *Isothecium cristatum* from rock and *I. stoloniferum* from decayed wood and living *Acer circinatum* were maintained from December 10, 1965 to May 18, 1966. Unfortunately only two forms were successfully cultured, the remainder being unavailable or producing very few sporophytes. An extensive population of the var. *myurellum* at Capilano Canyon Park, near Vancouver, produced very few capsules in the 1965-66 fruiting season, the spores of which failed to germinate.

MATERIALS AND METHODS

Growth Chambers

Initially the cultures were housed in a glass-walled chamber. A bank of fluorescent tubes provided side-lighting of 500-800 foot candles in 12 hour cycles. The chamber had no temperature control. After two-and-a-half months the cultures were transferred to a "Hotpack", floor model #TA

12SBBW, growth chamber with a constant temperature of 20-22°C and 12 hour light cycles of 200 to 450 foot candles.

Preparation of Media

A Bacto-agar concentration of 1% was used throughout the experiment. Concentrations greater than 3% resulted in aberrant germination as seen in plate 1 fig. 1.

(a) Mineral Medium

The following formula is used by Dr. D.J. Wort of the Botany Department at the University of British Columbia in making up a "complete" mineral solution.

To 3 liters of distilled water add:

1M $MgSO_4 \cdot 7H_2O$	6.9 ml.
1M $Ca(NO_3)_2 \cdot 4H_2O$	13.5 ml.
1M KH_2PO_4	6.9 ml.
Iron Solution	3.0 ml.
Microelement Solution	3.0 ml.

The iron solution is FeEDTA (an iron complex of ethylene-diaminetetra-acetic acid) containing 5 mg. of Fe per ml.

The microelement solution was made up by adding the following to one liter of distilled water:

H_3BO_3	2.86 g.
$MnCl_2 \cdot 4H_2O$	1.81 g.
$ZnCl_2$	0.11 g.
$CuCl_2 \cdot 2H_2O$	0.11 g.
$Na_2MoO_4 \cdot 2H_2O$	0.025 g.

(b) Soil Extract

One teaspoon of sandy loam per 150 ml distilled water was agitated 24 hours. The supernate was then either autoclaved or millipore-filtered three times with a .45 u filter to remove the microflora (the millipore-filter provides a cell free culture).

(c) Moss Extract

A homogenate of Isothecium stoloniferum var. spiculiferum growing on Acer circinatum was agitated 24 hours, then filtered through cheesecloth. The extract had to be centrifuged at 16,000 rpm. for 30 minutes to remove a colloidal suspension. The supernate was then either autoclaved or millipore-filtered as described above.

Inoculating Technique

Unopened capsules from freshly collected material were transferred to test tubes containing a sterilizing solution of 10% Pittchlor* (granular calcium hypochlorite with 70% available chlorine) for one minute. The capsules were then placed in petri dishes, where the spores were released by piercing the capsule wall with a flamed needle. A flamed platinum wire loop with a water film was used to transfer and apply the spores evenly over an agar surface.

* available from the Columbia - Southern Chemical Corporation, Pittsburgh 22, Pennsylvania.

OBSERVATIONS AND CONCLUSIONS

Effects of the various media on gametophyte development

The best growth, with gametophytes of 15-20 mm., occurred on the millipore-filtered soil extract supplemented with the millipore-filtered moss extract (see plate 9 fig. 32). The supplement was added when necessary to maintain 100% relative humidity in the petri dishes. Sterile-distilled water was added as a supplement to some cultures instead of the moss extract, providing a control. Gametophytic growth was consistently doubled in those plants where the moss extract was added as opposed to distilled water.

Spore germination to the young gametophyte (plates 1 to 9 fig. 32)

Prior to germination the spore imbibed and enlarged to twice its normal size, becoming green as the chloroplasts developed. On the sixth to eighth day the spore wall ruptured and a germ tube emerged. This tube branched when it became two or three cells long (see plate 1 fig. 3) and eventually formed a mat of filaments on, and below, the agar surface. Occasionally a spore produced more than one germ tube (see plate 1 fig. 4).

Spores were never seen to give rise to a rhizoid directly, as reported by Allsopp and Mitra (1958) for

Funaria hygrometrica and *Atrichum undulatum*; by S.L. Meyer (1947) for *Physcomitrium turbinatum* and K. Benson-Evans (1953) for *Mnium hornum*. The germ tube always grew into the chloronema, with hyaline cell walls, perpendicular cross-walls and abundant chloroplasts. Gradations between perpendicular and oblique cross-wall occurred on mature protonemal mats. The protonema of *Isothecium cristatum* consisted of dense, chlorophyllose, sparsely branched filaments while that of *I. stoloniferum* consisted of loosely arranged, profusely branched filaments (compare plate 2 fig. 6 & plate 5 fig. 16). The filaments of *I. cristatum* were twice the diameter of those in *I. stoloniferm* (compare plate 2 fig. 7 & plate 5 fig. 17).

Differentiation of the protonemal mat into an erect and prostrate portion, the so-called heterotrichous habit, reported by Allsopp and Mitra (1956) was observed in only a few cultures. The erect and prostrate filaments were identical, showing no differences in cell length and angle of cross-wall as illustrated for several mosses by Allsopp and Mitra (1958).

True rhizoids, with pigmented cell walls, oblique cross-walls, and filaments tapering to the growing point arose only from the bases of gametophytes. The chloronema and rhizoid appear to be homologous structures as the chloronemata graded into the rhizoids with differential elongation of the cell wall on one side of the cell causing a transition from perpendicular to oblique cell walls as the cells mature. At the same time the walls of the filaments became gradually pigmented from the base of the gametophyte to the growing point (see plate 2 fig. 6, 7 & 8). Rhizoids emerging from leafy stems gave rise to chlorophyllose filaments with perpendicular cross-walls when they touched the agar surface. Thus the transition can easily be made from chloronema to rhizoid and vice versa.

The protonemal mat which arose from one spore initially gave rise to one gametophyte. The gametophytes were first seen 75 days after inoculation. Many gametophyte buds were observed on rhizoids which developed from the initial gametophyte. These buds generally occurred singly, but occasionally in groups of five or more (see plate 5 fig. 18 & 19). Buds were also seen at the bases of well-differentiated gametophytes.

Alar regions were well-differentiated even in very young leaves (see plates 3 fig. 9; 6 fig. 22 & 8 fig. 28). Small quadrate cells differentiate at a very early stage in I. cristatum as a single row of cells extending up the outermost edge of the leaf (see plate 6 fig. 22). As a result of periclinal divisions of this row of cells the zone of quadrate cells increases in size (see plate 6 fig. 23). This zone increases in size until it forms a triangular zone extending up the edge of the leaf to 1/3 its length (see plate 7 fig. 25 & 27). This zone may become two or three cells thick due to divisions parallel to the flat plane of the leaf.

The leaves of the cultured gametophytes closely resembled those of the plants from which the spores were taken.

Conclusions

(1) Agar concentrations of 3% or more result in aberrant spore germination in Isothecium cristatum and I. stoloniferum.

(2) The supplement of moss extract, prepared as described, increases gametophyte growth two-fold.

(3) The chloronema and rhizoid are homologous structures each being able to transform into the other.

(4) The alar cells, which are small and quadrate in Isothecium, are differentiated very early in the stages of leaf development.

(5) Leaf morphology is genetically stable for Isothecium cristatum and I. stoloniferum var. spiculiferum from Acer circinatum and decayed wood.

Chapter 3

Herbarium Studies and Mapping

MATERIALS AND METHODS

Dried material for study was obtained from thirteen herbaria (see appendix). The following data were recorded for each specimen:

> Name; number (each specimen was given a number by the writer for future reference); substrate; growth habit; exposure; herbarium; locality; collected and determined by; date and comments.

An annotation label was affixed to every specimen and a permanent slide made of the leaves for the majority of the specimens. The locality for each collection was then recorded in a Rand McNally Road Atlas. Neither duplications of collections nor collections made from the same substrate which were in close geographic proximity to one another were recorded. The selected collection records were plotted on base maps (see maps I, II & III) to reflect the range of the taxa rather than to record every collection examined. A list of the collections plotted on the maps is found in the appendix.

RESULTS

Herbarium Studies

After twice examining the material, seven groups based on leaf morphology became evident. Leaf morphology is genetically stable and one of the primary taxonomic characters (see chapter 4). Growth-form on the other hand is genetically unstable as shown previously, but in nature it correlates well with leaf morphology and substrate. For this reason the following groups are discussed in the hope of aiding field identification.

(1) Decayed wood form (*Isothecium stoloniferum* var. *spiculiferum*): A form always found on decayed wood, having a very characteristic leaf shape (see drawing I, fig. 5-7). Although this form is distinct I have seen specimens of it which have features of both the decayed wood and pinnate branching form (i.e. *Isothecium stoloniferum* var. *stoloniferum*). This difficulty arises in the occasional specimen of the decayed wood form which has cells with large, conspicuous pits, so characteristic for the pinnate branching form.

(2) Pendulous (corticolous) form (*Isothecium stoloniferum* var. *spiculiferum*): The small, acuminate leaves of this form are very distinctive (see drawing II fig. 1-4).

It can be confused with no other form, not only because of its unique leaf shape, but also because of its pendulous growth-form (see plate 11 fig. 46).

(3) Wet stream valley rock form (Isothecium stoloniferum var. myurellum): This has not only a characteristic growth-form but also a characteristic leaf shape (see drawing II fig. 5). It is this leaf shape that allows the leaves to overlap one another, and gives the stem a julaceous appearance when dry. As the streams swell with water from the melting snow, this form is often subjected to spring floods. In contrast, during the summer it is subject to very hot and dry conditions, especially when exposed.

(4) Semi-exposed rock form (Isothecium stoloniferum var. myurellum): Although predominantly on rock this is sometimes corticolous. The leaf shape is very similar to that of the Isothecium cristatum shown in drawing I fig. 1 but twice the size, and, of course, lacking the distinctive quadrate cells characteristic of that species.

(5) Dry rock form (Isothecium stoloniferum var. myurellum): Characterized by a very small leaf (see drawing III fig. 9) and stems tightly julaceous. It is readily confused with Isothecium cristatum but lacks the large area of small quadrate alar cells found in that species. The similarity is so striking in some cases that it suggests that I. cristatum

and the dry rock form of I. spiculiferum hybridize. The similarity has led Andrews (1952) to say "one may ... well raise the question whether I. Brewerianum* could not be an extremely xerophytic development of I. stoloniferum."

(6) Pinnate branching form (Isothecium stoloniferum var. stoloniferum): The robust, pinnate branching habit, large leaves and conspicuously pitted walls (see drawing II fig. 1-7) make this the most distinctive of all the forms examined. Although predominantly corticolous, this form is also found on rock, decayed wood and humus. Two phases can be distinguished; a yellow phase north of Vancouver Island and a green phase, on, and south of Vancouver Island.

(7) Isothecium cristatum: This species shows much variability in leaf shape (compare plate 7 fig. 25 with drawing I fig. 1) but cannot be mistaken for other species of Isothecium because of the characteristic alar region (see plate 7 fig. 27 and drawing I fig. 4). Although distinctive at the microscopic level, its growth-form can sometimes be confused with that of the dry rock form of I. stoloniferum.

This species is not substrate specific. It grows predominantly on rock in the northern part of its range but also on tree bases and logs in the southern part of its range.

* Isothecium cristatum (Hampe) Robinson

Many more characters, other than leaf morphology, were examined in an attempt to crystallize the concept of the forms described earlier.

Stem and leaf cross sections were made but no differences could be found among the various forms. The stem cross section of Isothecium cristatum is illustrated in plate 12 fig. 54.

I. cristatum can be readily distinguished from I. stoloniferum on the basis of the capsules, which tend to be narrower, smaller and more erect in I. cristatum (see plate 12 fig. 53). The capsules of I. stoloniferum var. stoloniferum have a distinctive reddish to reddish-black hue and tend to be more urceolate than those of the other forms.

The outer peristome teeth are alike in all forms but those of I. stoloniferum var. stoloniferum tend to be somewhat larger. At first it was thought that the number of cilia between the teeth of the inner peristome would be a useful taxonomic character but a survey of the inner peristomes showed that the number of cilia can vary from one to three, even on the same capsule, and thus of no value as a taxonomic character. In plate 12 fig. 55 & 56 the inner and outer peristomes of the pendulous form are shown.

It should be emphasized that the seven forms discussed previously are not clearly discrete units. Intermediates were found but not in sufficient numbers that the units are rendered useless from the taxonomists point of view. It is hoped that the illustrations of the various forms will make identification an easier task.

CONCLUSION

(1) Seven forms of Isothecium in Pacific North America can be recognized on the basis of leaf morphology. These units are not totally discrete as intermediates exist between the various forms.

Chapter 4

Isothecium as a Taxonomic Unit, Distributions and General Conclusions

Isothecium as a taxonomic unit

The family concept in the bryophytes is rather poorly defined, especially in the pleurocarpous mosses. The boundaries within this group have probably been obscured by parallel evolution. For a discussion of the characters that have been used in distinguishing the various families see Robinson (1962).

Andrews (1952) feels that the Lembophyllaceae, a family erected by Brotherus, (in Engler and Prantl 1925) in which he included Isothecium, is a natural family. The family Lembophyllaceae is characterized by a group of small quadrate, densely chlorophyllose alar cells. Andrews is not supported by two recent monographers, Robinson (1962) and Takaki (1955-56). Robinson places Isothecium in the Brachytheciaceae and Takaki, who recognizes Grout's (1928) name Pseudisothecium, also places it in the Brachytheciaceae. Grout (1928) recognized two subfamilies under the Hypnaceae pertinent to the present discussion. In the Porotricheae, distinguished by strongly costate leaves and short and broad leaf cells, he included Bestia Breweriana*. In the Brachytheciaeae, distinguished by

* Isothecium cristatum

leaves plicate or sulcate at least when dry, and linear vermicular leaf cells, he included his new genus *Pseudisothecium* (where he placed *Isothecium stoloniferum*). It is difficult to understand why Grout considered these two taxa to belong to separate genera, and also to separate subfamilies, especially in view of his statement "if it were not for the much larger area of small thick-walled alar cells in *B. Breweriana* it would be almost impossible to distinguish sterile forms of one from the other."

In 1928 Grout erected the genus *Pseudisothecium*, the North American counterpart of the European genus *Isothecium*. In his description of *Pseudisothecium* he says that it "differs from *Isothecium* in its unsymmetric and cernuous capsules and peristomes with well-developed cilia." He justifies the creation of this new genus by saying: "I have consistently held to the opinion that the erect capsule together with the absence of cilia in the peristome is sufficient basis for generic distinction in the Hypnaceae." Robinson (1962) points out that this is not a sufficient difference since these characters are extremely variable and often not even of specific importance.

Key to the species of Isothecium in Pacific North America

A. Quadrate alar cells numerous, extending 1/4-1/3 of the way up the leaf as a well-defined triangular area, plants tightly julaceous when dry.........*Isothecium cristatum*

A. Quadrate alar cells few, forming a small area at the base of the leaf, not extending up the leaf margin, growth form various..B

B. Plants julaceous when dry.................... .... *Isothecium stoloniferum* var. *myurellum*

B. Plants not julaceous when dry...............C

C. Leaf cells conspicuously pitted from the base to 2/3 of the leaf length... *Isothecium stoloniferum* var. *stoloniferum*

C. Leaf cells not pitted or pitted only near the base......................... *Isothecium stoloniferum* var. *spiculiferum*

The taxa recognized in this study

ISOTHECIUM STOLONIFERUM Brid. *sensu lato*

Bryol. Univ. 2: 371 (1827)

Hypnum stoloniferum Hook. (holotype examined)

Musci Exot. 1: 74 (1818) (Hom. illeg.)

Hypnum myosuroides stoloniferum C. Muell.

Syn, 2: 500 (1851)

Hypnum spiculiferum Mitt. (holotype examined)

J. Linn. Soc. Bot. 8: 34 (1865)

Eurhynchium stoloniferum Jaeger & Sauerb.

