

The Rhacomitrium heterostichum complex
in British Columbia

by

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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

November, 1969

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The University of British Columbia
Vancouver 8, Canada

Date 17th November, 1969.

ABSTRACT

The Rhacomitrium heterostichum complex in British Columbia consists of four species and five varieties:

R. "laxum", R. heterostichum, R. heterostichum var. affine, R. sudeticum, R. sudeticum var. macounii, R. brevipes, R. brevipes var. "laevis", var. "eramulosum" and var. "microcarpiformis". Within each of these taxa minor variations occur.

R. sudeticum tends to be confined to sub-alpine and alpine localities and R. heterostichum to lower elevations, while R. "laxum" and R. brevipes show no altitudinal limitations.

There appears to be a positive correlation between nature of branching and details of leaf apex structure to moisture conditions: short branches, abbreviated hair point and shorter leaf cells in the leaf apex being commoner in specimens of wet sites than in specimens of dry sites. Experimental evidence is needed to determine phenotypic plasticity in these characters, since they are widely used to distinguish among the various taxa of the R. heterostichum complex.

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ACKNOWLEDGEMENT

The author gratefully acknowledges the guidance, advice and encouragement extended to her by Dr. W.B. Schofield throughout the progress of this investigation.

Sincere thanks go to Professor G.H.N. Towers, Dr. G. Hughes and Dr. J.R. Stein for their continued interest and advice during the study.

The author wishes to thank Dr. R.R. Ireland, Curator of the Bryological Herbarium, National Museum of Canada, who sent on loan specimens, particularly type specimens; Mr. V.L. Bourne for assistance in photomicrography and Dr. Q.A. Fattah for encouragement and help throughout her studies.

Acknowledgement is expressed to the Education Department, Government of East Pakistan, for granting study leave.

National Research Council, Canada, contributed financial assistance through a grant awarded to Dr. W.B. Schofield.

INTRODUCTION

Rhacomitrium, a genus in the family Grimmiaceae (Musci), was described by Bridel in 1819 to accommodate a number of species previously included in Trichostomum Hedw. The genus Trichostomum was so broadly interpreted that it included taxa belonging to the families Grimmiaceae, Pottiaceae and Ditrichaceae. In erecting the genus Bridel gave greater prominence to gametophyte characters than had previous workers, basing the genus largely on the very characteristic sinuous nature of the leaf cell walls. This type of areolation is virtually unique to Rhacomitrium and separates it clearly from all other genera except the closely related Grimmia.

Rhacomitrium contains seventy five species (Van der Wijk, Margadant and Florschütz, 1967) distributed throughout the world, eleven of which occur in North America (Crum, Steere and Anderson, 1965).

Rhacomitrium heterostichum is one of the most variable species in the genus possessing many ill-defined forms, thus the species has frequently been treated very broadly as the "Rhacomitrium heterostichum complex". Most representatives of this complex grow on rocks or sometimes on earth in mountainous regions, particularly in temperate climates of the Northern Hemisphere.

Taxonomists have frequently faced the problem of defining and correlating the characters found in the R. heterostichum complex (Dixon, 1924; Persson, 1947;

Nyholm, 1956). They have recognized this variability in different ways. Their decisions have been based on morphological and anatomical studies of herbarium specimens as well as experience with living plants in the field.

Dixon (1896) stated that "Racomitrium heterostichum is our most variable species and the multiple forms are so inconstant and so ill-defined as almost to defy classification. They depend chiefly on the mode of ramification, the relative length, or absence, of the hair point, the varying acuteness of the leaves, and the form, size and texture of the capsule. There appears to be little or no correlation between these characters and it is, therefore, unsafe to found even varieties on them."

Persson (1947) stated that the "Heterostichum group of the genus Racomitrium is everywhere a rather critical one and especially on the Pacific coast of North America." He examined some of the Alaskan-Yukon heterostichum group and observed that the leaf cells generally were clearly papillose, a feature not present in European material. Besides this character the specimens differed from European R. heterostichum in having the upper cells of the leaves of the same form as by R. microcarpon (Hedw.) Brid. (R. ramulosum Lindb.) i.e., pronounced elongate, and not isodiametrical as in R. heterostichum. In capsule shape, the specimens were most similar to R. heterostichum. Summarizing this, he concluded that "this common Alaskan Racomitrium had characters of both R. heterostichum (most related), R. microcarpon and R. sudeticum

(often given as a variety or subspecies of R. heterostichum) but besides had also its own important character: the papillose leaf cells."

Jones (1933) lists several varieties for R. heterostichum

var. affine (Schleich) C. Jens.

var. affine f. obtusum (sm.) Moenk

var. gracilescens B.S.G.

var. sudeticum (Funck) Jones

var. sudeticum f. occidentale (Ren. & Card.) Jones

var. macounii (Kindb.) Jones

var. ramulosum (Lindb.) Jones

Jones concluded that, with the possible exception of Grimmia apocarpa Hedw. and G. trichophylla Grev., R. heterostichum sens. lat. possesses the most variable species in the Grimmiaceae. Anderson (1958) stated that "... in spite of the wide choice of epithets available within this complex, I am unable to find satisfactory names for variations from North Carolina." He observed many specimens which exhibited complete intergradation of different characters.

The plants of the Rhacomitrium heterostichum complex are very difficult to determine. On habit sometime there is a remarkable resemblance to other species of the genus. R. heterostichum in its mode of growth is sometimes erect and not unlike a Grimmia, such as Grimmia trichophylla or G. decipiens (Schultz) Lindb.; R. sudeticum is quite often mistaken as Grimmia in the field.

Often plants with somewhat similar characters (e.g. upper leaf cells, nature of margin, capsule shape, etc.) are very different in habit. Colour and branching patterns of the gametophyte are highly variable. Thus forms with elongated upper leaf cells also possess a most widely different form of capsule and varying degrees of robustness and branching. It is also not uncommon to find plants with the majority of stems having numerous short lateral branches and others completely lacking short lateral branches. The upper cells of the leaf are sometimes highly variable. While in most leaves the upper cells are round, in some cases rectangular cells dominate or are sometimes mixed with round cells. Sometimes in a single plant there may be many leaves where the upper cells are elongated while others have the upper cells entirely rectangular or mixed with round cells.

It is possible that the nature of the hair point and the shape of the cells in the upper part of the leaf are related to the wetness of the habitat. Kawai (1965) in his study of Grimmia, noted that in G. apocarpa Hedw. in wet places cells of the leaf especially at the apex are short, hyaline point is usually not found and indentions are obscure or sometimes even absent, but in dry places the leaf cells tend to be long, hyaline point and indentions become conspicuous. A similar correlation has been noted in Rhacomitrium, particularly in the R. heterostichum complex. In some cases plants grow in seasonally wet habitats and active growth of the plant is confined to the time that

moisture is available (largely autumn to spring) while during the remainder of the year the habitat is dry and the plant desiccated.

Experimental studies need to be conducted in order to solve this problem. It is possible that such studies would considerably clarify the nature of the structural diversity within this species complex, though they would require a several years' duration to determine whether repeated environmental changes consistently produced the same morphological responses in the gametophyte.

The main object of the present investigation is two-fold: (1) to determine the extent of variability within the species complex in British Columbia and (2) to find out whether or not there is a sufficient correlation between different characteristics to delimit sub-specific taxa. Information was derived from both gross morphology and detailed anatomy, particularly of the leaf. Investigations were carried out on herbarium specimens collected in British Columbia and compared with European specimens. It was from European material that the species complex was first recognized. North American bryologists have compared American specimens with those from Europe, and attempted to fit the specimens into the circumscription of the European species. In cases where the differences were considered too marked, new taxa were described to accommodate them.

Because of the considerable variability within the R. heterostichum complex, this had led to a great inflation of

names, each accepted taxon in North America being accompanied by a vast array of synonyms.

Detailed attention was given to branching pattern; size and shape of leaves, leaf areolation, anatomy of leaves, nature of stratification of the leaf margin, lamina and costa; length and nature (twisting and papillosity) of seta; shape, size and nature of the capsule; characteristics of the peristome teeth; exothecial cells; presence and number of stomata; nature and shape of annulus and operculum; and shape, nature and size of spores. Diagnostic characters used in the construction of keys in manuals were carefully examined.

It was found that mounting material in Hoyer's solution (Anderson, 1954) gave greater clarity to the cellular details than water mounting. Although this involves a greater amount of work, the resulting clarity makes determinations more reliable and it leaves permanent reference slides of the material studied.

The key to the British Columbia taxa (page 40) is by no means ideal. Many atypical specimens simply will not fit into a key, unless it is made extremely long and cumbersome. I have tried to make the key as reliable as possible. The key should, however, produce reliable determinations for the majority of the specimens. It can be perfected only after considerable further use.

For a number of reasons it was not possible to borrow type specimens. In some cases the type specimen could

not be located; in some cases it may have disappeared. Since the type descriptions are frequently inadequate, the evaluation of these taxa is virtually impossible without examination of a type specimen.

Due to unavailability of some of the literature, plants from British Columbia could not always be compared with type descriptions. Thus a number of the taxa are tentatively given the names that seem to best apply to them. To others, for which no available name seems satisfactory, a provisional designation is given. In some cases, should the assumptions made in this thesis prove valid, new taxa will need to be carefully described and illustrated. Such should not be done, however, until a wider survey is made of the entire R. heterostichum complex.

All specimens cited, unless noted otherwise, are from the Bryophyte Herbarium, University of British Columbia (UBC). Specimens cited only by number are those of W. B. Schofield. Specimens from the herbarium of the National Museum of Canada are cited as CAN.

TAXONOMIC TREATMENT

The genus Rhacomitrium was first described by Bridel (1819) in Mantissa Muscorum. Rhacomitrium is related to Grimmia through the sub-genus Dryptodon. The most distinctive generic characters which separate it from Grimmia are the peculiar basal areolation of the lower third of the lamina, the deeply cleft peristome, and the subulate operculum. In R. patens (Hedw.) Hueben, the nature of the habit and leaf anatomy would place this species in the genus Grimmia, in which it is placed by many European authors (Nyholm, 1957; de Sloover & Demaret, 1968). The peristome, however, is characteristic of Rhacomitrium. In other species of the sub-genus Dryptodon, however, more characters are in common with Rhacomitrium than with Grimmia. Unfortunately no type species has been selected.

Description of the genus:

Rhacomitrium Brid. Mant. Musc. 78, 1819.

Gametophytes robust, mostly rupestral, usually loosely and widely caespitose, yellowish or blackish green; stems spreading, bearing rhizoids only at the base, leafy throughout, often with numerous short lateral branchlets; central cylinder absent, leaves numerous, imbricated when dry, mostly lanceolate, acuminate or obtuse, often with hyaline hair points consisting of linear, non-chlorophyllose cells; costa complete, usually broad and flat, homogeneous, single, usually percurrent or slightly sub-percurrent, leaf margins

sometimes bistratose, or revolute, usually entire except on the terminal hyaline portion, occasionally denticulate, leaf cells sometime papillose, usually more or less incrassate, the upper ones mostly small and roundish quadrate or somewhat elongated, the basal cells linear or rectangular, usually nodulose or sinuose, seldom entire; dioecious; antheridia and archegonia terminal on the stem and on short lateral branchlets.

Sporophyte: seta long, straight or arcuate, usually twisted to the right (with the exception of three species); usually smooth, capsule erect, exserted, ovoid or ellipsoid or cylindrical, narrow mouthed, smooth; stomata present at the base of the capsule; annulus present; calyptra non-plicate, mitrate, often papillose at the apex, usually long-beaked; operculum conical, long-beaked; peristome present, single; teeth 16, united at the base, but deeply cleft into 2-3 linear divisions, trabeculate, basal membrane not extending beyond the annulus; spores 0.8 - 35 μ in diameter. Sporophytes generally maturing in spring, commonly produced in most species.

Ecology: Essentially rupestral on acidic substrata; most species essentially xerophytes and tolerant of perennial desiccation; some tolerant of wet situations, but none essentially aquatic.

Geographic distribution: Essentially cosmopolitan, but most species confined to temperate and arctic climates; in tropical latitudes confined to the mountains; circumpolar

throughout the Northern Hemisphere in Eurasia and North America; in the Southern Hemisphere scattered in South America, Australasia and Africa; infrequent in the Pacific Islands.

Rhaconitrium "laxum" n. sp.

Gametophytes greyish green to dark brown; stems 5 - 16 cm long, with few or no elongated branches (if present, about 1 - 6 cm long), short tuft-like lateral branchlets none (Pl. I, fig. 1 & 2); rhizoids reddish brown, smooth, branched or unbranched, outer wall thick, cross wall oblique; stem densely covered with leaves; leaves loosely imbricate to divergent when dry (Pl. I, fig. 1 & 2), well spreading when wet, lanceolate from a broad base, acuminate, up to 6.2 mm long, usually about 5 mm including 0.5 - 2.7 mm long hyaline point (Pl. XVII, fig. 1-4) which is usually toothed only on the margin or with very few weak teeth on the surface as well, not papillose (Pl. I, fig. 3); upper leaf cells elongated, narrow, about $18 - 40 \mu : 2.5 \mu$ (Pl. I, fig. 7); lower cells about $24 - 40 \mu : 2.5 \mu$, all cell walls sinuose (Pl. I, fig. 4), appearing weakly papillose because of uneven thickening of the sinuose cell wall; margin of the leaf entire or appearing somewhat papillose in the upper portion, and entire downward, unistratose throughout (Pl. II, fig. 1, 2, 5 & 8) or occasionally irregularly bistratose toward the middle portion of the leaf (Pl. II, fig. 7), revolute either on one margin or both (Pl. XVII, fig. 1-4), usually one side more strongly revolute than the other, not or up to the apex; costa flat in the lower portion but distinctly 2-ridged in the upper portion (Pl. I, fig. 6), extending far into the hyaline point, 2 - 4 stratose in cross section, $70 - 90 \mu$ wide, usually cells in the upper row are larger than the lower row or more or less

similar in size (Pl. II, fig. 1-5 & 8); dioecious; perichaetial leaves much thinner and broader, cells mostly hyaline, with or without hyaline point.

Sporophyte: seta usually 4 - 5 mm long, rarely as short as 2.5 mm or up to 8.5 mm, corkscrew twisted to the right, smooth; capsule erect, ellipsoidal or cylindrical, 1.5 - 2.8 mm long and 0.6 - 0.9 mm broad (Pl. I, fig. 5); upper exothecial cells narrow, nearly transversely rectangular (Pl. III, fig. 2), brown, median cells rectangular to elongate (Pl. III, fig. 4), lower cells round or rectangular with 10 - 16 phaneropore stomata (Pl. II, fig. 3); operculum rostrate, about 0.8 mm long, beak usually straight, sometimes oblique, smooth; annulus 2 - 3 rows of golden brown cells (Pl. II, fig. 6); peristome teeth brownish yellow, 0.4 mm long, papillose (Pl. III, fig. 1), forked, forks joined or free, transverse band not prominent, mostly not swollen on the margin (Pl. III, fig. 3); calyptra conical, not papillose at apex; 5 - 8 lacerations at the base, 1.2 - 1.8 mm long; spores round, granular, greenish yellow, 12 - 13 μ in diameter (Pl. II, fig. 4). Sporophyte maturing late spring to summer.

Habitat: On dry, exposed or shaded rocks or humid, wet cliff, largely at lower elevations.

Specimens examined:

Queen Charlotte Islands: Dawson Inlet, Graham Island, 33438; Schofield & Vaarama, 24647; Anna Inlet, Moresby Island, Schofield & Vaarama 24292; Wells Cove, S. W. Moresby Island

31700; Chaatl Island, Schofield & Boas 18760; Takakia Lake, Moresby Island, 24898; Bigsby Inlet, Moresby Island, Schofield & Vaarama 24131; Richardson Island, Schofield & Vaarama 24222; Lagins Creek, Graham Island, 30021; Bigsby Inlet, Moresby Island, 32509; Van Inlet, Graham Island, Schofield & Sjors 32148; Echo Harbour, Moresby Island, 32496; Goose Cove, Graham Island, 30550; Blue Heron Cove, Moresby Island 31384; Kootenay Inlet, Moresby Island, 31146; Peel Inlet Area, Moresby Island, 30455;

Mainland and adjacent Islands: Keith Anchorage Area, Calvert Island, Schofield & Williams 27115, 27109; North Vancouver, 19924; Long Lake, Calvert Island, Schofield & Williams 27837, 27902, 27907; Wigwam Creek, Indian Arm, 20540; Horseshoe Bay, Schofield & Anderson 33378; Deeks Creek, Howe Sound, 20666; Lake between Britannia Beach and Squamish, 13119; W. of Wedgeborough Pt., Calvert Island, Schofield & Williams 27146; Halfmoon Bay, Sechelt Peninsula, Schofield & Boas, 18060; Murrin Park near Squamish, 20347.

In the following specimens the gametophytes are comparatively much shorter, 2 - 3.5 cm long (Pl. I, fig. 2), darker and the costa is not ridged in the upper portion (Pl. XVII, fig. 2 & 3).

Specimens examined:

Queen Charlotte Islands: Sperm Bay, Moresby Island, 31732; Keith Anchorage Area, Calvert Island, Schofield & Williams 27114, 26876; Centre Bay, Gambier Island, Dill 15562.

From sub-alpine areas of the Queen Charlotte Islands some specimens, otherwise typical, possess leaves with bistratose margins and with occasional portions of the lamina also bistratose (Pl. II, fig. 7).

Specimens examined:

Peel Inlet Area, Moresby Island 30438; Chaatl Island, Schofield & Boas 18760.

This is the most distinctive and least variable taxon of the heterostichum complex in British Columbia. The gametophytes are uniformly without any short lateral branchlets, possess long, lanceolate leaves with elongated upper cells, ridged costa in the upper portion and with transversely rectangular upper exothecial cells. These characters are consistent even in different habitats.

The unbranched habit and long upper leaf cells readily separates this taxon from other members of the heterostichum complex and the distinctly ridged costa, elongated upper leaf cells and long hyaline point from R. depressum Lesq. and R. aquaticum Brid. As this taxon is clearly different from all other known species it could be described as a separate species of Rhacomitrium.

Some specimens are distinctly bistratose in the margin; this might be separated as a variety as in the case of var. affine (Schleich) C. Jens. of R. heterostichum which is separated mainly on the basis of bistratose margin. Since so few specimens are available and only a single distinguishing

character is involved, it seems presently most reasonable not to give this variation any special taxonomic status. Instead it is considered within the variability of the taxon. The same holds true for the forms in which the costa is not ridged in the upper portion of the leaf.

Rhacomitrium heterostichum (Hedw.) Brid. Musc. Recent Suppl.
4:79, 1819.

Trichostomum heterostichum Hedw. Sp. Musc. 109, 1801.

Dryptodon carnosus Brid. Bryol. Univ. 206, 1826.

Trichostomum carnosum Dicks; Brid. Bryol. Univ. 206, 1826.

Trichostomum stenocarpum Hampe, in Hueben Musc. Germ. 208, 1833.

Grimmia heterosticha C. Muell. Syn. 1:807, 1849.

Rhacomitrium heterostichum Subsp. Vulgare Loeske,
Laub. Eur. 1:183, 1913.

Gametophytes greyish green to dark brown, often blackish; stem 2 - 8 cm long, erect or spreading usually with many short tuft-like lateral branches (about 1 - 3 mm long) and elongated branches (about 1 - 4 cm long) (Pl. IV, fig. 1 & 2); rhizoids long, branched or unbranched, few, thick walled, smooth; leaves loosely imbricated when dry (Pl. IV, fig. 1 & 2), erect spreading when moist, lanceolate, from a broad base, 2.2 - 3.1 mm long including the 0.2 - 0.8 mm hyaline point (Pl. XVIII, fig. 1-3) which is either toothed both on the margin and surface or only on the margin, never papillose (Pl. IV, fig. 5); margin entire to somewhat crenulate at apex and entire in the lower portion, recurved usually on both margins but with one side more recurved than the other (Pl. XVIII, fig. 1-3), unistratose throughout (Pl. V, fig. 1-4 and Pl. VI, fig. 5); upper leaf cells usually isodiametrical (Pl. IV, fig. 4), sometimes a few short rectangular, 5 - 8 μ in diameter, becoming gradually longer towards the middle of the leaf, median cells rectangular or elongate, about 13 - 23 μ long and 5 μ broad

(Pl. IV, fig. 7), lower cells elongated 15 - 38 μ long and 3 - 5 μ broad, sinuose (Pl. IV, fig. 6); alar cells not distinct, sometimes a few hyaline cells at the basal corner with smooth walls, broader than the rest, cells across base of leaf orange coloured; costa prominent, flattened (Pl. IV, fig. 3), about 0.1 mm wide at the base, gradually narrowing in the upper portion and extending into the hyaline point, 2 - 4 stratose, in cross-section the cells of the lower row usually bigger than the rest or more or less equal in size; dioecious; outer perichaetial leaves with hyaline point, cells elongated, longer than in ordinary leaves, upper cells not sinuose, inner perichaetial leaves without hyaline point, broad and thin, cells not sinuose at all; perigonial leaves broad, much shorter, thinner, brown with green tip, usually with no hyaline point, cells not sinuose.