St. Gall. Nat. Gesell. 1876-77: 347 (1878)

Isothecium spiculiferum L. et J.

Sensu Renauld & Cardot: Rev. Bryol 20: 20 (1893)

Pseudisothecium stoloniferum (Hook.) Grout

Moss Flora of North America 3: 12 (1928)

Isothecium spiculiferum (Mitt.) Ren. & Card.

Sensu Crum, Steere & Anderson: The Bryologist 67: 163 (1964)

Dioicous. Stems varying from 1.0 cm to over 30 cm in some pendulous forms, branches varying from .5 cm to 2 cm. Branching pinnate to irregularly pinnate. Leaves variable, lanceolate, elliptic to ovate, 0.8 cm to 3.5 cm in length, .3 cm to 1.0 cm in width, tightly appressed to divergent on stem; toothed from the base to the apex, teeth alternately large and small, rarely absent. Costa slender to broad, to 2/3 the leaf length, ending in a spine on the back of the leaf, generally single, but sometimes double. Distinct concave alar region of dense, quadrate, chlorophyllose cells. Leaf cells varying from linear to rhombic (rhombic in ovate leaves); minutely to obviously pitted; cell ends projecting on the dorsal surface towards the apex of the leaf. Stem terete in cross section with a central strand and thickened cortical cells. Capsule reddish to reddish-black; symmetric to unsymmetric; inclined to sub-erect. Phaneropore stomata at the base of the capsule. Outer peristome teeth sixteen, lanceolate, transversely striate at base, minutely papillose at tips. Inner peristome minutely papillose from a broad basal sheath as long as the keeled teeth; cilia between the teeth varying from one to three (even on the same capsule) but, usually two. Seta smooth.

Substrate highly variable; on most coniferous and deciduous trees, on rock, some shrubs and decaying wood. Throughout coastal Pacific North America from Alaska (Kodiak Island) to southern California (Santa Catalina Island). Also in the Columbia Mountain Range in British Columbia, Idaho and Montana.

I am indebted to Dr. T.M.C. Taylor for pointing out that, according to the strict interpretation of the International Rules of Botanical Nomenclature (1961) *Isothecium stoloniferum* Brid. is a legitimate name. Although *Hypnum stoloniferum* Hook., is an illegitimate homonym the epithet *stoloniferum* can still be used in a later combination. See Art. 72, the note of which reads:

> When a new epithet is required, an author may, if he wishes, adopt an epithet previously given to the taxon in an illegitimate name, if there is no obstacle to its employment in the new position or sense; the epithet in the resultant combination is treated as new.

Crum, Steer and Anderson (1965) reject the rule, saying "It seems to us that, regardless of the rule, the principle that an illegitimate epithet may be made legitimate by later recombination defeats the all-important rule of priority and ultimately leads to a greater confusion."

The fact remains that under a rigid application of the "Rules", Bridel's combination must be treated as a new name and cited as _Isothecium stoloniferum_ Brid.

ISOTHECIUM STOLONIFERUM Brid. VAR. STOLONIFERUM

Isothecium Cardoti Kindb. (holotype examined)

Cat. Canad. Pl. 6: 203 & 275 (1892) ("-ii")

Note: published as a Nom. nud. in Bull. Torr. Bot. Cl. 17: 278 (1890)

Eurhynchium stoloniferum var. _Cardoti_ (Kindb.) Grout.

Bull. Torr. Bot. Cl. 25: 253 (1898)

Pseudisothecium stoloniferum var. _Cardoti_ (Kindb.) Grout

Moss Flora of North America North of Mexico 3: 13 (1928)

Isothecium stoloniferum var. _cardotii_ (Kindb.) Wijk et Marg.

Taxon 9: 51 (1960)

Isothecium spiculiferum var. *cardotii* (Kindb. ex Mac. & Kindb.)
Crum, Steere & Anderson

The Bryologist 67 (2): 163 (1964)

Branching obviously pinnate giving a robust appearance to the loose mat growth-form. Leaves large, to 3.5 cm in length and 1.0 cm in width, cells linear with conspicuously pitted cell walls from the base of the leaf to 2/3 its length. Capsules urceolate, reddish-black. See plate 12 fig. 51 and drawings II fig. 1-7.

ISOTHECIUM STOLONIFERUM VAR. SPICULIFERUM (Mitt.) R.D. Williams Comb. nov.

Hypnum spiculiferum Mitt. (holotype examined)

J. Linn. Soc. Bot. 8: 34 (1865)

Eurhynchium stoloniferum Jaeger & Sauerb.

St. Gall. Nat. Gesell. 1876-77: 347 (1878)

Isothecium spiculiferum L. et J.

Renauld & Cardot: Rev. Bryol. 20: 20 (1893)

Isothecium pleurozioides Kindb.

Can. Rec. Sc. 6: 19 (1898) (Nom. nud.)

Pseudisothecium stoloniferum (Hook.) Grout

Moss Flora of North America 3: 12 (1928)

Isothecium spiculiferum (Mitt.) Ren. & Card.

Crum, Steere & Anderson: The Bryologist 67: 163 (1964)

Loose mat growth-form stems drawn into flagelliform shoots when pendulous. Leaves acuminate from a broad base. Cells linear, occasionally pitted in the basal portion of the leaf.

The type specimen of Hypnum spiculiferum is what I consider as the decayed wood form. I am placing the pendulous form under this variety as it is a close relative of the decayed wood form.

See plate 12 fig. 50, 55 & 56 and drawings 1 fig. 5-7 & III fig. 1-4.

ISOTHECIUM STOLONIFERUM VAR. MYURELLUM (Kindb. ex Mac.) Wijk et Marg.

Taxon 9: 190 (1960)

Note: Wijk and Margadant did not acknowledge the orthographic correction of Macoun (see below)

Isothecium myurcellum Kindb.

Bull. Torr. Bot. Cl. 17: 78 (1890) ("myurellum")

Orthographic error corrected in Macoun's Cat.

Canad. Pl. 6: 204 (1842)

Isothecium obtusatulum Kindb.

Rev. Bryol. 22: 83 (1895)

Note: published as a Nom nud. by Macoun in Canad.

Rec. Sc. 6: 19 (1894)

Eurhynchium stoloniferum var. myurcellum (Kindb.) Grout

Bull. Torr. Bot. Cl. 25: 254 (1898)

Pseudisothecium stoloniferum var. myurellum (Kindb.) Grout

Moss Flora of North America 3: 13 (1928)

Isothecium spiculiferum var. myurellum (Kindb. ex Mac.) Crum, Steere & Anderson The Bryologist 67: 163 (1964)

Loose to dense mat growth-form. Appearing julaceous when dry. Leaf shape highly variable, resembling Isothecium cristatum, acute to acuminate apex, elliptic to ovate. Cells seldom linear, most rhombic, sometimes pitted in the basal portion of the leaf.

A very complex variety made up of many ecotypes.

See plate 12 fig. 52 and drawings III fig. 5-11.

ISOTHECIUM CRISTATUM (Hampe) Robinson

The Bryologist 65: 95 (1962)

Leptohymenium cristatum Hampe (holotype examined)

Linnaea 30: 459 (1860)

Hypnum acuticuspis Mitt.

J. Linn. Soc. Bot. 8: 34 (1865)

Hypnum aggregatum Mitt.

J. Linn. Soc. Bot. 8: 35 (1865)

Hypnum Brewerianum Lesq.

Trans. Amer. Phil. Soc. 13: 12 (1865)

Isothecium aggregatum (Mitt.) Jaeg.

Ber. S. Gall. Naturn. Ges 1876-77: 300 1878

(Ad. 2: 366)

Hypnum brewerianum var. lutescens Lesq. & James

Manual of the Mosses of North America p. 349 (1884)

Isothecium Brewerianum (Lesq.) Lesq. & James

Cat. Canad. Pl. 6: 204 (1892)

Note: This is a citation error of Macoun's, for Lesquereux and James, in their Manual of the Mosses of North America (1884) p. 349 put Brewerianum in the subgenus Isothecium but left it in the genus Hypnum.

Isothecium acuticuspis (Mitt.) Macoun et Kindb.

Cat. Can. Pl. 6: 204 (1892)

Isothecium brewerianum var. lutescens (Lesq. & James) Ren & Card. Rev. Bryol. 20: 20 (1893)

Isothecium howei Kindb.

Rev. Bryol. 22: 92 (1895)

Tripterocladium Brewerianum (Lesq.) Fleisch.

Laubm. von Java (1906)

Bestia Breweriana (Lesq.) Grout

Moss Flora of North America 3: 10 (1928)

Bestia breweriana var. howei (Kindb.) Grout

Moss Flora of North America 3: 10 (1928)

Bestia cristata (Hampe) L.F. Koch

Leafl. West. Bot. 6: 25 (1950)

Bestia cristata var. howei (Kindb.) L.F. Koch

Leafl. West. Bot. 6: 25 (1950)

Bestia cristata var. lutescens (Lesq. & James) L.F. Koch

Leafl. West. Bot. 6: 25 (1950)

Isothecium cristatum var. howei (Kindb.) Crum, Steere & Anderson

The Bryologist 67: 163 (1964)

Isothecium cristatum var. lutescens (Lesq. & James) Crum, Steere & Anderson

The Bryologist 67: 163 (1964)

Dioicous. Plants tightly julaceous, compacted growth-form, rich glossy green to dark green, almost black. Leaf shape variable, elliptic to ovate, acute to acuminate, teeth alternating large and small. Cells rhombic. Alar region 2 to 3 cells in thickness, composed of dense quadrate, chlorophyllose cells which angle up the side of the leaf to 1/3 its length.

This species is composed of a complex of ecotypes which probably interbreed in nature. Until the variation is studied experimentally I do not wish to recognize the varieties lutescens and howei of others, for example Grout (1928), Koch (1950) and Crum, Steere & Anderson (1964).

Distributions

The four taxa of *Isothecium* are Pacific Coastal Elements with *Isothecium stoloniferum* var. *spiculiferum* and var. *myurellum* being Cordilleran Elements as well (see maps I, II & III). The following hypothesis is put forward to account for this disjunct distribution.

Mathews and Rouse (1963), on the basis of geofloral evidence, suggest that the climate in south-central British Columbia in the late Miocene-early Pliocene "was cool temperate, with a higher annual precipitation and warmer annual temperature than are found in the same area today." They suggest that, during that time, Quesnel had an average annual rainfall of 40 inches with an average annual temperature of 45-55^{o}F as opposed to 19.7 inches and 41^{o}F today. Such conditions would have been favorable for the growth of *Isothecium*. It is conveivable then that *Isothecium* was widespread over much of southern British Columbia, as well as many of the western states of the U.S. With the uplift of the Cascade Mountains probably in the late Eocene, and of the Coast Mountains later than Miocene-Phiocene times (G.E. Rouse, personal communication) an extensive rain shadow area was created eastward, which could have caused the extinction of *Isothecium* in that area. Presumably it was only able to survive in the Columbia Mountains to the east (see Map I), in areas with an average annual rainfall of greater than 30 inches. The elevation of the Sierra Nevada Mountains in late Pliocene-Pleistocene times (Axelrod 1957) had the same effect as the Columbia Mountains to the north do today, i.e. picking up moisture from the westerly winds. Thus Isothecium would have been able to survive on the western slopes of the Sierra Nevadas (see Maps I & III).

As the glaciers radiated from the principal mountain ranges during the Pleistocene, Isothecium probably became extinct over much of its range. It is unlikely that Isothecium survived in the Columbia mountains as the refugia were, for the most part, on mountain tops over 6500 feet (see Daly (1912) and Economic Geology Series No. 1 4th ed., pp. 458-462 (1957).

Recent evidence supports the theory that refugia of limited extent existed on the west coast of the Queen Charlotte Islands during the Pleistocene glaciation. The evidence for this has been based on animals (J.B. Foster (1965)); on plants (Calder and Taylor (1966) and W.B. Schofield (1962)); and paleobotanical evidence (Heusser (1955)). Isothecium stoloniferum var. spiculiferum and var. myurellum may have survived in these refugia. According to Heusser (1960) refugia also existed in parts of coastal Alaska, north-central Vancouver Island and south of the ice in Washington.

Upon recession of the ice, Isothecium presumably extended its range southward from coastal Alaska and northward from the northwestern states, and possibly also radiated from the various nunataks. This recolonization continued until Isothecium occupied its present area of distribution.

Isothecium stoloniferum var. stoloniferum is strictly a Coastal Element occurring in areas with an average annual rainfall greater than 50 to 60 inches. One collection was made on Saltspring Island which has an average annual rainfall of 40 inches. This is most unusual and probably the result of local edaphic conditions. Its occurrence along the Oregon Coast to the Prairie Creek Redwoods in northern California is best explained by the relatively high rainfall in these areas which exceeds 65 inches. Without a high rainfall to maintain a high relative humidity this variety probably could not survive.

Isothecium cristatum is a Coast Element occurring in areas with less than 35 inches average annual rainfall or on exposed outcrops with slightly greater rainfall. Although found predominantly in areas with an average annual rainfall of 20 to 30 inches, it also occurs on Santa Catalina Island, off southern California, which has an average annual rainfall of 12 inches.

General Summary and Conclusions

Isothecium stoloniferum is highly polymorphic. Its many variants differ not only in leaf shape but also in growth-form. These are ecotypes, their leaf morphology being stable under cultivation and their growth-form unstable under cultivation.

As Grout (1928) suggests "short, thick-walled leaf cells are so frequently correlated with a xerophytic habitat as to suggest a causal relation." Correlated with these short rhombic cells is a more ovate leaf shape. This leaf shape is further correlated with the julaceous appearance of the dried stems. As discussed previously, julaceousness and a dense mat growth-form appear to be important in the survival of *Isothecium* in dry habitats.

The greatest difficulties in identification arise between the dry rock form of *I. stoloniferum* and *I. cristatum*, also an inhabitant of dry sites. It is possible that these hybridize, as Grout (1928) speculates, but *I. cristatum* still remains a distinct species.

More, ecologic, cytogenetic, and hybridization work is needed before the *Isothecium* complex is fully understood.

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(to face plate 1)

Isothecium cristatum

(1) Aberrant spore germination on 4% agar, 60 days, x575

Isothecium stoloniferum var. spiculiferum - decayed wood form

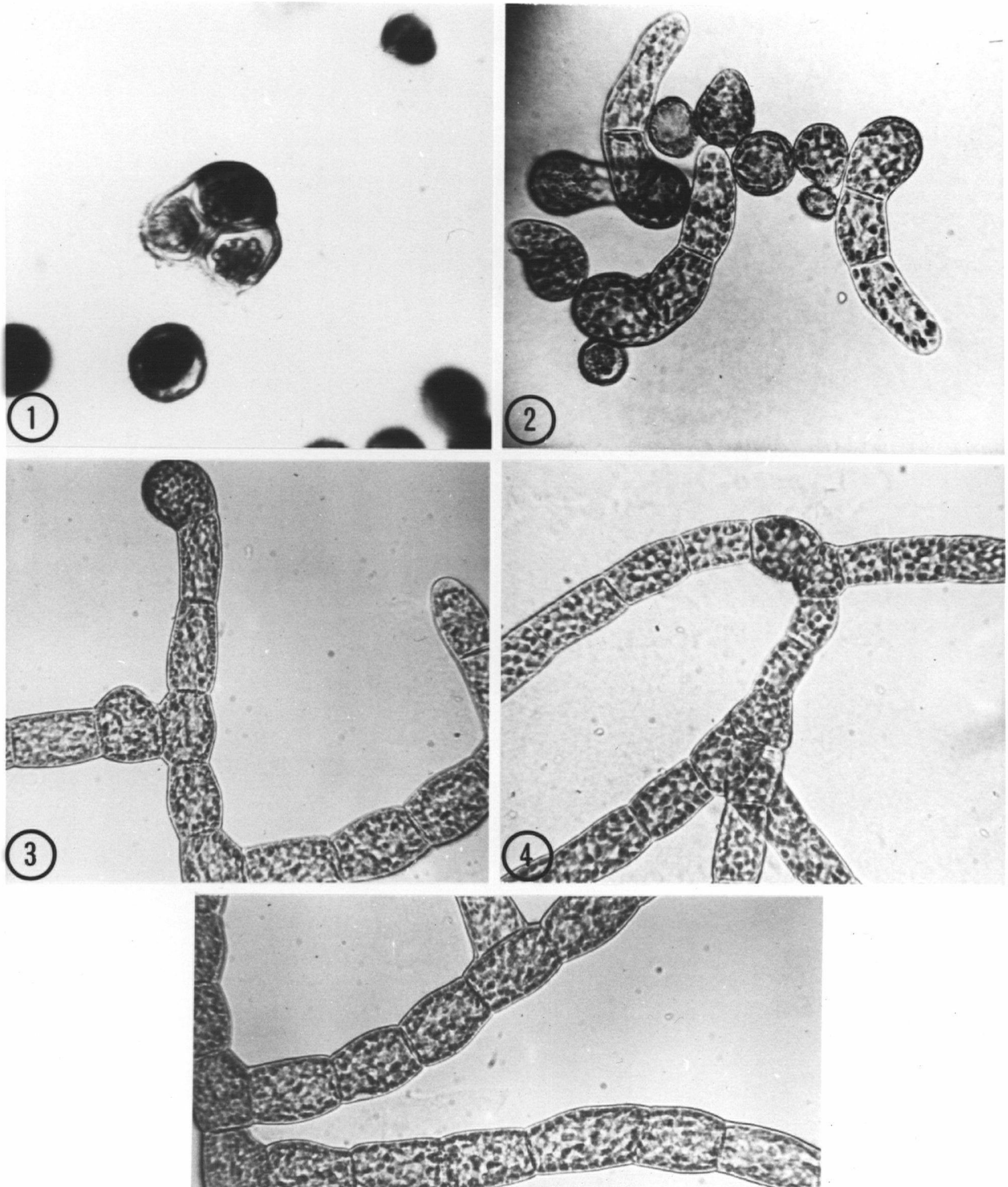
(2) Showing various stages of germination, 14 days. x575

Isothecium stoloniferum var. spiculiferum - pendulous form

(3) Young protonema below agar surface, 31 days. x575

(4) Spore which germinated by two germ tubes, one of which immediately branched, 31 days. x575

(5) Branching of protonema below agar surface, 31 days. x575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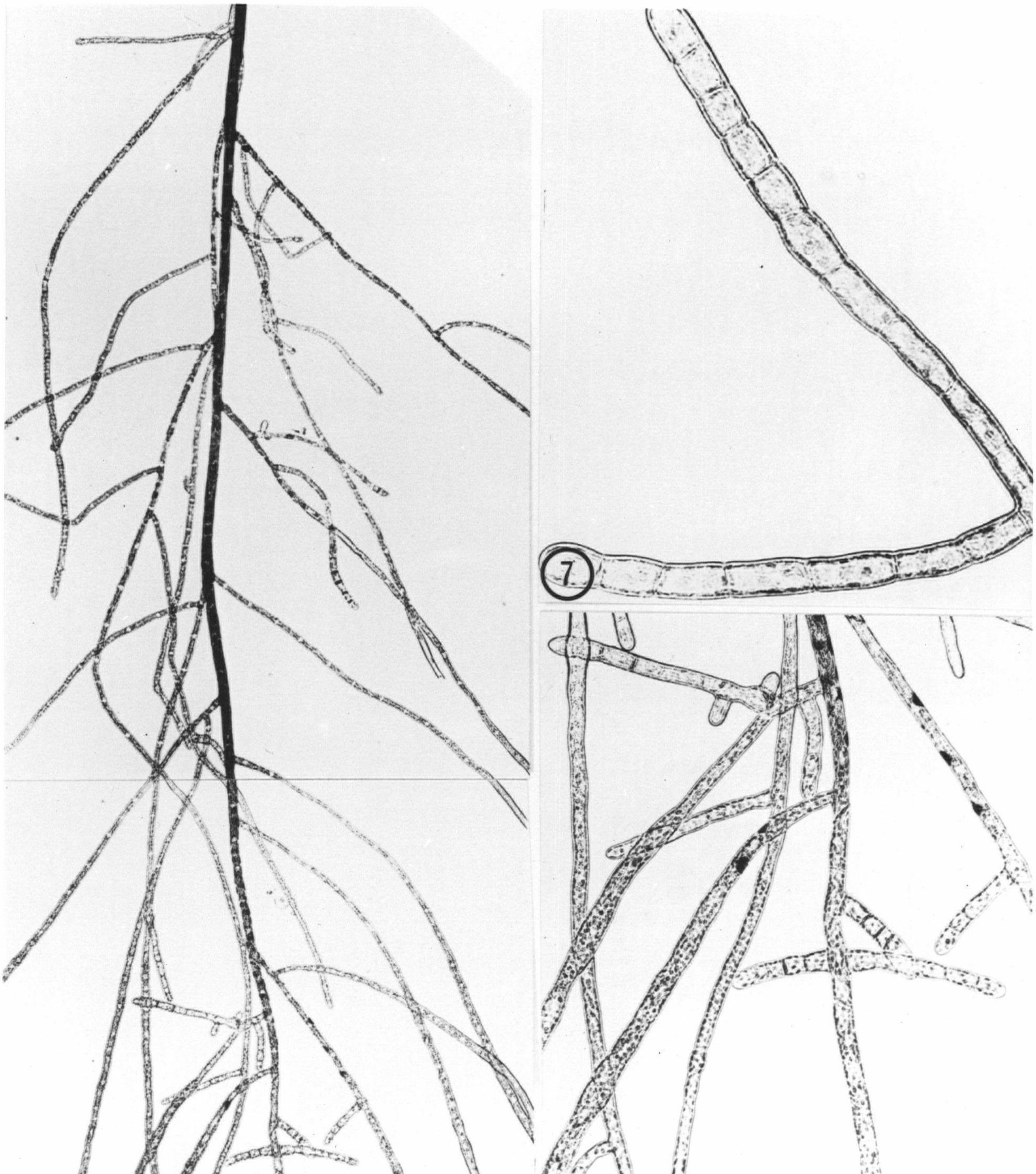
(to face plate 2)

Isothecium stoloniferum var. *spiculiferum* - decayed wood form

(6) Showing gradual differentiation of a rhizoid from the base of a gametophyte (top of picture) to the growing point. x110

(7) Detail of the growing point. x470

(8) Detail of the critical zone of rhizoid differentiation. Note the gradual pigmentation of the cell walls towards the base of the gametophyte and less oblique walls closer to the growing point (bottom of picture). x250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(to face plate 3)

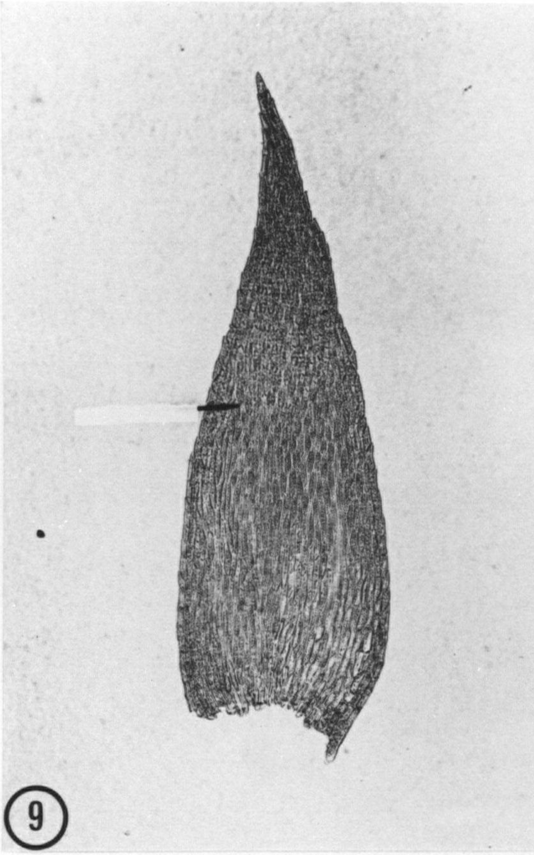
Isothecium stoloniferum var. spiculiferum - decayed wood form

(9) Young leaf. x110

(10) Alar region of (9). x425

(11) Apex of (9). x425

(12) More mature leaf. x110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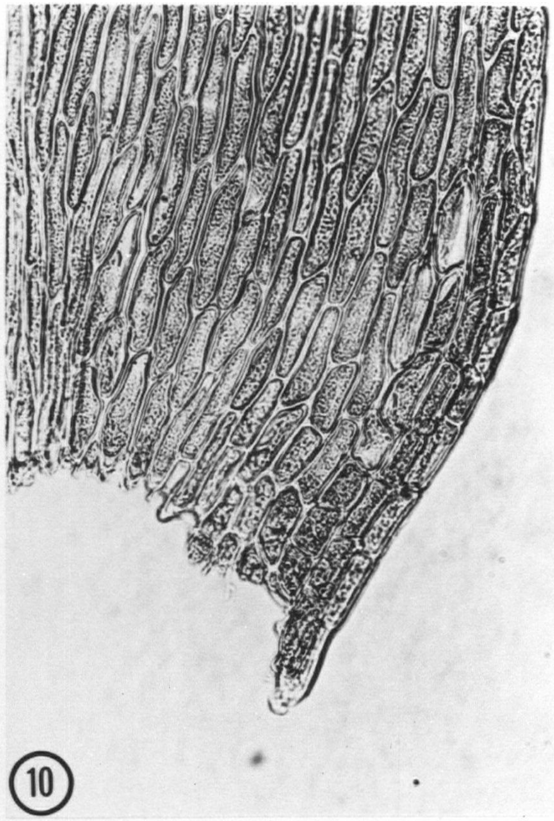
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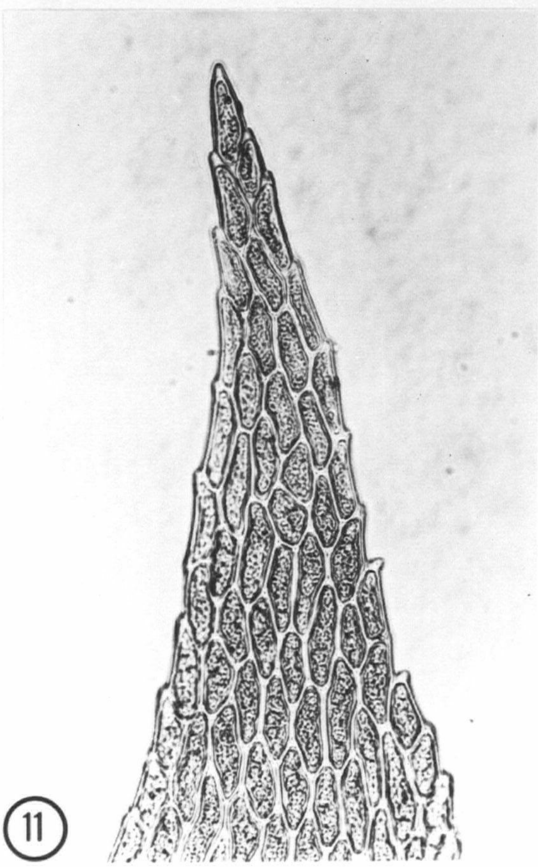
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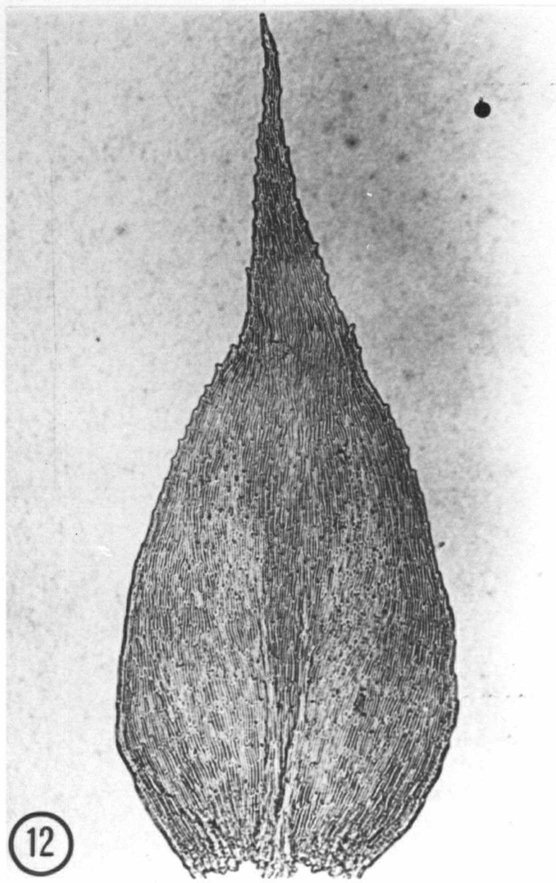
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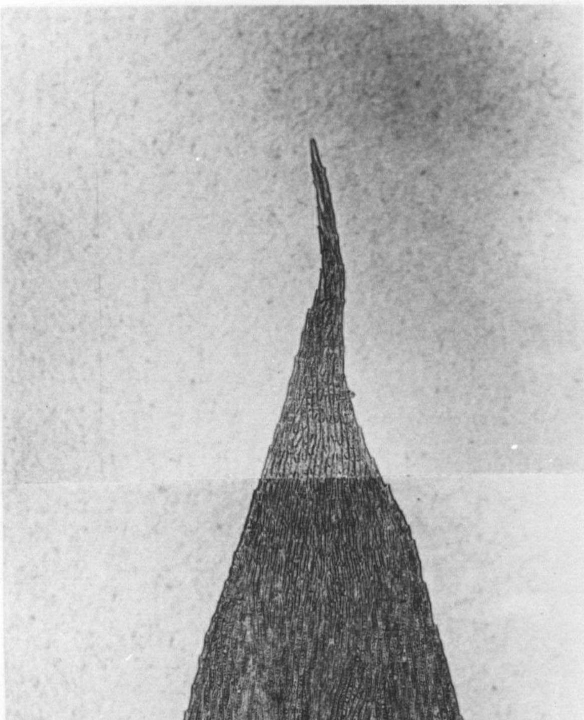
(to face plate 4)

Isothecium stoloniferum var. *spiculiferum* - decayed wood form

(13) Near-mature leaf. x110

(14) Apex of (13). x425

(15) Alar region of (13). x425



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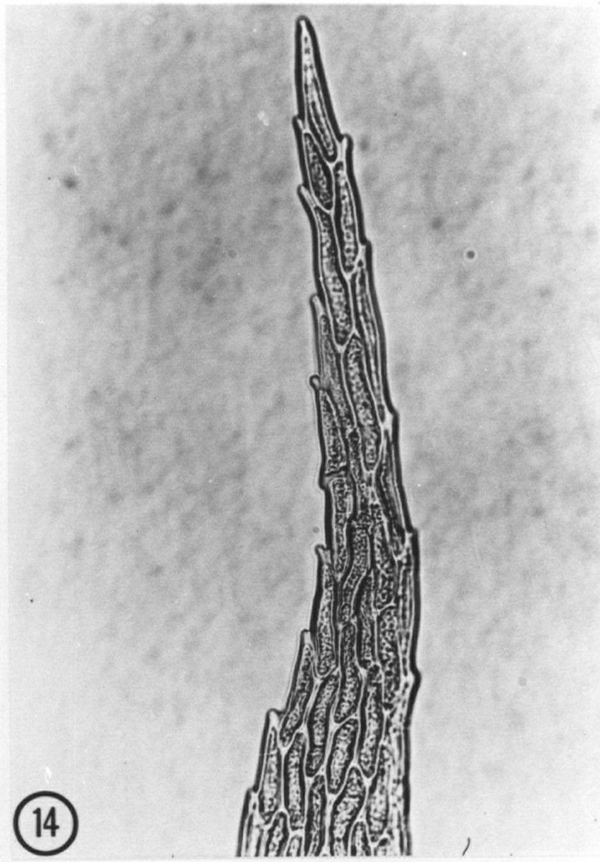