Sporophyte: seta straight, 4 - 7 mm long, twisted to the right, smooth; capsule erect, cylindric, 1.8 - 2.7 mm long and 0.7 - 1.1 mm broad (Pl. V, fig. 6), yellowish brown, upper exothecial cells round, quadrate or mixed type for 4 - 5 rows (Pl. VI, fig. 1), dark coloured, middle cells elongate or rectangular (Pl. VI, fig. 4), lower cells mixed type with about 16 phaneropore stomata; peristome teeth 16, about 0.2 - 0.35 mm long, forked into 2 - 3 filiform divisions, usually of different size (Pl. VI, fig. 1), papillae irregularly placed, transverse band prominent, swollen at the margin, divisions joined at various places or only at the base (Pl. VI, fig. 3); calyptra mitrate, papillose at apex; operculum rostrate (Pl. V, fig. 5);

annulus of 2 - 3 rows of reddish cells, deciduous (Pl. VI, fig. 7); spores finely granular, 12 - 18 μ in diameter (Pl. V, fig. 7). Sporophyte maturing in summer or late spring.

Habitat: Usually on dry cliff faces and outcrops, occasionally in damp shaded cliff walls, usually near sea level.

General distribution: Circumboreal in the Northern Hemisphere: In North America from Alaska to Greenland and Labrador, southward in Eastern America to the southern Appalachian mountains of North Carolina and Tennessee, southward in Western America to California. In Eurasia from Iceland to Kamtchatka, southward in Japan, Korea and Himalayan area; also (according to Van der Wijk et al, 1967) in southern South America, North and South Africa and Australasia.

Specimens examined:

Queen Charlotte Islands: Tuft Island, East of Lyell Island, Schofield & Vaarama 24013,

Vancouver Island: Otter point, 29453,

Mainland and adjacent Islands: Gambier Island, Centre Bay, 20755; Yale, Fraser River Bank, 25586; Point Atkinson, North Vancouver, 13240; Mt. Maxwell, Saltspring I, Boas 436; Gabriola Island, 22873; between Spuzzum and Yale, Krajina s.n., Aug. 23, 1958.

Var. affine (Schleich) C. Jens, Danmarks Mossor 2:238, 1923.

Trichostomum affine Schleich, Cat (Ed 2) 31, 1807.

Trichostomum alopecurum Schkuhr, Deutschl Moose, 77, 1810.

Rhacomitrium alopecurum Brid. Mant. 79. 1819.

Rhacomitrium fastigiatum Wallr. Fl. Krypt. 1:175, 1831.

Rhacomitrium heterostichum var. β alopecurum Hueben
Musc. Germ. 208, 1833.

Trichostomum fasciculare, var., Tayl. in Mack. Fl. Hib. 2:20,
1836.

Trichostomum saxatile Tayl. Trans. Bot. Soc. Edib. 2:1, 1845.

Grimmia heterosticha β alopecura C. Muell, Syn 1:808, 1849.

Rhacomitrium affine Lindb. Acta Soc. Sci. Fenn. 10:552, 1857.

Grimmia affinis Lindb. Musc. Scand. 29, 1879.

Rhacomitrium heterostichum, Subsp. micropoides Kindb. Hedwigia
35:65, 1896.

Grimmia sublurida Stirt, Scot. Nat. 9:36, 1900.

Grimmia calvescens Stirt, Ann. Scot. Nat. Hist. 10:112, 1901.

Grimmia papillulata Stirt. Op. Cit. 11:110, 1902.

Rhacomitrium heterostichum subsp. affine, Amann Fl. Mouss.
Suisse, 2:143, 1912.

Rhacomitrium heterostichum var. Limprichtii Loeske Laubm.
Eur. 1:184, 1913.

Stem slender, elongated or short, 4 - 7 cm long,
with numerous slender fasciculate branches (Pl. VII, fig. 1);
plants yellowish green to dark green; leaves ovate-lanceolate,
1.8 - 3 mm long with hyaline points shorter (Pl. XVIII, fig. 4),
often almost obsolete, margin bistratose in upper part of leaf
(Pl. VII, fig. 2, 4, 6), unistratose in lower part (Pl. VII,
fig. 3); capsule cylindrical, 2 - 2.9 mm long and 0.6 - 1 mm

broad (Pl. VI, fig. 2). Sporophytes maturing in late spring or summer.

Habitat: On dry rocks.

General distribution: In Europe from the Faeroe Islands, Scandinavia and Siberia, southward to Spain and Italy; in North America from Newfoundland and Nova Scotia and from Alaska to British Columbia and Washington.

Specimens examined:

Queen Charlotte Islands: Moresby Island, 30805 A; Dass Peninsula, Schofield & Vaarama 24482,

Mainland and adjacent Islands: Point Atkinson, North Vancouver, 13242; Grafton Bay, Bowen Island, Dill 20462; Saturna Beach, Gulf of Georgia, 14399; Mill Creek, Mc.Fadden s.n., Oct. 19, 1923.

R. heterostichum sen. str. is very variable in size, colour and mode of branching. In general, it is close to R. canescens Brid. and R. fasciculare (Hedw.) Brid. in habit but the very strong and distinct papillose leaf cells and hyaline point of R. canescens, and elongated upper cells, muticous leaf of R. fasciculare immediately separate these species. The character of branching pattern and unistratose margin suggests a strong relationship between R. heterostichum and R. ramulosum Lindb., but the very short and pale capsule of R. ramulosum and elongated upper cells are distinctly different from the long, cylindric capsule and isodiametric

upper cells of R. heterostichum. It is also close to the R. brevipes Kindb. group especially with var. "microcarpiformis" having more or less similar type of branches, unistratose margin, long cylindrical capsule but differs in the character of upper cells which are isodiametric in R. heterostichum but elongate in R. brevipes var. "microcarpiformis".

Var. affine is very difficult to separate from R. heterostichum because all the characters are the same except for the bistratose nature of the leaf margin.

- Rhacomitrium sudeticum (Funck) B. S. G. Bryol. Eur. fasc. 25-28, 1845.
- Trichostomum microcarpon Hedw. Sp. Musc. 112, 1801.
- Trichostomum sudeticum Funck, Moost. 26, 1821.
- Dryptodon sudeticus Brid. Bryol. Univ. 1:195, 1826.
- Rhacomitrium microcarpon β sudeticum Hueben Musc. Germ. 302. 1833.
- Trichostomum gracile Hueben Op. Cit. 1. C.
- Grimmia procera Bals & Not. Pugill. no. 17, 1836.
- Rhacomitrium sudeticum Br. & Sch. Bryol. Eur. fasc. 25-28, 1845.
- Grimmia microcarpa. C. Muell. Syn. 1:804, 1849.
- Rhacomitrium microcarpon Lindb. Acta. Soc. Sci. Fenn. 10:524, 1875.
- Rhacomitrium heterostichum, Subsp. sudeticum. Dixon. Stud. Handb. Brit. Mosses (Ed. 1) 154, 1896.
- Rhacomitrium heterostichum var. sudeticum Jones Moss Fl. N. Amer. II: 57, 1933.

Gametophytes yellow to dark green to almost black, usually short, loose wide patches (Pl. VIII, fig. 2); stem usually 1 - 3 cm, (rarely up to 8 cm) long, branches ascending, usually 0.5 - 3 cm (rarely 5 cm long), short lateral branches few or none (if present, about 1 - 3 mm long) (Pl. VIII, fig. 1); rhizoids at the base of the stem, branched or unbranched, thick walled, smooth; leaves not twisted or curled when dry but erect, usually spreading or loosely imbricated, long lanceolate from a broad base, about 2.5 - 3.3 mm long including the 0.1 - 0.3 mm hyaline point (Pl. XIX, fig. 1-4), hyaline point denticulate either only on the margin or both on the margin as well as on the surface (R. sudeticum var. occidentale (Ren. & Card.) Frye, R. heterostichum var. sudeticum f. occidentale

(Ren. & Card.) Jones) not papillose (Pl. VIII, fig. 6); upper cells round to short rectangular, about $0.5\ \mu$ in diameter or $10:5\ \mu$ (Pl. VIII, fig. 3), median cells usually rectangular, sometime round, about $12:5\ \mu$ (Pl. VIII, fig. 4); lower cells elongate, sinuose $30 - 40 : 5\ \mu$ (Pl. VIII, fig. 5); alar cells not distinct, a few of the lowermost cells linear, not sinuose, broader than the rest and yellow brown in colour, leaf cells almost smooth or very weakly papillose in the lower portion; margin entire, revolute only on one side (Pl. XIX, fig. 1-4), lower few marginal cells smooth walled and hyaline; bistratose for few rows at least in the upper half of the leaf (Pl. IX, fig. 1-3); costa flat, extending up to or into the hyaline point, about $80\ \mu$ wide, usually broader in the middle, 2 - 4 stratose (Pl. IX, fig. 1-4); dioecious; perichaetial leaves thin, broader than rest of the leaves, cells linear, entire except a few in upper portion, with hyaline point, inner leaves larger than the outer; perigonial leaves much shorter, darker and thinner than the rest of the leaves, usually without hyaline point, costate.

Sporophyte: seta straight, twisted to the right, 3 - 3.5 mm long, not papillose; capsule erect, ellipsoidal, usually small, 0.6 - 2 mm long and about 0.5 mm broad, light to dark brown, not papillose (Pl. IX, fig. 5); upper 2 - 3 rows of exothecial cells round or quadrate, reddish brown, lower cells of mixed shape with about 8 stomata, slightly darker than rest of the cells; peristome teeth 16, about 0.3 mm long, reddish brown at the base, yellow-brown in the upper portion,

papillose (Pl. IX, fig. 9) and divided into 2 - 3 filiform prongs, usually straight and of same size, united at the base, transverse band not prominent, margin thickened at bands (Pl. IX, fig. 6); annulus 1 - 2 rows of golden yellow cells (Pl. IX, fig. 7); operculum rostrate, usually with a straight beak, sometimes oblique, not papillose, about 1 mm long (Pl. X, fig. 8); calyptra nearly smooth at apex, lacerate and smooth at base; spores round, granular, greenish yellow, about 12 - 15 μ in diameter (Pl. IX, fig. 8). Sporophyte maturing in summer.