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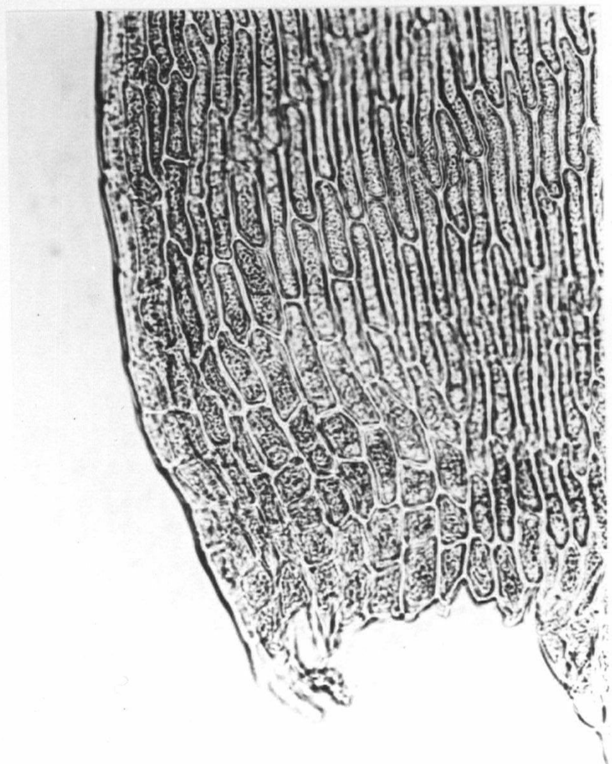

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(to face plate 5)

Isothecium cristatum

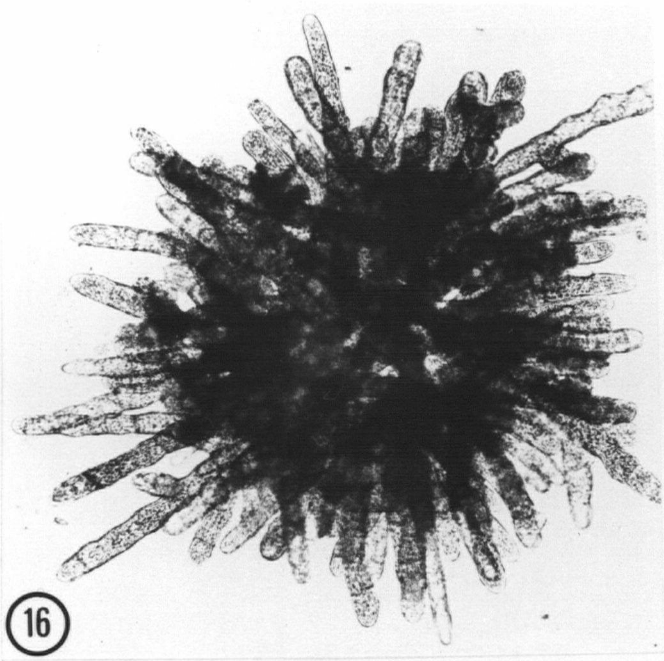
(16) Protonemal clump which has arisen from one spore. x110

(17) Detail of protonemal filaments. x470

(18) Gametophyte bud (gb) on a rhizoid. Note the oblique wall (ow) of the rhizoid. x600

Isothecium stoloniferum var. *spiculiferum* - pendulous form

(19) Group of gametophyte buds. x600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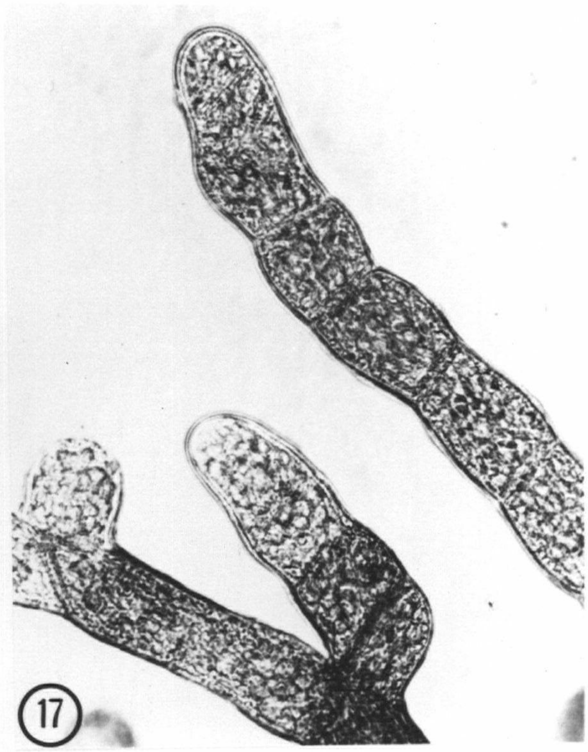
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gb
ow
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(to face plate 6)

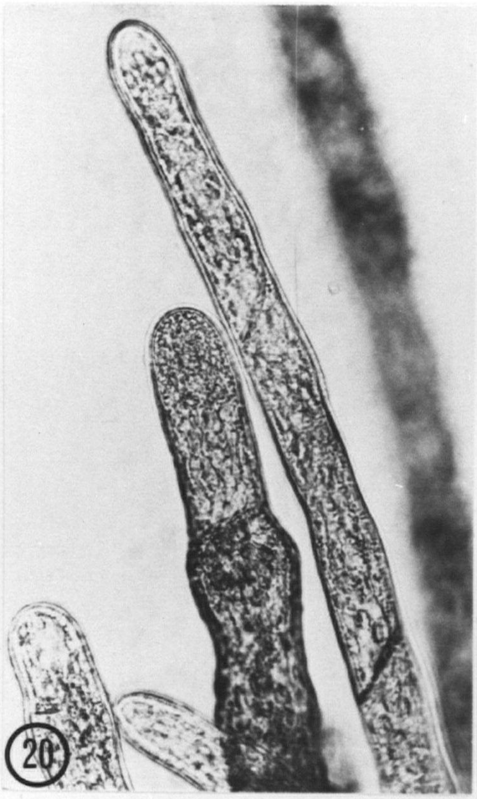
Isothecium cristatum

(20) Detail of chloronema (on left) and rhizoid (on right). x470

(21) Young gametophyte (yg) on a rhizoid (r). x250

(22) Very young leaf. Note single row of quadrate cells extending from the leaf base along the edge of the leaf to 1/3 its length. x470

(23) More mature leaf. Note the broadening of the quadrate cell zone by periclinal divisions in the direction of the arrows. x470



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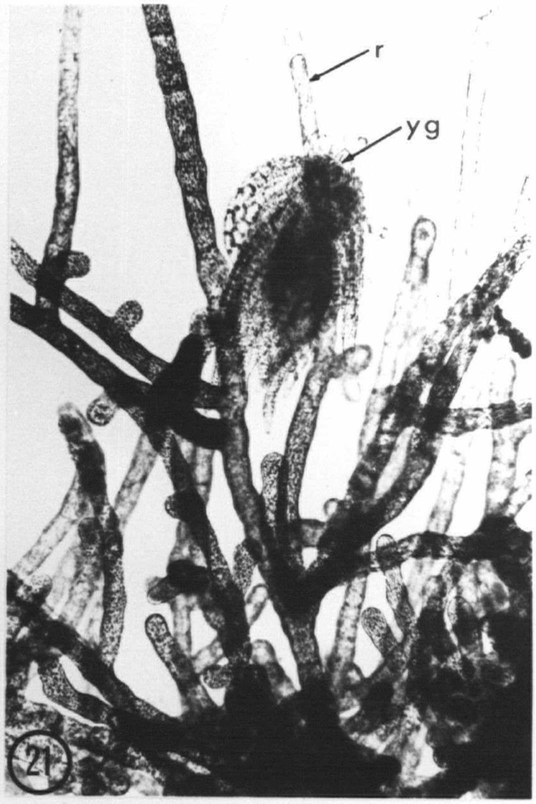

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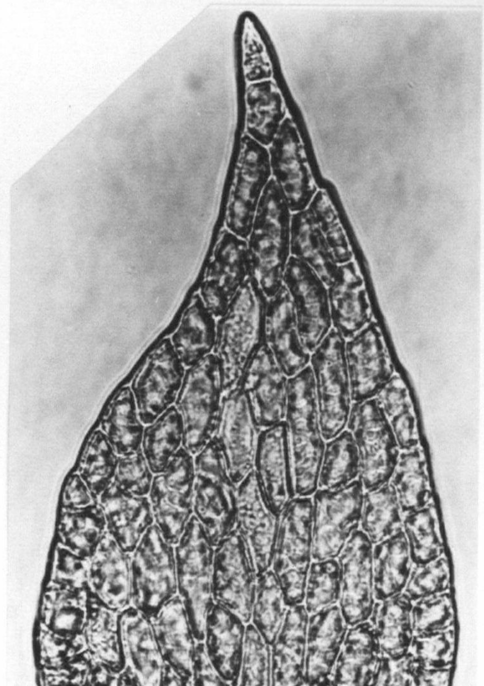

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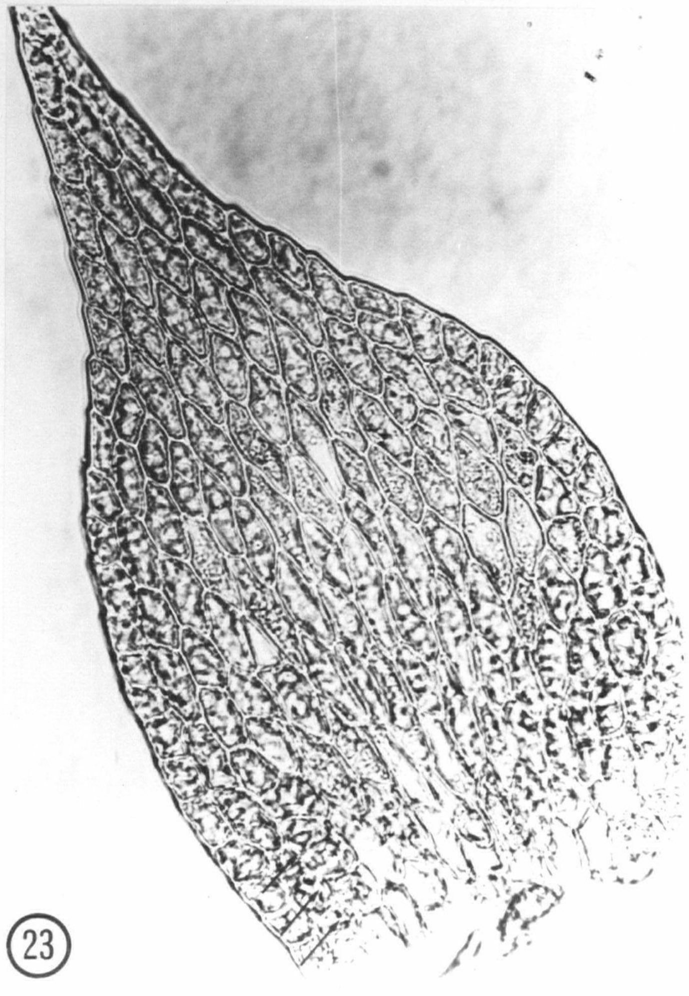


23

(to face plate 7)

<u>Isothecium cristatum</u>

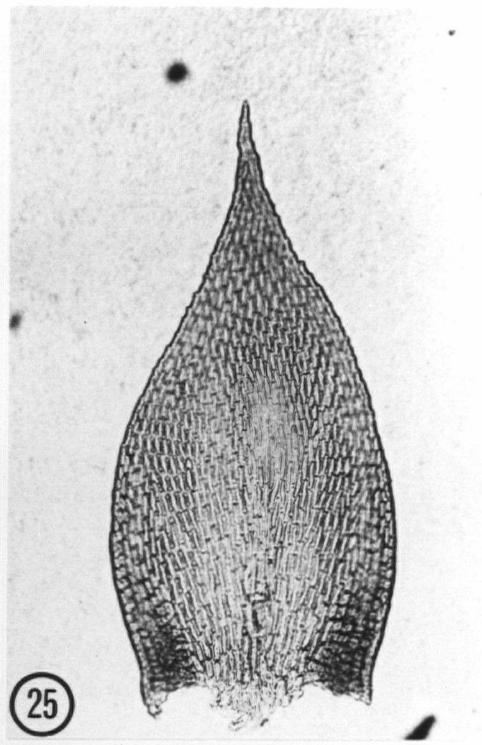
(24) Young gametophyte. x110

(25) Mature leaf. x110

(26) Apex of (25). x470

(27) Alar region of (25). x470


24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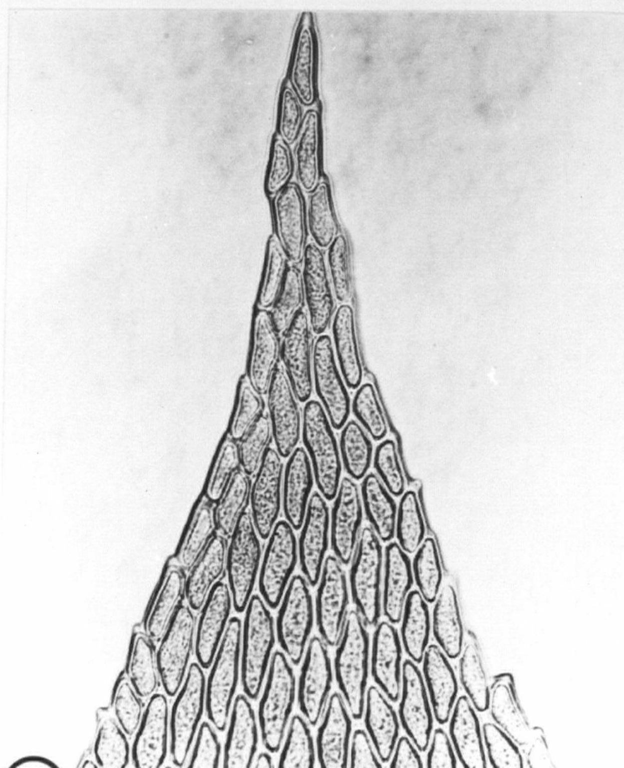
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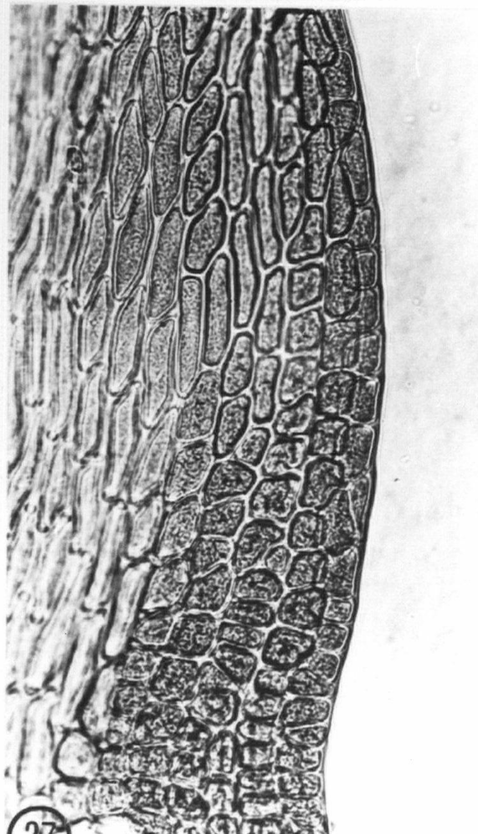

27

(to face plate 8)

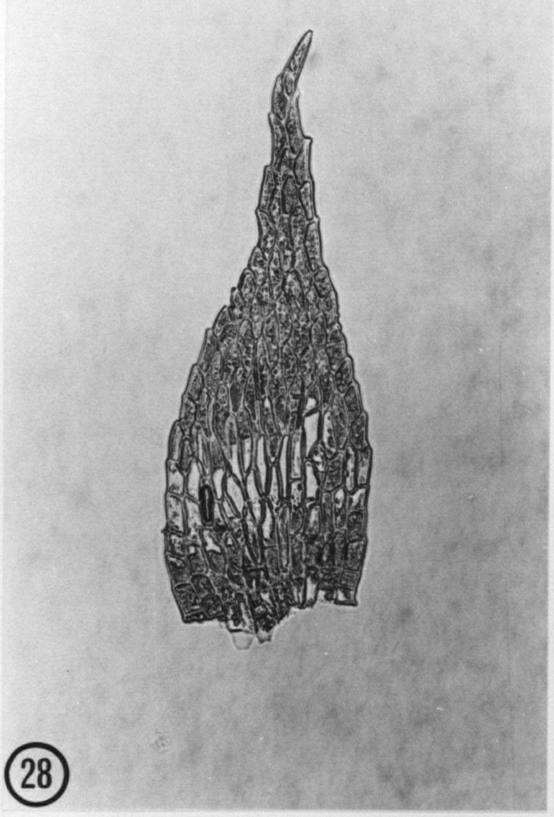
Isothecium _stoloniferum_ var. _spiculiferum_ - pendulous form

(28) Young leaf. x220

(29) Near-mature leaf. x110

(30) Apex of (29). x420

(31) Alar region of (29). x420



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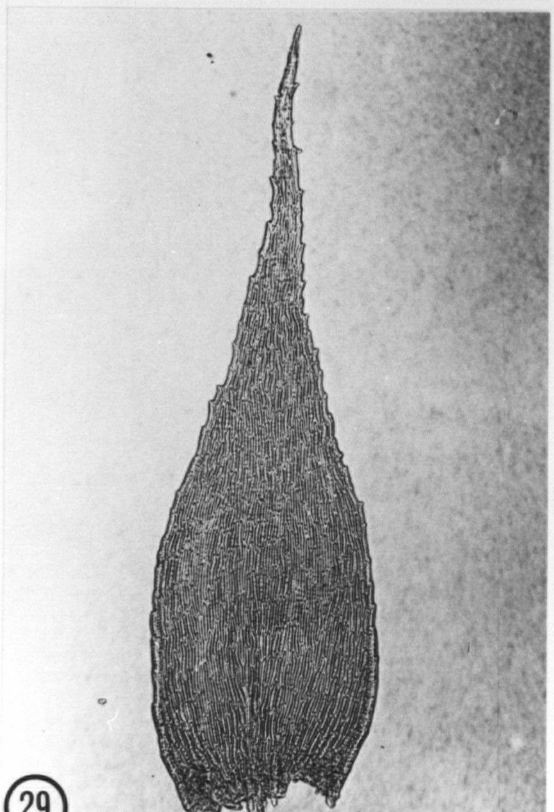

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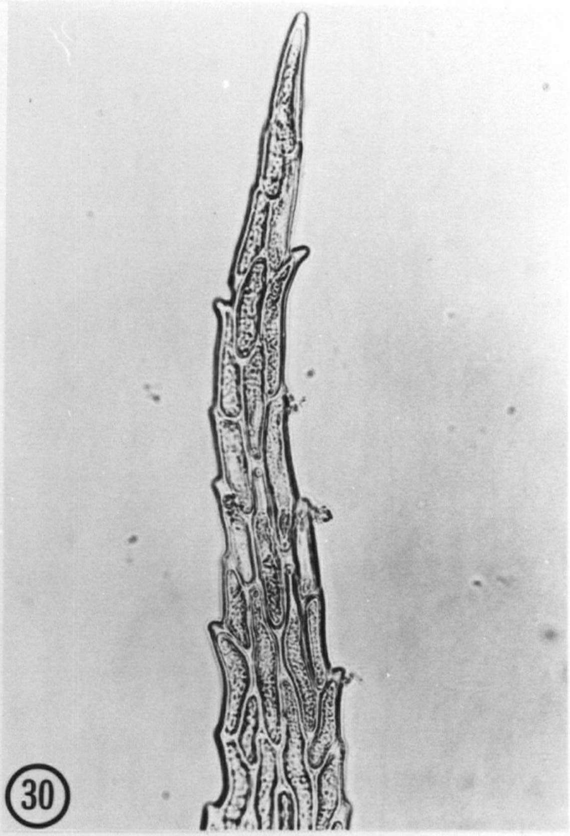

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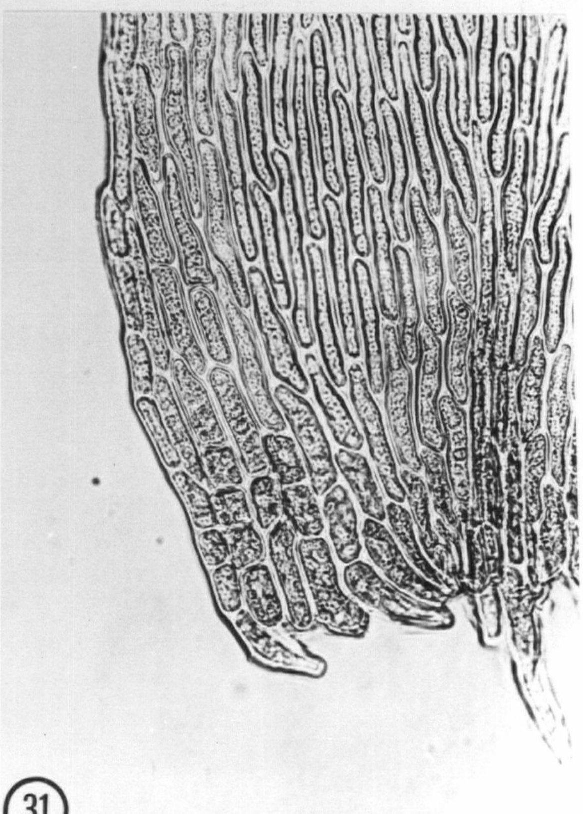


31

(to face plate 9)

Isothecium stoloniferum var. spiculiferum - decayed wood form

(32) Best growth obtained in spore culture experiments. Grown 5 months on a 1% agar-millipore-filtered soil extract supplemented with the moss extract.

Isothecium cristatum

(33) Showing the small dense mat with the julaceous habit.

Isothecium stoloniferum var. myurellum

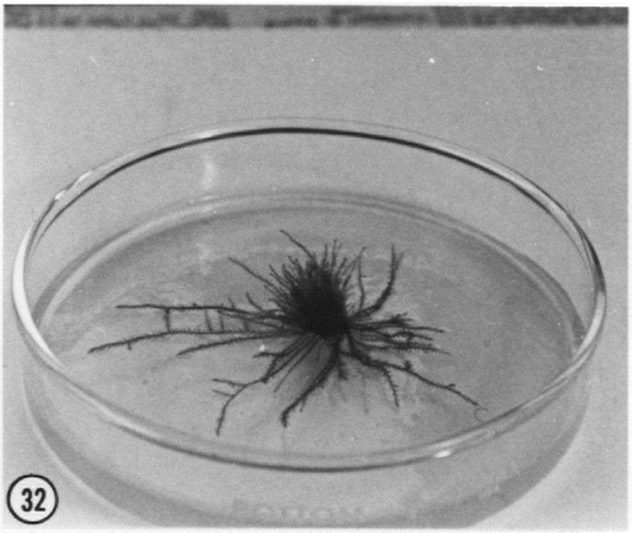
(34) Dry exposed rock form.

(35) Wet stream valley rock form.

Isothecium stoloniferum var. spiculiferum - decayed wood form

(36) Specimen collected from Lynn Valley Park near Vancouver.

(37) New growth of (36) in humid coldframe.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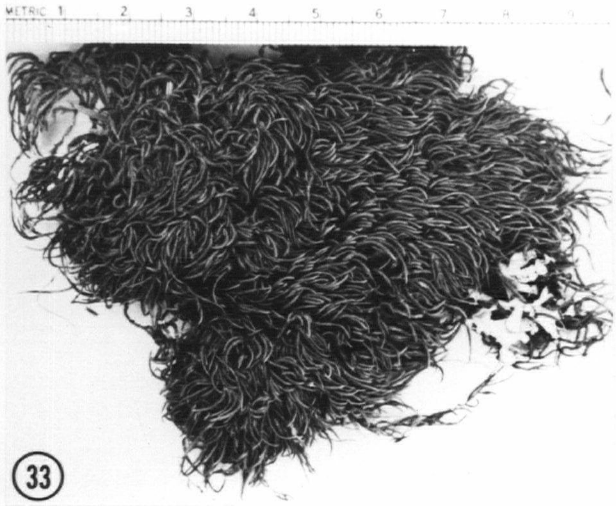
METRIC 1 2 3 4 5 6 7 8 9
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1 2 3 4 5 6
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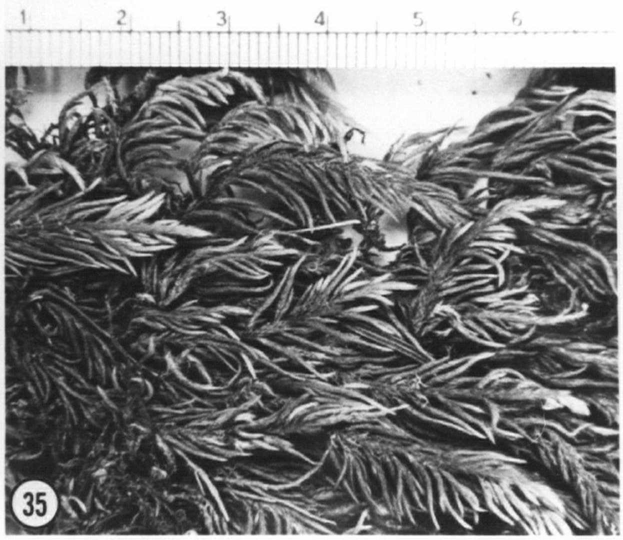
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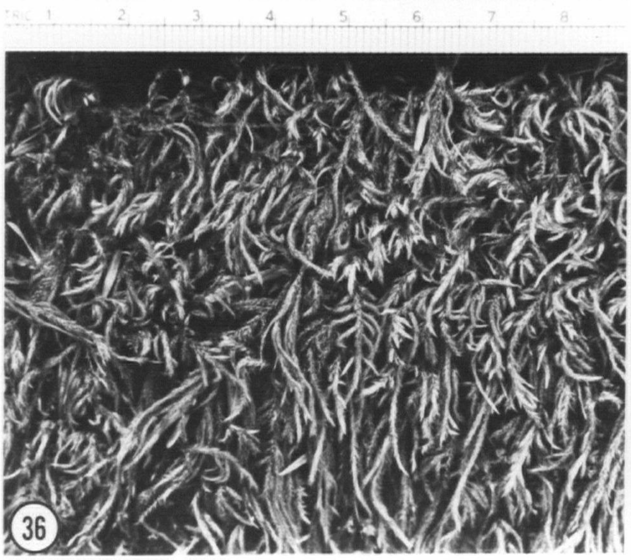
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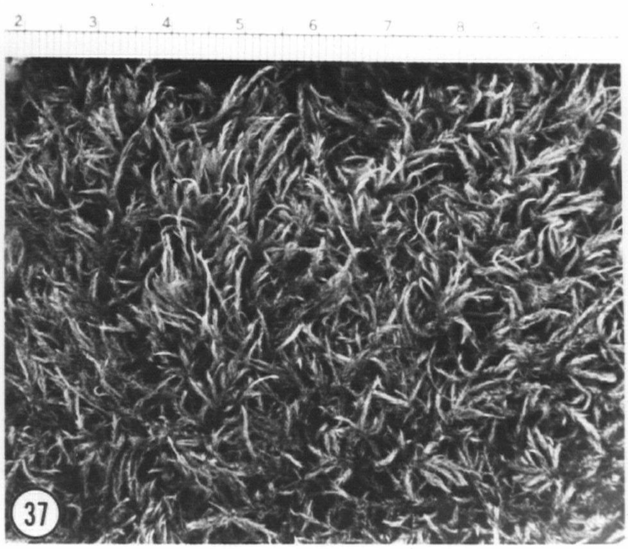
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37

(to face plate 10)

Isothecium stoloniferum var. *myurellum*

(38) Specimen from Horseshoe Bay near Vancouver - semi-exposed rock form.

(39) New growth of (38) in humid coldframe.

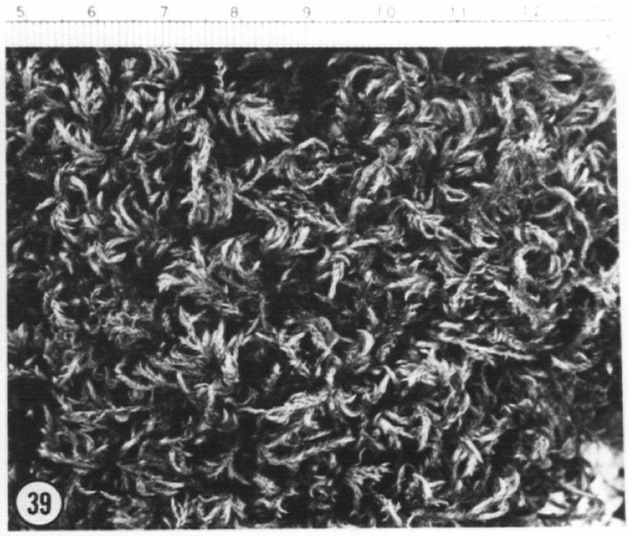
(40) Specimen from Capilano Canyon Park - wet stream valley rock form.

(41) New growth of (40) in humid coldframe.

(42) Dry rock form from O'Brien, Oregon.

(43) New growth of (42) in humid coldframe.


38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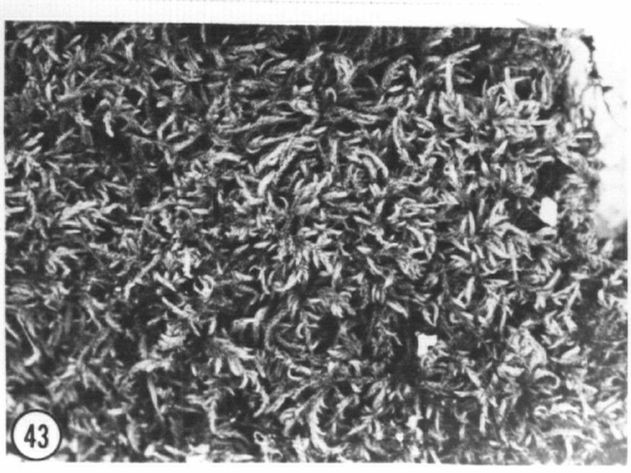

43

(to face plate 11)

Isothecium stoloniferum var. *stoloniferum*

(44) Specimen from Calvert Island (north of Vancouver Island) growing on *Thuja*.

(45) New growth of (44) in humid coldframe.