Habitat: On dry exposed rocks and soil, usually in high altitudes and latitudes, sub-alpine to alpine.

General distribution: Alaska and Yukon to Oregon and Idaho; across arctic and boreal Canada to Greenland, Labrador and Nova Scotia, southward to New Hampshire and Pennsylvania; in Europe from Iceland to Fennoscandia, southward to the Alps, Tatra Carpathians and Caucasus, also from Asia Minor, and northeastern Asia in Japan.

Specimens examined:

Queen Charlotte Islands: Mt. de la Touche, Moresby Island, Foster & Bigg. s.n., June 28, 1961; Mt. Needham Area, Graham Island, Foster & Bigg, s.n., June 18, 1961; Takakia Lake, Moresby Island, 24891; 24965, 25025, 25170; Moresby Mt., Moresby Island, 32308; Head of Dawson Inlet, Graham Island, 15880;

Vancouver Island: Mt. Maxwell, Mackenzie s.n., August, 1930; Victoria, Savale 57; Mt. Arrowsmith, Elvidge K 1070.

Mainland and adjacent Islands: Long Lake, Schofield & Williams 27940; Whatshan Lake, Bell SB 56; Garibaldi Park, Archer s.n. 12th August, 1962; Wells Gray Provincial Park, Leena & Ahti 14230, 14193; Mt. Buxton, Calvert Island, 28042; Mt. Seymour, 12553; Lion's Bay Trail, 19936; Small Creek, Dam Mt., Krajina s.n., Aug. 28, 1959; Tonquin Valley, Jasper Park, McFadden s.n., July, 1926; Fisher Maiden Lake, Silverton, McFadden s.n. June 27, 1926.

Var. Macounii (Kindb.) N. Comb.

Rhacomitrium macounii Kindb. Bull. Torr. Club. 16:93, 1889.

Rhacomitrium robustifolium Kindb. Op. Cit. 17:272, 1890.

Rhacomitrium alternuatum. C.M. and Kindb. in Mac. Cat. Can.
Pl. 6:73, 1892.

Rhacomitrium attenuatum C.M. and Kindb. l. C.

Grimmia robustifolia Kindb. Eur. and N. Am. Bryin, 225, 1897.

Grimmia attenuata Kindb. l. C. 228.

Rhacomitrium heterostichum var. macounii Jones Moss. Fl.
N. Amer. II:57, 1933.

Gametophytes green or brownish, yellowish green on the top of ascending branches, short lateral branchlets absent, stem 3 - 8 cm long; leaves lanceolate, somewhat twisted or curled when dry (Pl. X, fig. 2), loose, with or without hyaline point, if present, short, usually blunt (Pl. X, fig. 3 & 6), upper leaf cells usually round or short rectangular, gradually longer and narrower downward (Pl. X, fig. 5 & 7); margin revolute only on one side (Pl. XX, fig. 1-3), bistratose for few rows in more than half the whole leaf.

Sporophyte: seta about 3 - 5 mm; capsule ellipsoidal or cylindrical, 1 - 1.8 mm long and 0.3 - 0.6 mm broad (Pl. X, fig. 4). Sporophyte maturing in summer.

Habitat: On alpine and sub-alpine rocks and soil.

General distribution: Probably endemic to Western North America: Alaska southward to British Columbia, Alberta, Montana and Washington.

Specimens examined:

Queen Charlotte Islands: Mosquito Lake, Moresby Island, 25433.

Vancouver Island: Arrowsmith Trail, Boas 1530, 1532, 1505; Albert Edward Mt., Forbidden Plateau, Boas 1598; Lillooet Macoun s.n. July, 1916.

Mainland and adjacent Islands: Garibaldi Park, Peterson BP 52; Archer s.n., 6th August, 1962, 23rd September, 1962; North East Garibaldi, Archer s.n., 22nd September, 1961; Grouse Mountain, Peterson BP 96, BP 100; Mt. Seymour 12432, 15985, 15947, 16013, 16000; Sentinel Glacier Area, Garibaldi Lake, Schofield & Worley 32936; Wells Gray Provincial Park, Leena & Ahti 13953; Lion's Bay Trail, 19906.

R. sudeticum is fairly consistent in most of its characters. The slender habit, absence of any short lateral branches, bistratose margin and short ovoid capsule are distinctive.

This taxon is related to R. heterostichum in its possession of upper leaf cells predominantly isodiametric but the habit, branching pattern, margin of the leaf and also capsule shape and size are much different from R. heterostichum. Though some taxonomists have recognized R. sudeticum as a subspecies or variety of R. heterostichum (Dixon 1896, Jones 1933, Nyholm 1956), I feel that R. sudeticum is sufficiently distinct from R. heterostichum to merit specific rank. This is also the

general opinion of several current European bryologists (Martensson, 1956, Augier, 1966).

Var. macounii, in habit, branching pattern, leaf margin, etc. is closer to R. sudeticum than to R. heterostichum. Except for the hyaline point which is short or even absent and leaves somewhat curled or twisted when dry it is similar to R. sudeticum. Indeed it is possible that R. macounii may ultimately prove to be identical to R. sudeticum.

Rhacomitrium brevipes Kindb. Bull. Torr. Club. 17:272, 1890
(Nov)

Rhacomitrium heterostichum var. occidentale Ren & Card.
Bot. Gaz. 15:41, 1890 (Feb.)

Rhacomitrium micropus Kindb. in Mac. Cat. Can. Pl. 6:97, 1892.

Rhacomitrium occidentale Ren. & Card. Musc. Am. Sept. 25, 1893.

Rhacomitrium heterostichum subsp. sudeticum var. occidentale
(Ren. & Card.) Frye Bryologist 21:3, 1918

Rhacomitrium heterostichum var. sudeticum f. occidentale
(Ren. & Card.) Jones Moss. Fl. N. Amer. II:57, 1933.

Gametophyte dark brownish or yellowish green; stem
3 - 6 cm long with few to numerous short lateral branchlets
(about 1 - 4 mm long) and also ascending branches (about 1 - 4
cm long) (Pl. XI, fig. 1 & 2); rhizoids branched, smooth,
thick walled; leaves loosely imbricated when dry, spreading
when wet, ovate-lanceolate, 2.5 - 5.6 mm including 0.5 - 1.4 mm
hyaline point (Pl. XXI, fig. 1 & 2); hyaline point strongly
toothed both on the margin and on the surface, not papillose
(Pl. XI, fig. 3), upper cells elongated, sometimes mixed with
rectangular or quadrate cells, usually $8 - 23 \mu : 5 \mu$, sinuose,
not or slightly papillose (Pl. XI, fig. 5), median cells
elongate, sinuose, $8 - 38 \mu : 3 - 5 \mu$ (Pl. XI, fig. 6), lower
cells long, sinuose $18 - 64 \mu : 4 - 5 \mu$, slightly papillose or
not (Pl. XI, fig. 4); margin entire to somewhat crenulate at
the apex, entire in the lower portion, bistratose, mostly not
in the upper portion but in the middle portion, sometimes
lamina also bistratose (Pl. XII, fig. 3, 5 & 6), laminal cell
walls appear papillose in cross section largely due to the

greatly thickened cross walls, never papillose over the lumen (Pl. XII, fig. 3-6), margin revolute either on one or both sides (Pl. XXI, fig. 1 & 2), sometimes up to the apex; costa flat, extending into the hyaline point, broader in the middle, about 0.1 mm wide, gradually becoming less wide in the upper portion, 2 - 4 stratose (Pl. XII, fig. 2, 3, 5 & 6); dioecious; inner perichaetial leaves broader and thinner, cells longer, wider, usually not sinuose and without hyaline point; perigonal leaves shorter, broader and darker (brown) than rest of the leaves, cells usually not sinuose except at the tip.

Sporophyte: seta straight, twisted to the right not papillose, usually 4 - 7 mm long, sometimes longer; capsule erect, cylindric 2 - 3 mm long and 0.6 - 0.9 mm broad, light to dark brown in colour, not papillose (Pl. XII, fig. 1); upper 2 - 4 rows of exothecial cells more or less round (Pl. XIII, fig. 3), reddish brown, lower cells round or rectangular with 14 - 32 stomata, stomata prominent, cells darker than rest of the cells (Pl. XIII, fig. 2); peristome teeth 16, about 0.3 mm long, forked, branches united or free, of same or of different length, papillose, transverse band not or swollen at the margin, not prominent (Pl. XIII, fig. 1); annulus 1 or 2 rows of yellow cells, deciduous (Pl. XIII, fig. 4); operculum rostrate, about 1 mm long, not papillose (Pl. XIII, fig. 5); calyptra conical, about 2 mm long, divided into 7 lacerations which are further divided into 2 - 3 parts, somewhat rough in the apex (Pl. XIII, fig. 6); spores round, granular, greenish brown in colour 12 - 15 μ in diameter.

Sporophytes maturing in spring.

Habitat: On dry rocks, sub-alpine.

General distribution: Endemic to Western North America: Alaska southward to Washington. Type locality on sloping garnetiferous rocks near the summit of the Gold range, North of Griffin Lake, British Columbia, altitude 6,700 feet.

Specimens examined:

Vancouver Island: Teanook Lake, 13627,

Mainland and adjacent Islands: Decanso Bay, Gabriola Island, 13627; Lion's Bay Trail, 19907; Keith Anchorage Area, Calvert Island, Schofield & Williams 26900; Mts. N. of Griffin Lake, Macoun, s.n., Aug. 9th, 1889, CAN; Selkirk and Gold Range Mountains, Macoun 614, CAN.

Var. "laevis". var. nov.

Gametophytes in loose brownish green, often bright green tufts; stems 2.5 - 8 cm long with few to numerous short lateral branchlets (about 1 - 4 mm long) and also ascending branches (about 1 - 4 cm long) (Pl. XIV, fig. 1); leaves lanceolate from a broad base (Pl. XXI, fig. 3 & 4); upper cells rectangular or elongated, margin bistratose (Pl. XIV, fig. 3 & 6), laminal cell walls not papillose in cross section, little thickening on cross wall (Pl. XIV, fig. 2-6), hyaline point either toothed only on the margin or both on the margin and surface but denticulations never as strong as in R. brevipes sen. str.