Isothecium stoloniferum var. *spiculiferum*

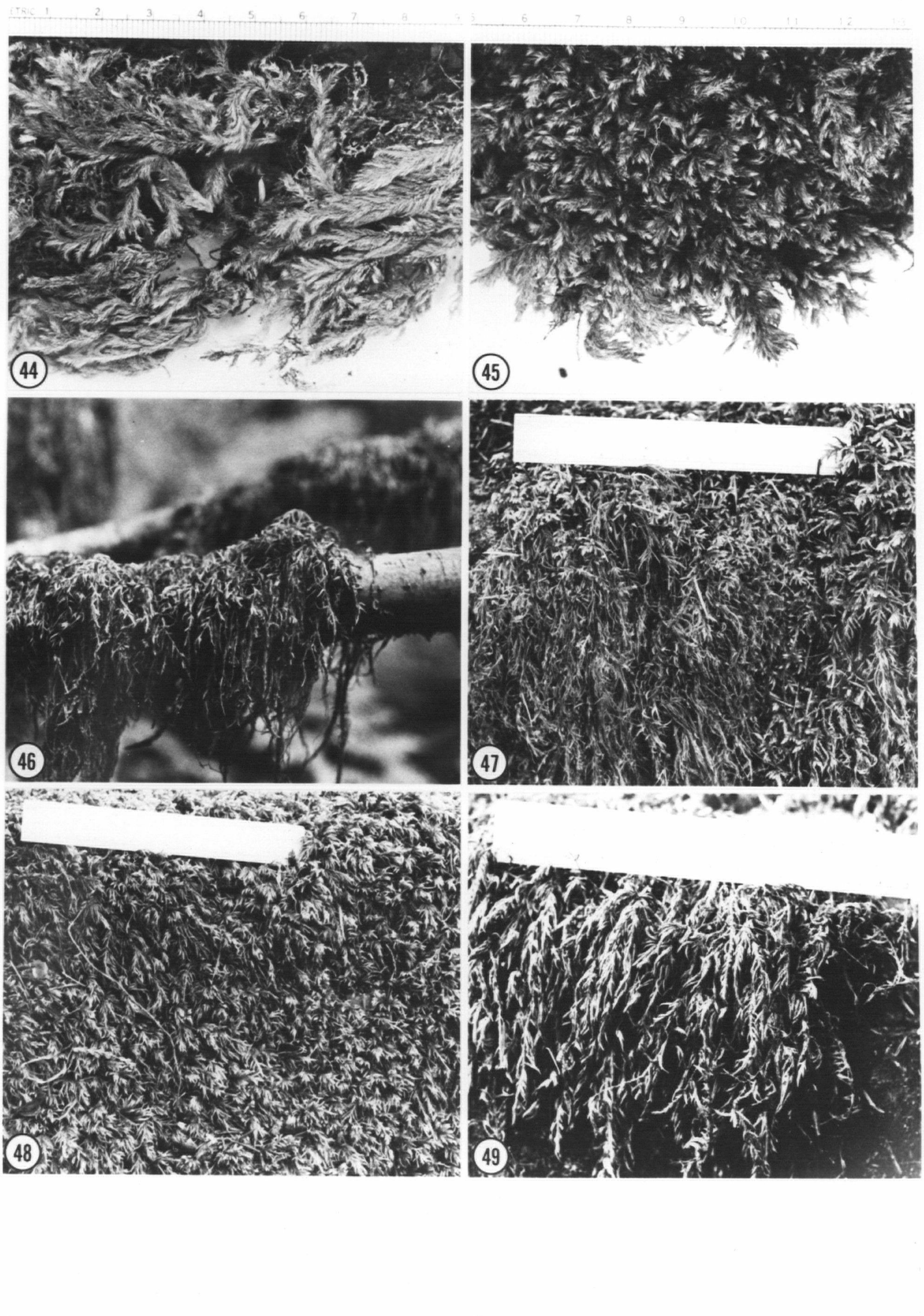
(46) Pendulous form overhanging an *Acer circinatum* branch.

(47) Transplant of (46) to semi-exposed rock in Horseshoe Bay (48).

Isothecium stoloniferum var. *myurellum*

(48) Growth habit of the semi-exposed rock form growing at Horseshoe Bay.

(49) Transplant of (48) to decayed wood.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(to face plate 12)

<u>Isothecium</u> <u>stoloniferum</u> var. <u>spiculiferum</u> - decayed wood form

(50) Type specimen of <u>Hypnum</u> <u>spiculiferum</u> Mitt. x3.5

<u>Isothecium</u> <u>stoloniferum</u> var. <u>stoloniferum</u>

(51) Type specimen of <u>Hypnum</u> <u>stoloniferum</u> Hook. x3.5

<u>Isothecium</u> <u>stoloniferum</u> var. <u>myurellum</u>

(52) Capsules. x3.5

<u>Isothecium</u> <u>cristatum</u>

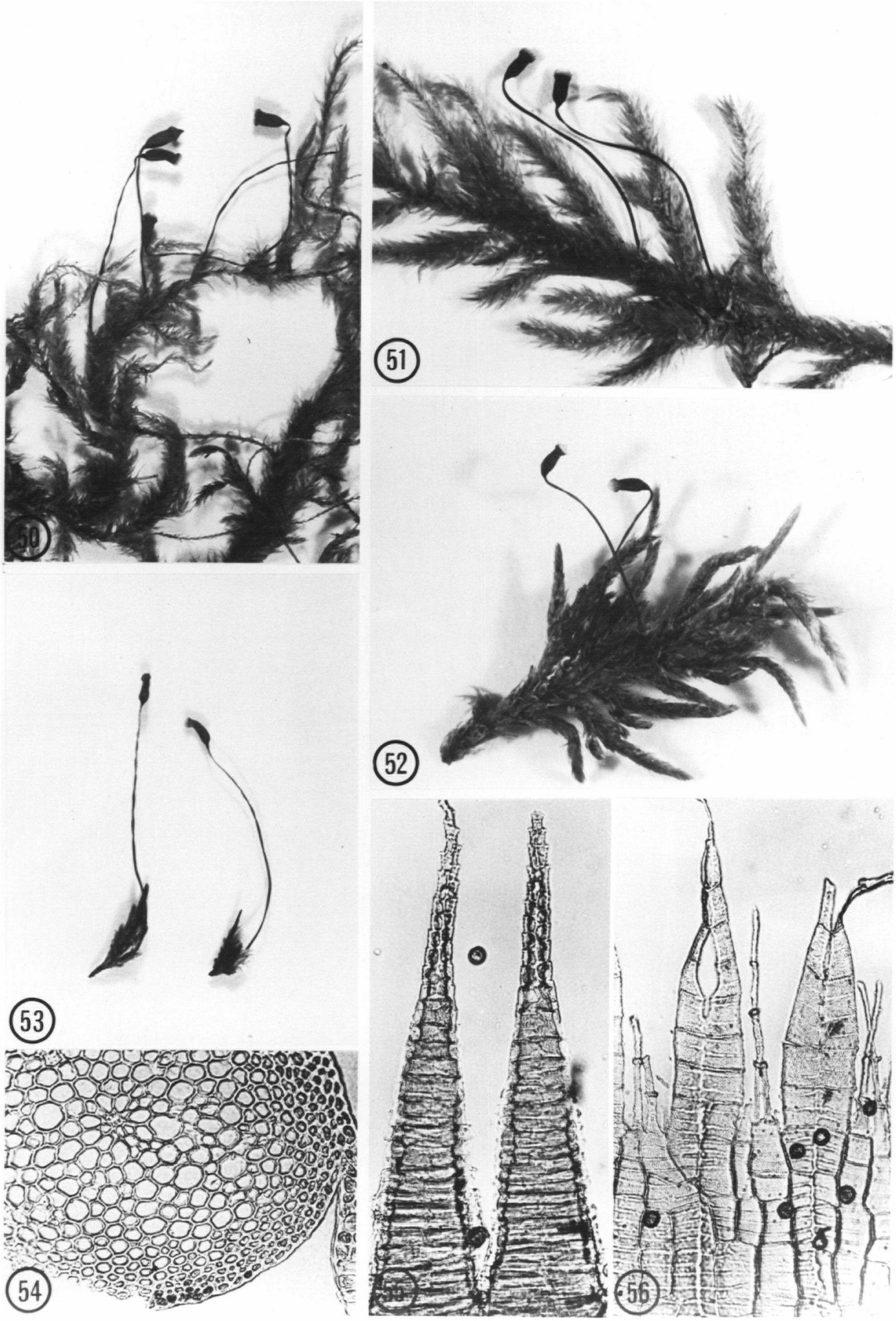
(53) Capsules. x3.5

(54) Cross section of stem. x200

<u>Isothecium</u> <u>stoloniferum</u> var. <u>spiculiferum</u> - pendulous form

(55) Outer peristome teeth. x200

(56) Inner peristome. x200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(to face Drawings I)

Isothecium _cristatum_ - branch leaf

(1) Leaf. x85

(2) Detail of leaf edge. x360

(3) Leaf apex. x360

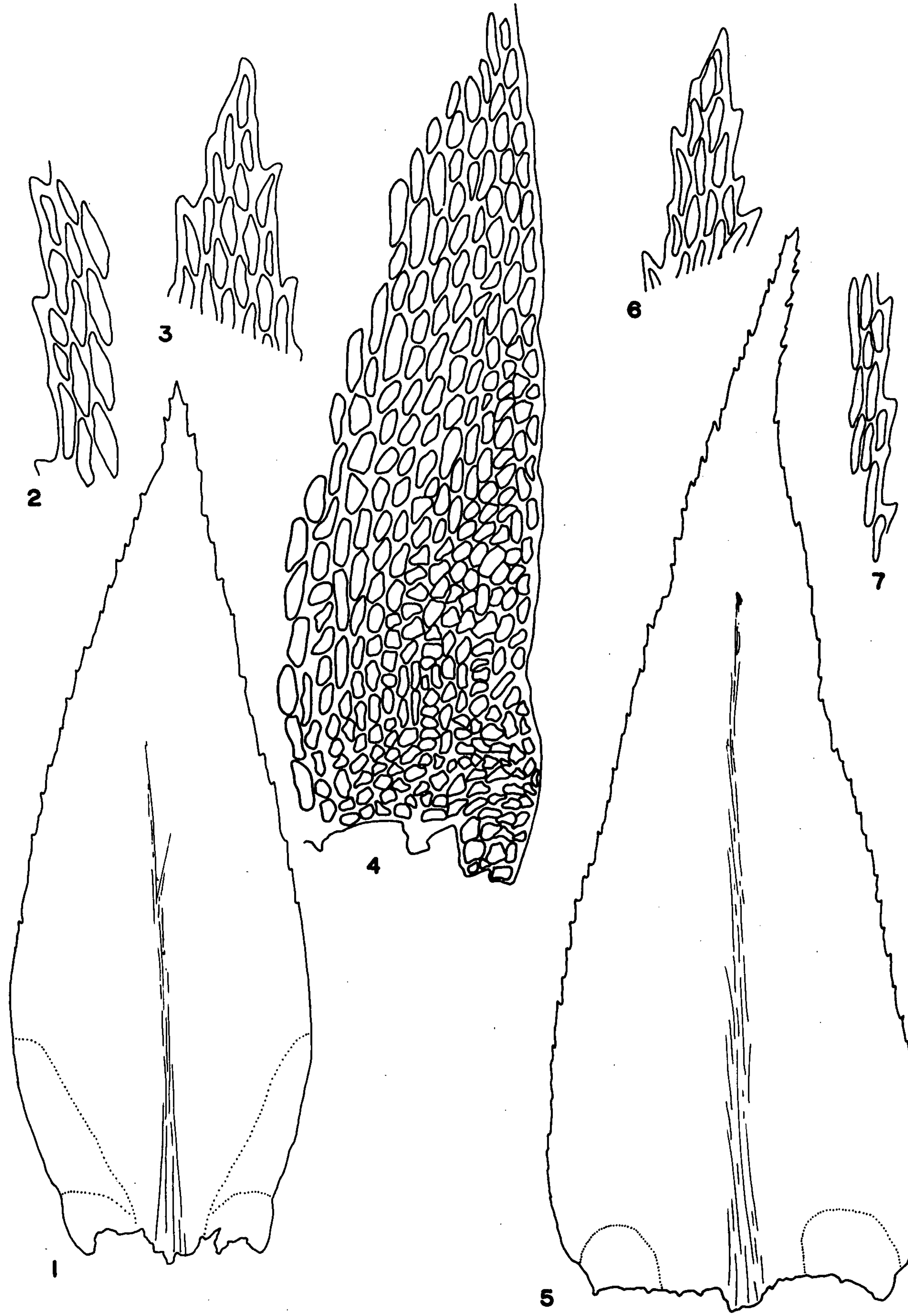
(4) Alar region. x360

Isothecium _stoloniferum_ var. _spiculiferum_ - stem leaf of decayed wood form

(5) Leaf. x85

(6) Apex. x360

(7) Detail of leaf edge. x360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(to face Drawings II)

Isothecium stoloniferum var. *stoloniferum*

(a) Stem leaf

(1) Leaf. x85

(2) Apex. x360

(3) Detail of leaf edge. x360

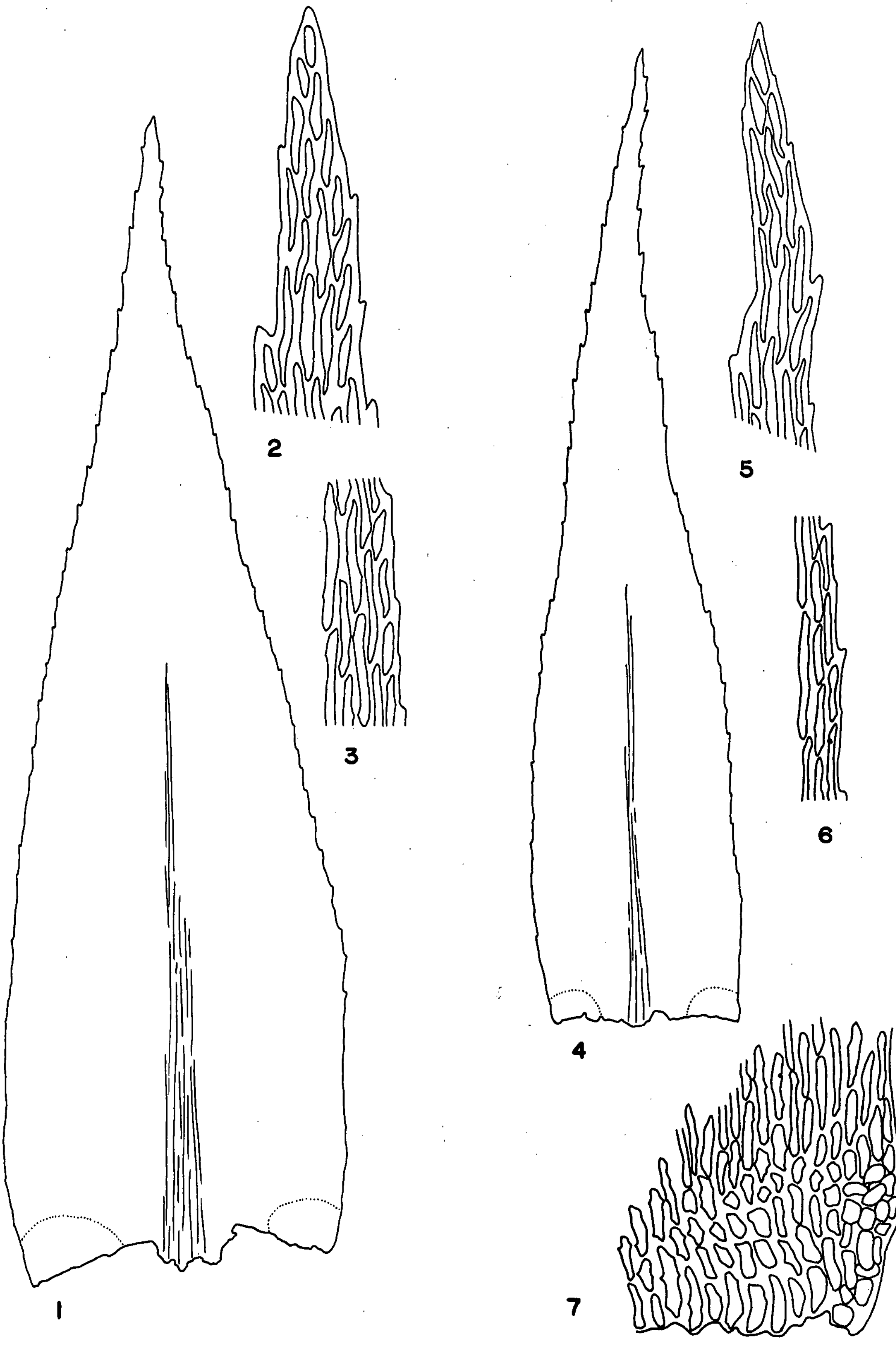
(b) Branch leaf

(4) Leaf. x85

(5) Apex. x360

(6) Detail of leaf edge. x360

(7) Alar region. x360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(to face Drawings III)