Sporophytes: seta straight, 4 - 8 mm long, capsule cylindric, 2 - 3.7 mm long and 0.7 - 1 mm broad. Sporophyte maturing in spring to summer.

Habitat: On dry exposed rocks.

Specimens examined:

Queen Charlotte Islands: Graham Island, 29768; Dass Point Peninsula, Schofield & Vaarama 24430; Tuft Island, Schofield & Vaarama 24018; Lagoon Inlet, 31983,

Vancouver Island: Mt. Tolmie, Boas 1174; Otter Point, 29444; Mt. Bruce, Saltspring I, Boas 313; Golden Hinda Area, Dollery - Pardy s.n., June 8, 1963; Long Beach, 26544.

Mainland and adjacent Islands: Horseshoe Bay, Krajina 3023; Shames, Skeena River, Schofield & Boas 21442; Long Lake,

Mt. Buxton, Schofield & Williams 27914; Paul Ridge, Garibaldi Park, 14469; Deek's Creek, Howe Sound, 35757; Armstrong, Wilson s.n., October 26, 1963; Junction of Lilloet and Fraser River, 36145; Lund, Malaspina Peninsula, Schofield & Boas 18182; Point Atkinson, North Vancouver, 13242.

Var. "eramulosum" var. nov.

Gametophytes with light green to brownish green stems, 2 - 8 cm long with usually no short lateral branches or few, elongated branches about 1 - 3.5 cm long (Pl. XV, fig. 1); leaves lanceolate from a broad base (Pl. XXII, fig. 1); upper cells elongated or rectangular, sometimes mixed with round cells, margin bistratose, laminal cell walls not papillose in cross section; hyaline point short to long, toothed only on the margin or both on the margin and surface.

Sporophyte: seta straight, 3 - 6 mm, sometimes up to 9.5 mm long; capsule erect, cylindric 1.7 - 2.7 mm long and 0.3 - 0.9 mm broad (Pl. XV, fig. 2). Sporophyte maturing in late spring to summer.

Habitat: On rocks; sub-alpine.

General distribution: Probably endemic to Northwestern North America, west of the Rocky Mountains.

Specimens examined:

Queen Charlotte Islands: Takakia Lake, 25144; Skedans, 31896.

Vancouver Island: Arrowsmith Trail, Boas 1457; Mt. Bruce, Saltspring I, Boas 301.

Mainland and adjacent Islands: U.B.C. Forest, Haney, Krajina 37; West pass Lake, Cariboo district, Boas 428; Howard Lake, Hazlewood 4; Calvert Island, 28000; Pochahantas Lookout,

Straight of Georgia, Schofield & Boas 18255; Mt. Seymour,
Peterson BP 27; Isaac Lake, Boas 606; Garibaldi Lake Trail,
28098; Halcyon, McFadden 393.

Var. "microcarpiformis". var. nov.

Gametophytes light green to dark green, rarely brown to almost black; stem 2 - 6 cm long with few to numerous short lateral branchlets (about 1 - 4 mm long) and also ascending branches (about 1 - 4 cm long) (Pl. XV, fig. 4); leaves 2 - 5 mm long, lanceolate with 0.5 - 2.5 mm hyaline point (Pl. XXII, fig. 2-4) which is denticulate either on the margin only or both on the margin and surface; upper cells elongated or rectangular (Pl. XV, fig. 3) gradually longer and narrower downward (Pl. XV, fig 5 & 6) margin revolute on one side or both (Pl. XXII, fig. 2-4), unistratose throughout (Pl. XVI, fig. 1-4), laminal cells not papillose in cross section; costa extending into or up to hyaline point, 2 - 4 stratose.

Sporophyte: Seta 4.5 - 7.5 mm long; capsule erect, 1.5 - 3.6 mm long and 0.5 - 0.9 mm broad (Pl. XIII, fig. 7); operculum rostrate or conical; peristome teeth always forked, usually all of equal length, either free or joined at various places; spores round, granular, 10 - 15 μ in diameter (Pl. XVI, fig. 6). Sporophytes maturing throughout the year.

Habitat: On dry, exposed rocks or damp, shaded cliffs or boulders in forest.

Specimens examined:

Queen Charlotte Islands: Louise Island, Schofield & Vaarama 23911-A; Rose Harbour, 31869; Tow Hill, 29859; Moresby Island, 30737, 30746 A, 25296; Hotspring, 31888; Skedans, 31910;

Moresby Camp, 30531; Cumshewa Head, 32368.

Vancouver Island: Colwood, 16404; Mt. Bruce, Boas 290; Elk Falls, 16198; Beaver Lake, Macoun s.n., 17. 3. 1914; Sidney, Macoun s.n., 13. 12. 1912, 31. 3. 1916, 16. 4. 1916; Saanich Pen, Schofield & Chuang 35845; 2nd Bridge, Nanaimo River Valley, Mueller - Dombois, 104-7; Kangaroo Road, 35938; Langford, Schofield & Chuang 35864; Halibut Island, 20445; Humpback Road, 35976; Thetis Lake, Boas 1352; Beaver Lake, Macoun s.n., 17. 3. 1914; Mt. Douglas, Boas 953; Mill Hill, 29486; Amphitrite Point, Schofield & Boas 19016; Tofino, along Taylor River, 13486.

Mainland and adjacent Islands: Benett Bay, Schofield & Boas 17497; Point Atkinson, N. Vancouver, 13258, 13256; Ashlu Valley, Widdowson s.n., Sept. 1963; Revelstoke, 27775; Burns Bog, Schofield & Taylor 35767; Gambier Island, Howe Sound, Schofield 20724; Brittania Beach, Howe Sound, 12603; Cypress Creek, 14348; Hall's Gate, Fraser River Gorge, Schofield & Boas 17689; Highway # 1, Revelstoke, Anastasiou s.n., May 7, 1963; Lois River, Long Bay, Schofield & Boas 18374; Big Oliver Creek, Skeena River, Schofield & Boas 21171; Kaslo, Kootenay district, Bell. s.n., Aug. 21, 1959; Acadia Camp, U.B.C., 11435; Wilson Lake, Bell. s.n., June 17, 1959; Haney, University Forest, Schofield & Orloci 16312; Indian Arm, 20559; Hope, Schofield & Williams 23428; Junction of Lilloet and Fraser River, 36140; Head of Knight Inlet, Widdowson, s.n., July 7, 1962; Dam of Cheakamus River, Schofield & Lang 26156; Lynn Creek Canyon, W. Vancouver, 13343; Burton, Bell s.n., June 27,

1959; Keith Anchorage Area, Calvert Island, Schofield & Williams 27006; Wigwam Creek, Indian Arm, 20527; Yale, Schofield & Boas 17788; Murrin Park, 14507; New Denver, Fadden s.n., June 9, 1923; Trout Lake, Sechelt Peninsula, Schofield & Boas 18038; McDonell Lake, Boas 564; Martha Creek, Krajina s.n., July 23, 1954.

In British Columbia the commonest representatives of the R. heterostichum complex (R. brevipes sens. lat.) are plants characterized by relatively elongated upper cells, few to numerous short lateral branchlets, fairly long hyaline point, and smooth or seemingly papillose leaf cells. In these characters R. brevipes resembles R. microcarpon Brid., a species endemic to Europe. But many plants of R. brevipes in British Columbia are distinctly bistratose in the leaf margin and the capsules are moderate to long which is not the case in R. microcarpon. Nor do they look like European specimens. R. brevipes sens. lat. differs from R. heterostichum Brid. in its possession of upper elongated or rectangular cells and, except for var. "microcarpiiformis", have bistratose leaf margins and match the type of R. brevipes Kindb. In the type description the capsule of R. brevipes is described as short but in the type specimen at the National Museum of Canada no capsules are present.

R. brevipes Kindb. is sometimes treated as a synonym of R. heterostichum var. occidentale Ren. & Card. or R. heterostichum var. sudeticum f. occidentale (Ren. & Card) Jones, but the description and type specimen of R. brevipes

show that it has few to numerous short lateral branches, rectangular to elongate upper leaf cells and thus cannot be considered identical to R. sudeticum. Moreover, the character of the denticulate hyaline point both on the margin and on the surface, used to separate R. occidentale Ren. & Card. from R. sudeticum is unreliable since in all other members of this complex I have seen, this character is not correlated with any other. Thus it cannot be taken as a character by which we can separate a variety or even a form. In consequence here I have separated R. brevipes as being quite distinct from R. sudeticum or R. occidentale no matter what category these taxa are accorded.

Var. "laevis" and var. "eramulosum" have been separated from R. brevipes sens. lat. based on the fact that their leaf cells are not papillose in cross section which I consider quite an important character since the anatomical characters appear to be less affected by environmental changes than the gross morphology. Based on the character of branching pattern var. "laevis" and var. "eramulosum" have been separated from each other.

Var. "microcarpiformis" forms a distinct variety characterized by the presence of rectangular or elongated upper cells, few to numerous short lateral branchlets but unistratose leaf margin. This variety could be placed in R. microcarpon except for the very different capsules and the habit. As to the character of branching pattern, upper cells and hyaline point they are like R. brevipes and are, therefore, placed as variety of that species.

Key to the Racomitrium heterostichum complex in British Columbia

- A. Upper cells quadrate or round (1:1)
occasionally mixed with rectangular
cells (2-3:1) ... B
- A. Upper cells predominantly elongate
(4-20:1) sometimes mixed with
rectangular cells (2-3:1) ... E
- B. Margin unistratose in upper part
of leaf ... R. heterostichum
sen. str.
- B. Margin bistratose (rarely with
unistratose portions) in upper
part of leaf ... C
- C. Bistratose portions confined to
one to two rows of marginal cells;
short lateral branches usually
more than 10 ... R. heterostichum
var. affine
- C. Bistratose portion extending well
into lamina; short lateral branches
usually fewer than 3 ... D
- D. Hyaline point usually 0.1 - 0.3 mm
long (at least on upper part of the
stem), and with up to 14 teeth on
one side ... R. sudeticum
- D. Hyaline point absent to very short
(less than 50 μ), and with less
than 4 teeth on one side if hyaline
point is present ... R. sudeticum var.
macounii
- E. Leaf in cross section with cross-
walls conspicuously ridged,
resembling papillae; hyaline point
strongly toothed both on margin
and surface ... R. brevipes sen. str.
- E. Leaf in cross section with cross-
walls smooth, never appearing
papillose; hyaline point usually
toothed only on margin or sometimes
weakly toothed on surface as well ... F

CONT.