Isothecium _stoloniferum_ var. _spiculiferum_ - branch leaf of pendulous form

(1) Apex. x360

(2) Leaf. x85

(3) Detail of leaf edge. x360

(4) Alar region. x360

Isothecium _stoloniferum_ var. _myurellum_ - wet stream valley rock form

(5) Leaf. x85

(6) Alar region. x360

(7) Apex. x360

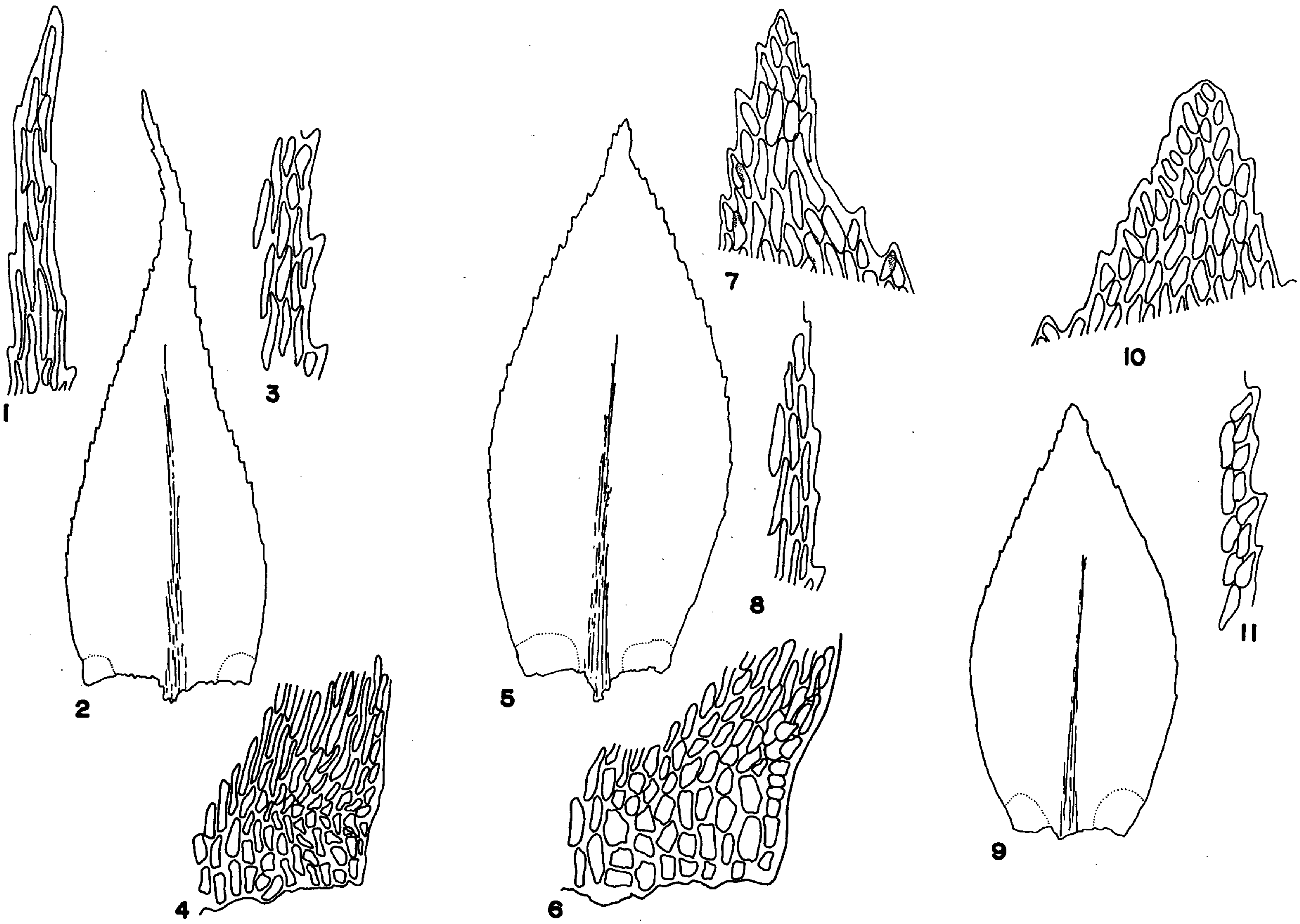
(8) Detail of leaf edge. x360

Isothecium _stoloniferum_ var. _myurellum_ - dry rock form

(9) Leaf. x85

(10) Apex. x360

(11) Detail of leaf edge. x360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COLLECTIONS RECORDED ON MAP I

ALASKA: on rock, sea cliff, Kodiak Is., E. Lepage #25542 (COLO, S-PA)*; on a spruce log, Thum Bay Knight I., Pr. Wm. Sound, W.J. Eyerdam #785 (MICH, S-PA); Wingham Island, (60°03' N., 144°24' W.), Art Mathieson #427 (UBC); rotten log. Yukutat, road to Ocean Cape, L.D. Stair #4959 (MICH); beside lake under conifers, Head of Leo Anchorage, Khaz Peninsula, southwest Chicagof Island, 30 miles NW. of Sitka, D.E. McAllister (CAN); Coronation Island, Art Mathieson #96 (UBC); coniferous woods, Kasaan, south eastern Alaska, E.H. Looff #E-12 (MICH); Cape Bartolome (55°14.3' N., 133°36' W.), Art Mathieson #214 (UBC).

BRITISH COLUMBIA: Gunia Point, Graham Island, (54°10' N., 132°56' W.), Queen Charlotte Islands, Art Mathieson #339 (UBC); common on alders, Chaatl I., Queen Charlotte Islands, W.B. Schofield #18831 (UBC); dry exposed cliff, N. face Mt. Moresby, Moresby Island, Queen Charlotte Islands, (53°08' N., 132°05' W.), W.B. Schofield #25317 (UBC); over alder, Peel Inlet, NW. Moresby Island, Queen Charlotte Islands (head of Inlet) mainly on S. side, W.B. Schofield #15325 (UBC); tree branches, pine-cedar-fir

* The following abbreviations are taken from the INDEX HERBARIORUM Part 1 the Herbaria of the World, compiled by J. Lanjouw and F.A. Stafleu 5th Ed. (1964).

bog near shore, Porcher Island, Oona River, Prince Rupert area, F.M. Boas #170 (UBC); cliff face, Lakelse, 20 mi. E. of Kitimat, W.B. Schofield #20894 (UBC); on bark of yew tree, long lake at N. base of Mt. Buxton, Calvert Island, W.B. Schofield #27910 (UBC); on Alnus bark, road to lighthouse, Cape Scott, V.I., R.D. Williams #63 (UBC); Checkakaklis Is., entrance of Ououkinsh Inlet, W. Vancouver Island, Art Mathieson (UBC); Vancouver Island, Salmon River Valley, 15 miles southeast from Sayward, Alt.: 65 m., V.J. Krajina #3439 (UBC); cliff wall, 30 miles E. of Tofino on Ucluelet Highway along Taylor R., V.I., W.B. Schofield #13482 (UBC); Long Beach area, Vancouver Island, L.K. Wade (UBC); Cowichan Lake, Vancouver Island, Alt.: 228 M., V.J. Krajina #2939 (UBC); rock, Becher Bay, Sooke, Vancouver Island, F. Boas #517 (UBC); on trunks and logs in woods, Victoria, Vancouver Island, J. Macoun #308 (CAN, MICH, NY); dry exposed cliff, Lund, Malaspina Peninsula, W.B. Schofield #18177 (UBC); dry cliff face, Saturna Beach, Saturna I., Gulf of Georgia, W.B. Schofield #14412 (UBC); basalt cliff, near McGuire, Garibaldi area - extensive volcanic area, W.B. Schofield #26242 (UBC); damp boulder face, a small lake S.W. of Squamish, W.B. Schofield #12885 (UBC); wet cliff face, Haney, Blaney Creek Gorge, W.B. Schofield

#16329 (UBC); on boulder, Hope, cliffs above road, W.B. Schofield #23436 (UBC); sloping cliff face, Hells Gate, Fraser River Gorge, W.B. Schofield #17732 (UBC); on boulder in forest, about 8 miles W. of Allison Pass, Manning Park, W.B. Schofield #24741 (UBC); on rocks near hot springs, Halcyon Hot Springs, F.A. MacFadden #95 (NY, UBC).

WASHINGTON: Clallam Co., low limb of a tree, Cape Flattery, F. Kubsch #1875 (MICH); Grays Harbor Co., on windswept boughs of fir trees on shore, Copalis Beach, W.J. Eyerdam #3603 (DS); Clallam Co., Olympic National Park, Hurricane Ridge, R.A. Pursell (COLO); Pierce Co., on stump in fir woods, near Tacoma, G.N. Jones #9823 (NY, US);Scagit Co., tree base, headland of S. end of Fidalgo Is., Deception Pass, W.B. Schofield #23499 (UBC); Whatcom Co., hanging in great mats on trees, Baker lake, A.H. Smith (MICH, NY); Snohomish Co., on logs, Index, E.T. & S.A. Harper (MICH, NY, UC): Kittitas Co., up along the Cle Elum River, P.O. Schallert #306 (NY); Skamania Co., bark of Taxus, W.A. Weber #2705 (COLO).

IDAHO: Bonner Co., in dense masses on branches of coniferous trees, Shady Canon, Lake Pend Oreille, J.B. Leiberg #262 (NY, UBC, US); Kootenai Co., exposed granite ledges at high water mark, Lake Pend Orielle, J.B. Leiberg #173 (NY);

Latah Co., _Pseudotsuga taxifolia_ Association, Douglas Fir Zone. Dense near-climax forest, north slope. West end of Thatuna Ridge, one-half mile west of U.S. 95, 3100 ft., V.G. Cooke #23125 (WS); Clearwater Co., boulder up Skull Creek from North Fork Clearwater, S. Biddulph and N. & B.W. Higinbotham #257 (WS).

MONTANA: Flathead Co., on rock, Columbia Falls, R.S. Williams #299 (NY, WTU); Missoula Co., on the ground, Lolo Hot Springs, T.C. Frye (WTU).

OREGON: Clatsop Co., trunk of _Acer macrophyllum_ in woods along U.S. 30, along Columbia River, 9 miles east of Astoria, F.J. Hermann #18662 (UBC); Multnomah Co., bark of trees, Larch Mountain near summit, Alt. 4056 feet, (Annual Foray of the American Bryological Society) P.L. Redfearn, Jr. #11527 (COLO, US); Marion Co., decaying wood in woods, Salem, E. Slavens #50 (NY); Douglas Co., rotten log, near Curtin, Route 99, W.B. Schofield #22955 (UBC); Josephine Co., on boulder in woods, O'Brien, T.C. Frye Moss Exsiccati #101 (NY); Jackson Co., on basalt, Rogue River Valley near Big Creek, J.B. Leiberg #344 (UBC, US).

CALIFORNIA: Del Norte Co., in "Big Trees" park four miles north of Klamath on Highway 101, L.F. Koch #2323 (MICH, NY, UC, US); Trinity Co., walls of West Weaver Canyon, G.R. Kleeberger (NY); Humboldt Co., on stems of huckleberry bushes in dense moist forest, Eureka, Alt. 200 ft., H.E. Parks & J.P. Trace (UC); Humboldt Co., on trees, Petrolia Steve Ross #650300 (UBC); Humboldt Co., on boulders, slopes by roadside in open *Quercus, Aesculus, Pseudotsuga, Umbellularia* woodland, ca. 5 mi. N. of Garberville, W.B. Schofield #28688 (UBC); Mendocino Co., on old redwood stumps and logs, 10 miles west of Laytonville, I.L. Wiggins #C-122 (J.A. McCleary Herbarium*); Mendocino Co., on cliff, ca. 5 mi. W. of Calpella, W.B. Schofield #28965 (UBC); Butte Co., forested gully above Highway 24 along the Feather River, L.F. Koch #1853 (MICH); Placer Co., on rocks and bases of trees, Canyon Creek, Dutch Flats, F.A. MacFadden #53 (NY, US); Eldorado Co., on rock in shade in American River Canyon, Placerville, Alt. 1350 ft., G.J. Ikenberry #24 (NY); Sonoma Co., Santa Rosa Canyon, M.S. Baker (UC); Marin Co., Mill Valley, M.A. Howe #12 (NY, US); Alameda Co., shaded rock, Oakland, M.A. Howe (DS, NY); San Mateo Co., near Lake Pilarcitos, M.A. Howe (DS, NY); Santa Clara Co., outcrop of stream canyon, Los Altos Hills, Chaparral hills, W.B. Schofield #23060 (UBC); Santa Cruz Co.,

* California State College at Fullerton, 800 N. State College Blvd., Fullerton, Calif., 92631.

6 miles southwest of Santa Cruz, R. & J. Koch (det. by L.F. Koch #2224)(MICH); San Benito Co., along trail, Pinnacles National Monument, L. Koch (UC); Monterey Co., on log, Big Sur-Palo Colorado Road, R.W. Becking #650916 (UBC).

COLLECTIONS RECORDED ON MAP II

ALASKA: Sitka, C.H. Townsend, Albatross Collections #491 (COLO, DS, NY, S-PA); on *Chamaecyparis nootkatensis*, Washington Bay, Kuiu Island W.J. Eyerdam #5260 (WS, S-PA); forest floor, Coronation Island, B.J. Neiland #703 (CAN); Annette I. (near Ketchikan), G.W. Gasser #36 (S-PA).

BRITISH COLUMBIA: in spruce forest and festooning trees, Masset, Graham Island, Queen Charlotte Islands, W.B. Schofield #14259 (UBC); base of tree, seaside cliffs of East Narrows, Skidegate Channel, Moresby Island, Queen Charlotte Islands, W.B. Schofield #14073 (UBC); on branch, Digby Island, Prince Rupert area, F.M. Boas #31 (UBC); on boulders in forest, long lake at N. base of Mt. Buxton, Calvert Island, W.B. Schofield #27829 (UBC); raw humus on rock wall by sea, Bay at N. tip of Vancouver Island, R.D. Williams #93 (UBC); on living timber, Holberg, North V.I., E.C. Mackenzie #398 (MICH); Johnson Lagoon, Brooks Peninsula, W. Vancouver Island, Art Mathieson (UBC); Salmon R. Valley, 15 mi. SE. from Sayward, Vancouver Island, V.J. Krajina #3420 (S-PA, UBC); Gold Stream Canyon, Cumberland, Vancouver Island, J.W. Bailey #85 (CAN, DS, MICH, NY, S-PA); Mt. Arrowsmith 5000', Vancouver Is., J. Macoun (CAN, S-PA); encasing tree-trunks, 17 mi. E. of Tofino, on Ucluelet Hwy. along Kennedy R., W.B. Schofield #13494 (UBC); Pt. Renfrew, Van. Is., Waldron #16 (NY); alder root, Laundry's Farm, Saltspring I., F. Boas #540 (UBC); rock, Stanley Park, Vancouver, V.J. Krajina #2679 (UBC); cliff in canyon, Wigwam Crk., Indian Arm, near Vancouver, W.B. Schofield #20506 (UBC).

WASHINGTON: Jefferson Co., on *Acer circinatum* trunk and branches, Lower Hoh River, B.I. Brown and W.C. Muenscher #72 (MICH, NY, UC, US, WTU); Jefferson Co., on *Picea sitchensis*, lower trunk, near shore, Queets, B.I. Brown and W.C. Muenscher #74 (MICH, NY, UC, US, WTU); Jefferson Co., Olympic Mtn. C.V. Piper #74 (NY, US); San Juan Co., base of tree in moist woods, C.M. Roberts #251 (NY); Snohomish Co., on rotten logs, Darrington, Mnt. loop highway, 2400 ft. elev., R.W. Becking #5210346 (WTU); Snohomish Co., on trees in shady places, Big Four, Alt. 2500 ft., J.W. Bailey (MICH); King Co., up base of tree, Green River Canyon, near Black Diamond, W.B. Schofield #26333 (UBC); Pierce Co., Mt. Rainier, P.O. Schallert #921 (US).