- F. Upper leaf cells mainly elongate (9-15:1) leaf strongly keeled in upper part, thus the upper surface strongly V-shaped in cross section ... R. "laxum"
- F. Upper leaf cells mainly rectangular (2-3:1) or elongate (5:1) or sometimes mixed with 1:1 cells; leaf not strongly keeled in upper part, thus the upper surface broadly U-shaped in cross section ... G
- G. Margin unistratose throughout ... R. brevipes var. "microcarpiiformis"
- G. Margin with occasional bistratose portions ... H
- H. Short lateral branches fewer than 3 or absent ... R. brevipes var. "eramulosum"
- H. Short lateral branches usually 4-15 ... R. brevipes var. "laevis"

TABLE I

Comparison between different species of the R. heterostichum complex
in British Columbia

Characters	<u>"laxum"</u>	<u>heteros-</u> <u>tichum</u>	<u>sudeticum</u>	<u>brevipes</u>
Plants usually very long (L) short (l) or medium (l'); size of stem	L 5-16 cm	l' 2-8 cm	l 1-3 cm	l' 3-6 cm
Short lateral branches usually present (S), absent (s)	s	S	s	S
Hyaline point always prominent and long (H); very short (h)	H	h-H	h-H	H
Hyaline point usually toothed both on the margin as well as surface (T) only on the margin (t)	t	t-T	t-T	t-T
Upper leaf cells predominantly elongate (E), round (e), rectangular (e')	E	e	e	e'-E
Margin of leaf revolute on both sides (R), only one side (r)	r-R	R	r	R
Margin unistratose throughout (U) bistratose (u)	u-U	u-U	u	u-U
When bistratose, usually for many rows (B), for only one row (b)	b	b	B	b
Costa flat (F), ridged in the upper portion (f)	f	F	F	F

(CONT.)

Characters	"laxum"	<u>heteros- tichum</u>	<u>sudeticum</u>	<u>brevipes</u>
Length of seta	4-5 mm	4-7 mm	3-3.5 mm	4-7 mm
Capsule cylindric (C), ovoid (c)	C	C	c	C
Length of capsule	1.5-2.8 cm	1.8-2.7 mm	0.6-2 mm	2-3 mm
Upper exothecial cells round (R), flat rectangular (r)	r	R	R	R
Length of peristome teeth	0.4 mm	0.2-0.35mm	0.3 mm	0.3 mm
Transverse banding in peristome teeth very prominent (T), not prominent (t)	t	T	t	t
Branches of peristome teeth usually joined at various places (B), free (b)	b-B	b-B	b	b-B
Branches more or less equal in size (E), not equal (e)	E	e	e	e-E
Length of operculum	0.8 mm	1 mm	1 mm	1 mm
Length of calyptra	1.2-1.8 mm	-	1-1.2 mm	2 mm
Dimension of spores	12-13 μ	12-18 μ	12-15 μ	12-15 μ

DISCUSSION

In treating any group of apparently related species an attempt is made to select those characters that are assumed to be genetically controlled and are not greatly modified by environmental differences.

The gametophyte in several bryophytes is markedly altered by environmental change, particularly changes in moisture available to the plant. Buch (1919, 1920) noted a conspicuous phenotypic response in species of several hepatic genera. Lodge (1959, 1960) noted gross morphological changes in the moss genus Drepanocladus, although the areolation of the leaves remained constant, thus the recognized species were considered genetically distinct.

In Rhacomitrium the nature of the branching pattern appears to be highly plastic, and it is possible that the nature of the hair point and the upper leaf cells are also affected by moisture conditions. Kawai (1965) has suggested such a correlation in the closely related genus Grimmia. Unfortunately these characters are utilized to separate the various taxa in the Rhacomitrium heterostichum complex.

Thus any attempt to separate the various elements of the R. heterostichum complex must be highly tentative, and a number of reasonable arrangements are possible.

In Table I a comparison is made among all taxa considered in the present study. An attempt has been made to group those individuals of greatest similarity together. In

order to do so a certain bias is necessary and certain assumptions are made. The most basic assumption is that a number of the characters are genetically controlled and are thus valid criteria to utilize in recognition of a taxon. A second assumption is that the conditions of alpine versus non-alpine environment have served to select out genetically distinct taxa and that a very plastic species is not involved. In one case various taxa are involved, while in the other a single taxon is involved, producing a different phenotype in differing environments. Thus R. sudeticum is considered a species restricted to arctic and alpine environments while R. heterostichum is essentially of lower elevations, at least in British Columbia. Both R. "laxum" and R. brevipes show a wider environmental range. Using these assumptions the following segregation has been made for the R. heterostichum complex in British Columbia; Four species are involved: R. "laxum", R. heterostichum, R. brevipes and R. sudeticum. Variation within these species is represented by R. heterostichum var. affine, R. sudeticum var. macounii and R. brevipes var. "laevis", var. "eramulosum" and var. "microcarpiiformis". Within the species other minor variation occurs.

The nomenclature of taxa within the complex is greatly complicated because many names are available. Until these available names are evaluated it would be foolhardy to apply any to the taxa recognized in this study. It would be equally hazardous to introduce further new names without thoroughly assessing those available.

To come closer to an acceptable solution to the nature of the taxa within the R. heterostichum complex a number of further steps are suggested. First, reciprocal transplantation should be made of the presumed taxa of the complex to contrasting environments. These populations should be left to grow for several years to note the phenotypic response, assuming that they survive in the new environment. Second, a number of the taxa could be grown together under controlled moisture and light conditions and changes in morphology noted. Third, a relatively simple experiment might determine whether greatly increased moisture made available to a growing gametophyte of any taxon in this complex would result in changes in the nature of the hair point or the nature of the upper leaf cells.

Fourth, specimens from a considerably wider geographic range should be examined to note the total variation in this species complex throughout its range. This would be a rather extensive undertaking since the complex has an extremely wide geographic range and shows considerable diversity through this range.

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APPENDIX

PLATE I

R. "laxum"

- Figures 1 & 2 - Habit showing branching pattern (X 1.5)
- Figure 3 - Hyaline point of leaf (X 280)
- Figure 4 - Cells from lower portion of leaf (X 280)
- Figure 5 - Sporophytes (X 5)
- Figure 6 - Costa from upper portion of leaf (X 280)
- Figure 7 - Cells from just below hyaline point of leaf (X 280).

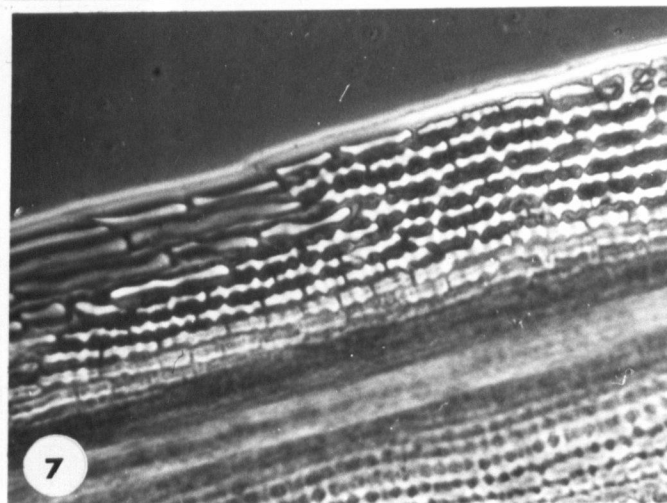
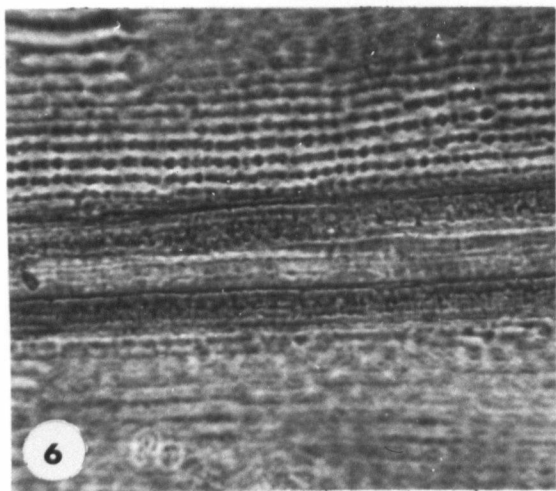
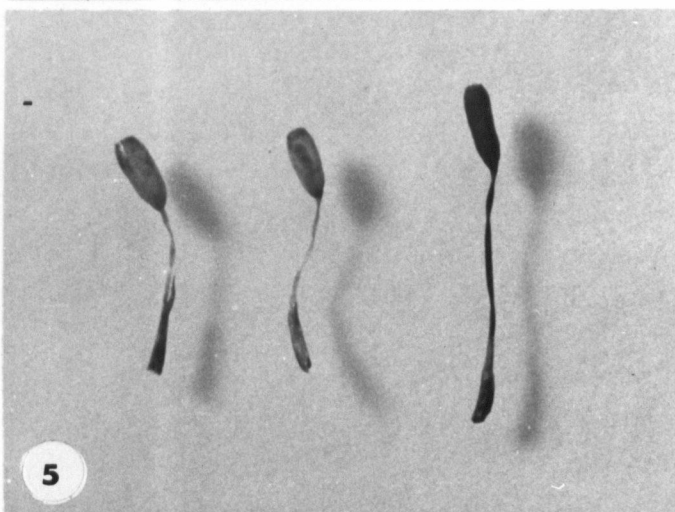
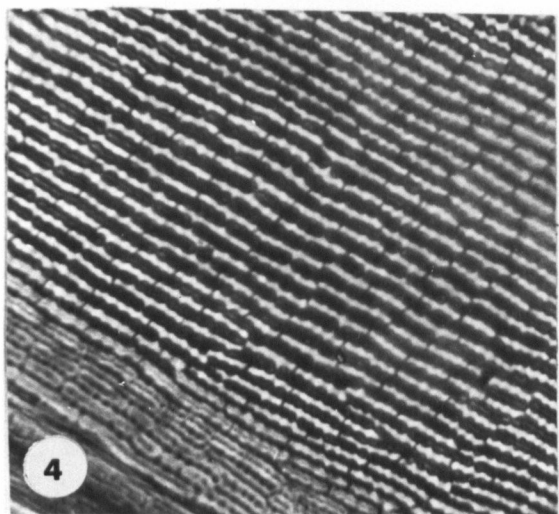
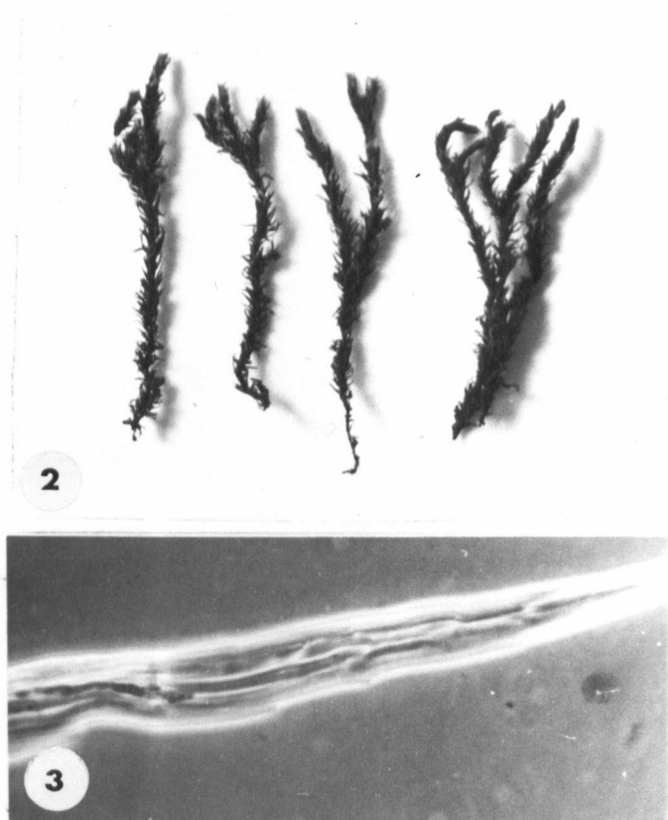


PLATE II

R. "laxum"

- Figure 1 - Cross section from lower portion of leaf (X 280)
- Figure 2 - Cross section from middle portion of leaf (X 280)
- Figure 3 - Stomate (X 1120)
- Figure 4 - Spores (X 1120)
- Figure 5 - Cross section from upper of leaf just below
hair point (X 280)
- Figure 6 - Portion of annulus (X 280)
- Figure 7 - Cross section from middle portion of the leaf
showing bistratose margin (X 280)
- Figure 8 - Cross section from lower edge of upper 1/3
of leaf (X 280).

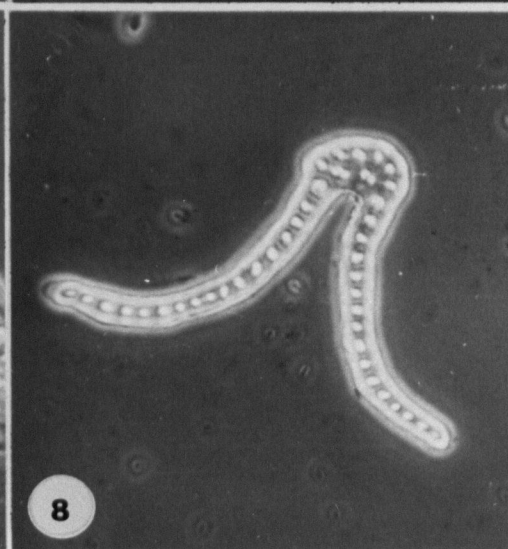
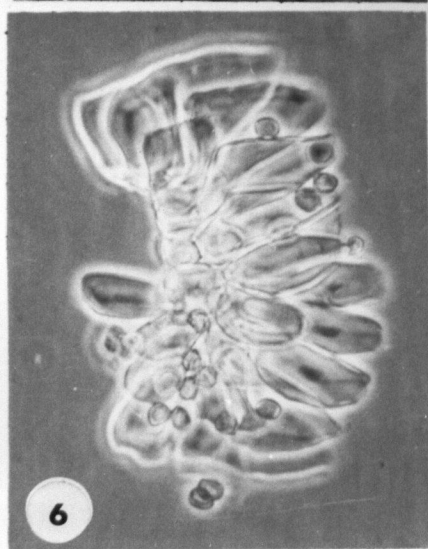
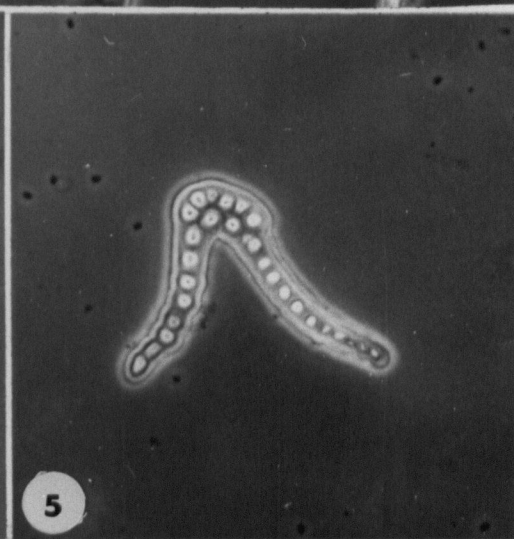
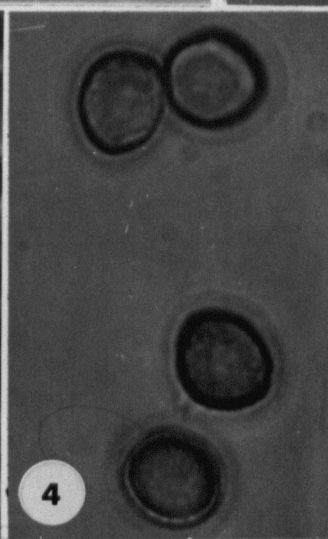
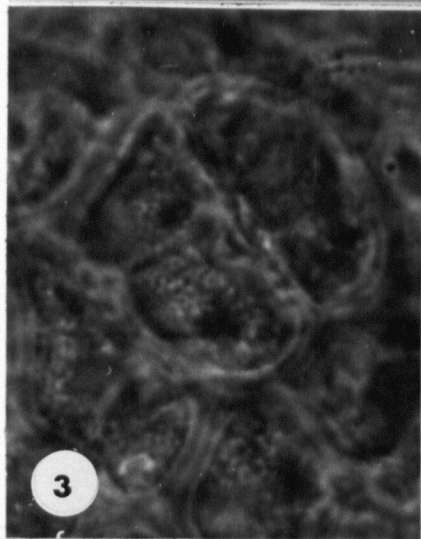
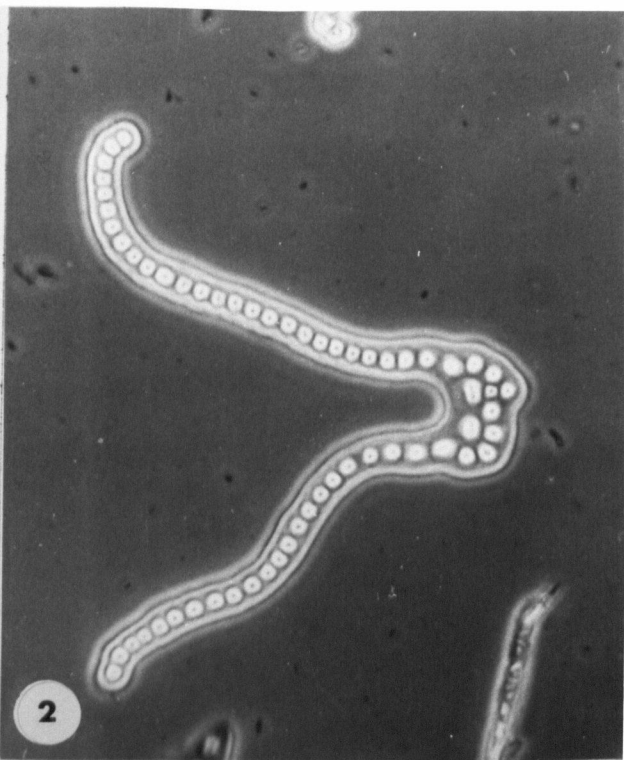
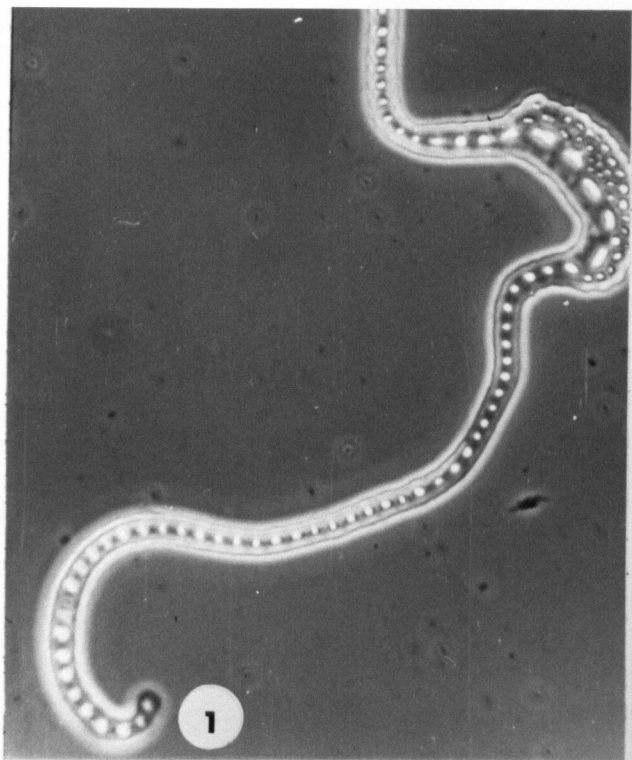


PLATE III

R. "laxum"

- Figure 1 - Peristome teeth showing papillosity (X 1120)
- Figure 2 - Upper exothecial cells (X 1120)
- Figure 3 - Peristome teeth (X 280)
- Figure 4 - Exothecial cells from middle of capsule wall (X 280).