OREGON: Lincoln Co., on trunk of huge alder tree, U.S. Highway 101, 2 mi. S. of Yachats, Cape Perpetua Forest Camp, Campsite 31, K. Young (WTU); Curry Co., log near streamlet, Humbug Mt. State Park, W.B. Schofield #21926 (CAN, UBC).

CALIFORNIA: Humboldt Co., on alder near stream Prairie Creek Redwoods, W.B. Schofield #28797 (UBC).

COLLECTIONS RECORDED ON MAP III

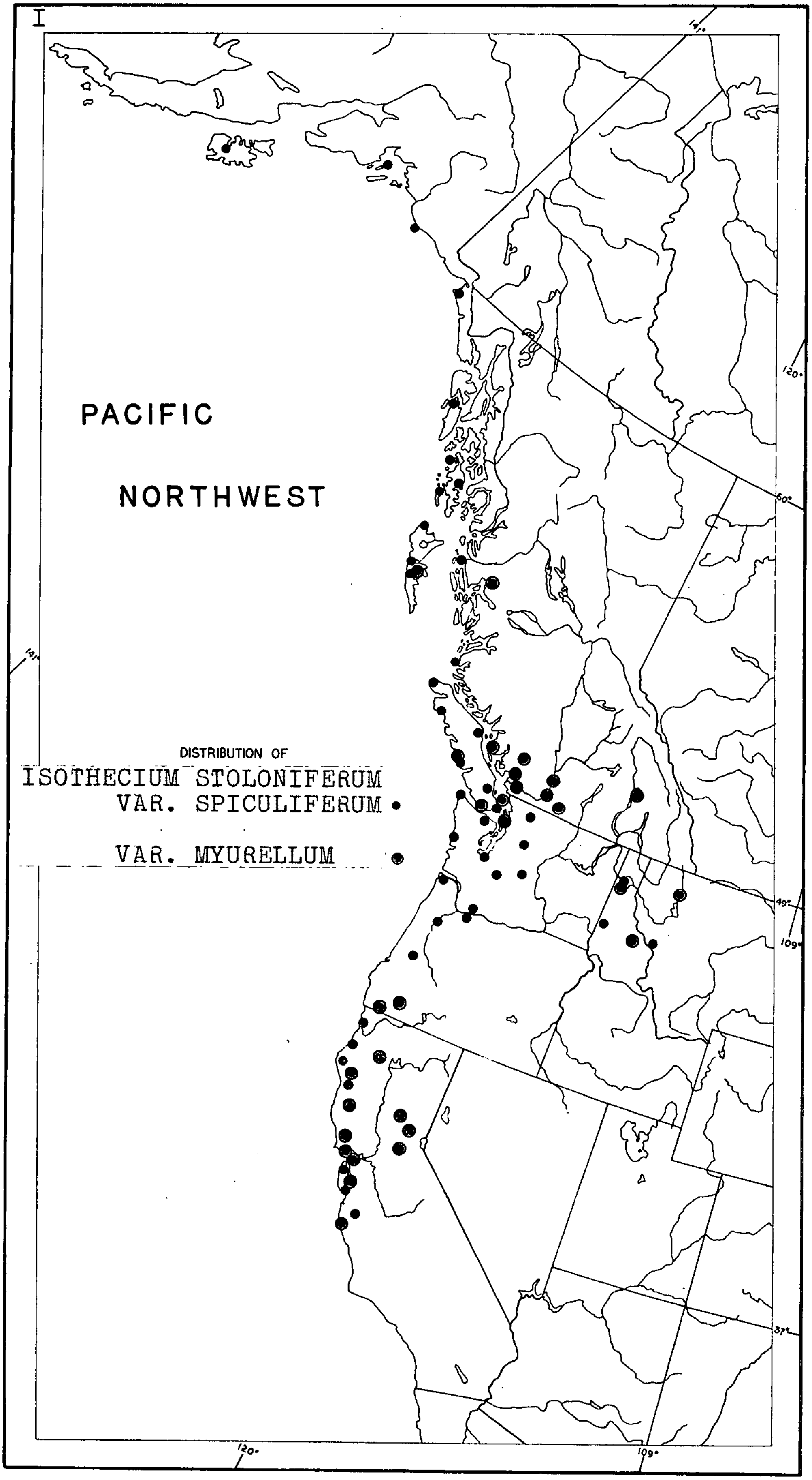
BRITISH COLUMBIA: boulders of open slope, ca. 13 mi. N. of Alice Lake, near Garibaldi, W.B. Schofield #26101 (UBC); on boulder of scree near Lion's Bay, Howe Sound, Vancouver area, W.B. Schofield #22445 (UBC); on rocks, North Arm Burrard Inlet, J. Macoun #125 (CAN, NY); up base of Douglas fir, near west end of Hoggan Lake, Gabriola Island, W.B. Schofield #22841 (CAN, UBC); dry cliff face, Bodega Hill, Galiano Is., S. Strait of Georgia, W.B. Schofield #17384 (CAN, S-PA, UBC); on logs and bases of trees - roadside, Plumper Bay, South Pender Island, W.B. Schofield & F.M. Boas #17007 (CAN, UBC); on rocks in woods, Sea's Farm, Victoria, V.I., J. Macoun #310 (CAN, NY); rock, Becher Bay, Sooke, Vancouver Island, F. Boas #524 (CAN, UBC).

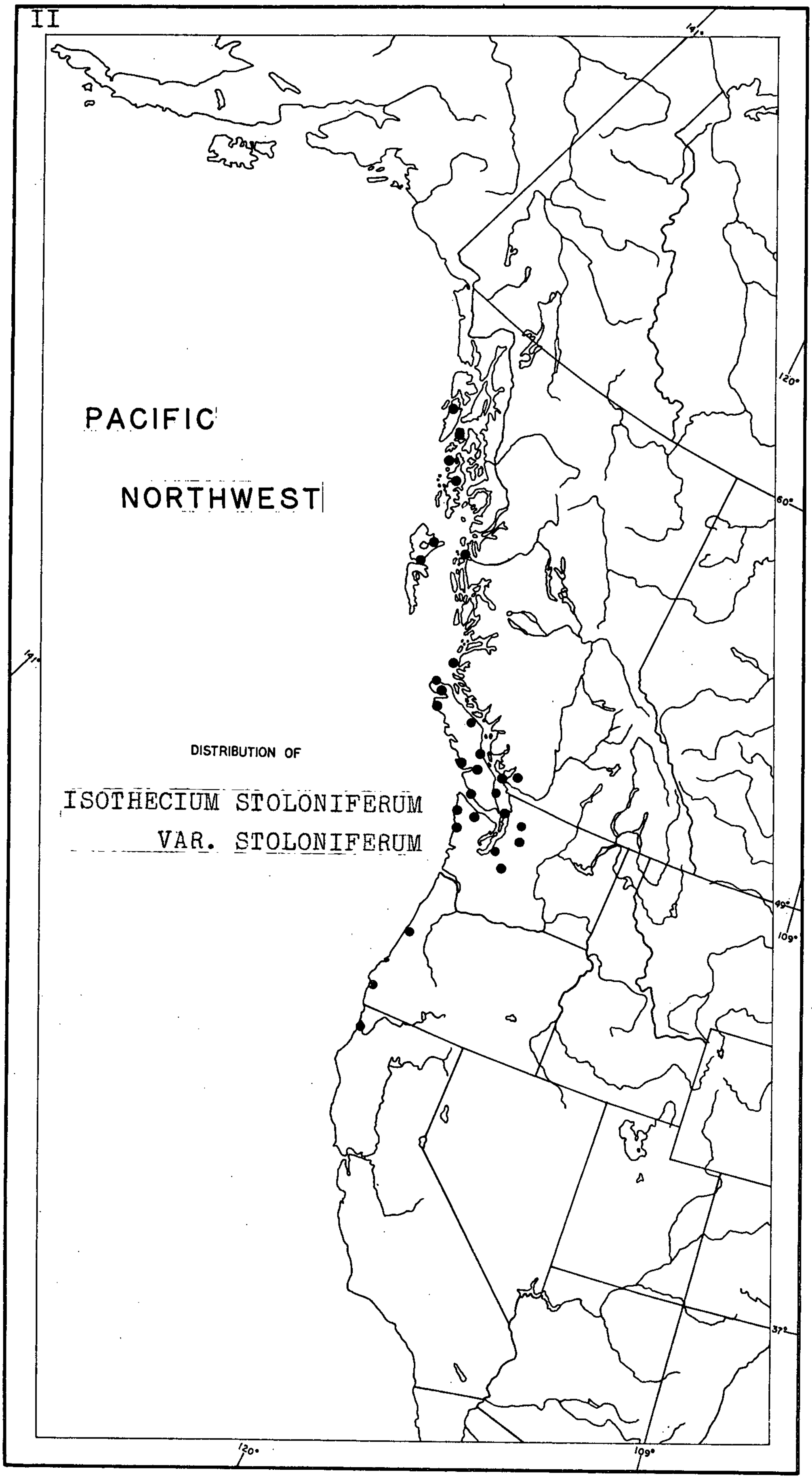
WASHINGTON: Island Co., on ground, Whidby Island, N.L. Gardner #140 (NY, UC); Clallam Co., on log, Krause's Bottom area Elwha River, Olympic National Park, W.B. Schofield #19400 (CAN, UBC); King Co., on ground, Lake Nash H.L. Gardner, (NY, UC).

OREGON: Multnomah Co., on fir trees near the ground, J.T. Howell #15 (NY); Multnomah Co., ground near Portland, L.T. Henderson (MICH); Benton Co., on log N.W. of Corvallis, H.C. Gilbert #10 (NY); Lane Co., 5 to 6 miles southwest of Eugene, Spencer Creek Valley, on road to Lorane, in woods,

E. Lawton #3396 (UAC); Douglas Co., rotten Douglas fir log, Canyon Creek, near Canyonville, W.B. Schofield #23016 (UBC).

CALIFORNIA: Humboldt Co., on log, Arcata, J.W. Howe (COLO); Humboldt Co., in redwood grove, Richardson's Grove, P.C. Hutchinson #915 (UC, US); Trinity Co., walls of West Beaver Canyon, (checked by A.J. Grout) H-38a (NY); Mendocino Co., on huge boulder in open forest, 10 mi. N. of Longvale, Long Valley Creek, W.B. Schofield #29342 (UBC); Mendocino Co., redwood log, 16 mi. E. of Noyo on Rte. 20, W.B. Schofield #28915 (UBC); Butte Co., boulders under oaks on river bank, Enterprise on South Fork Feather River, W.B. Schofield #23217 (UBC); Sonoma Co., on log, Cazadero, M.A. Howe (DS, NY); Napa Co., Walter Springs on Monticello-Pope Valley road, L.F. Koch #2341a (MICH); Marin Co., near summit of East Peak, Mt. Tamalpais, J.T. Howell (MICH); Contra Costa Co., shaded rock, Moraga Ridge, J.T. Howell (MICH, NY); Santa Clara Co., on log, Los Altos Hills - chaparral hills, W.B. Schofield #25252 (CAN, UAC, UBC); San Mateo Co., on rocks, near Mission Dolores, San Francisco, M.A. Howe (NY); San Mateo Co., on old log of redwood forest floor margining Pescadero Creek, ca. 3 miles NE. of La Hondo Road from Pescadero, W.B. Schofield #11211 (UBC); Santa Cruz Co., Aptos, C.F. Baker #1978 & #1974 (NY); Monterey Co., Big Sur Park, P.O. Schallert #16583 (MICH); on base of tree in ravine behind White's Landing, 5 miles N. of Avalon, Santa Catalina I., W.C. Steere (DS).


I
PACIFIC
NORTHWEST
DISTRIBUTION OF
ISOTHECIUM STOLONIFERUM
VAR. SPICULIFERUM
VAR. MYURELLUM
141°
120°
60°
49°
109°
37°


II
141°
120°
60°
49°
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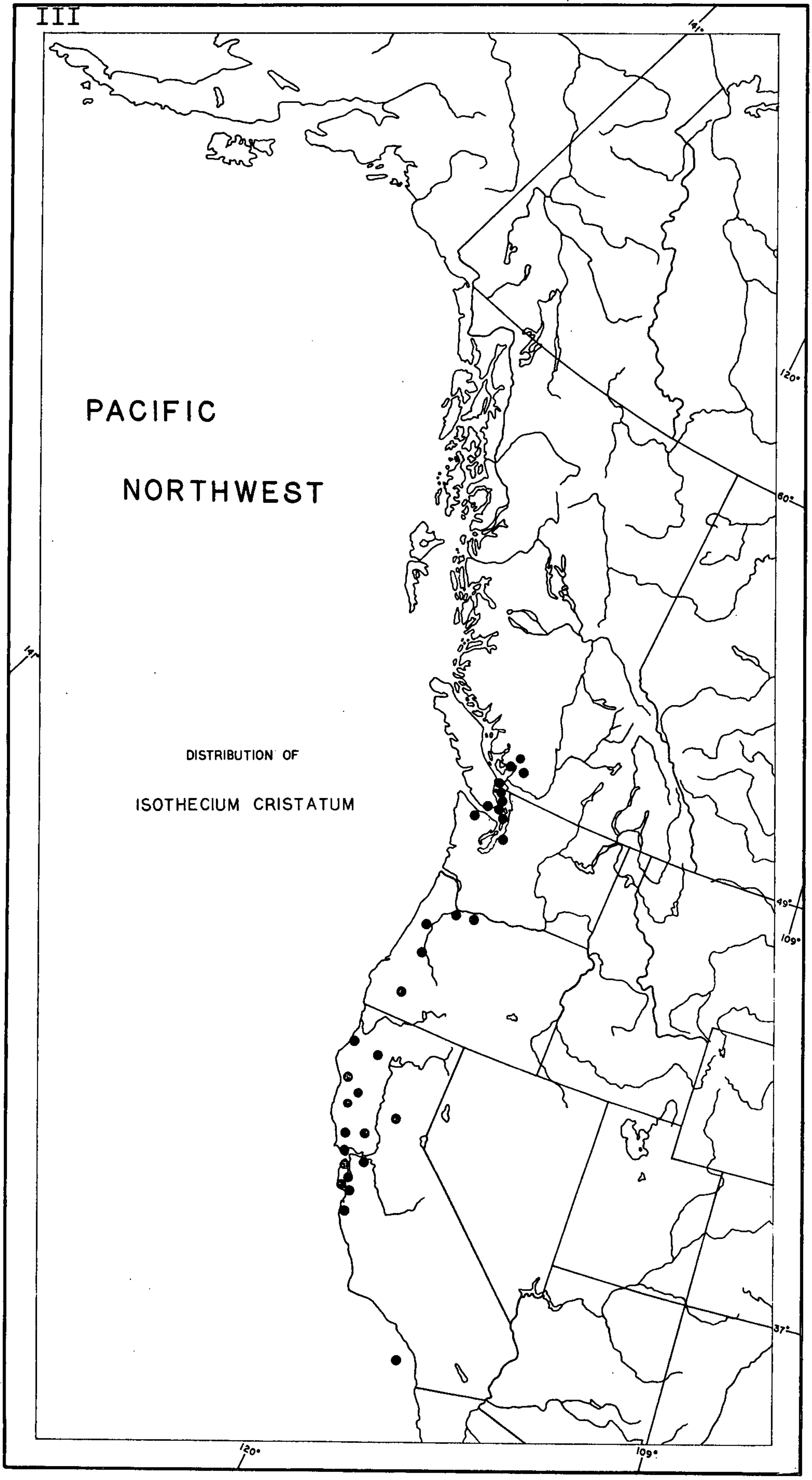
37°
PACIFIC
NORTHWEST
DISTRIBUTION OF
ISOTHECIUM STOLONIFERUM
VAR. STOLONIFERUM


III
PACIFIC
NORTHWEST
DISTRIBUTION OF
ISOTHECIUM CRISTATUM
141°
120°
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49°
109°
37°
141°
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