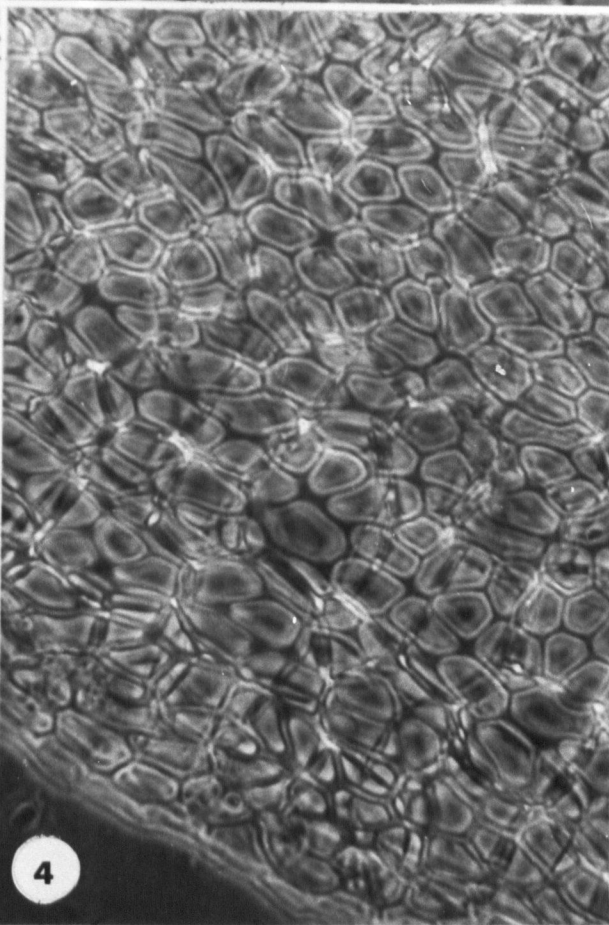
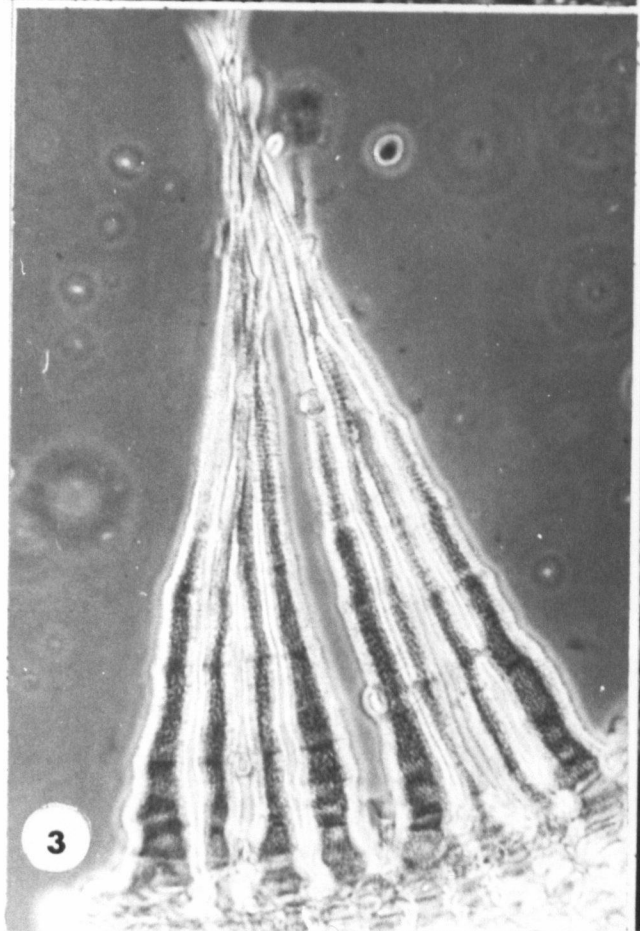
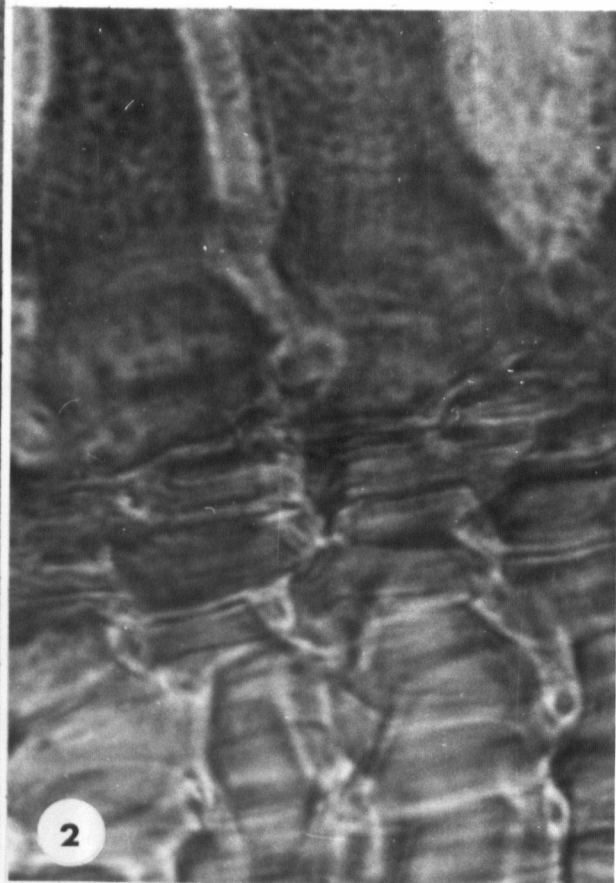
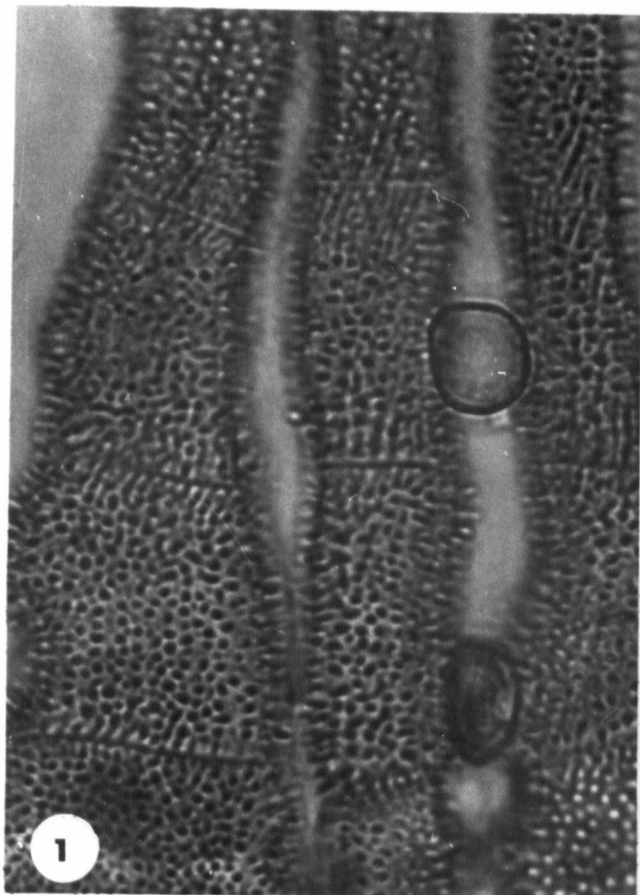


PLATE IV

R. heterostichum

- Figures 1 & 2 - Habit showing branching pattern (X 1.5)
- Figure 3 - Middle portion of the leaf showing costa (X 280)
- Figure 4 - Cells from upper portion of leaf (X 280)
- Figure 5 - Hyaline point of leaf (X 280)
- Figure 6 - Cells from lower portion of leaf (X 280)
- Figure 7 - Cells from middle portion of leaf (X 280).

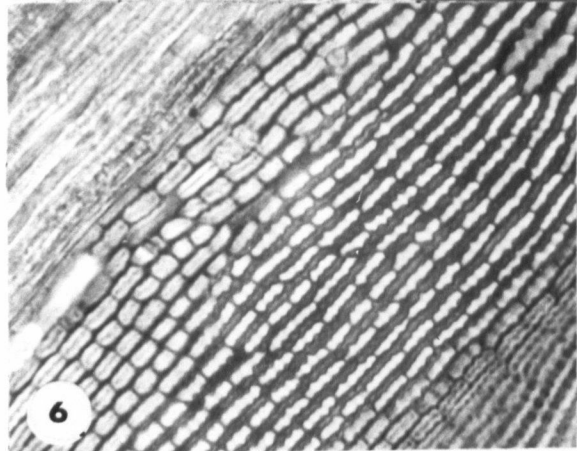
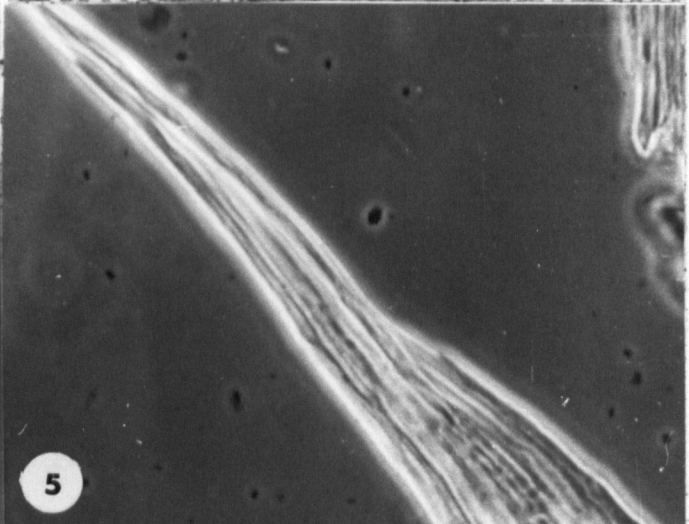
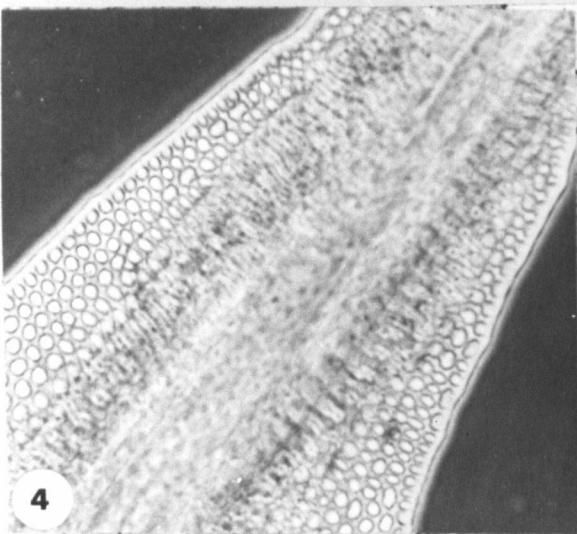
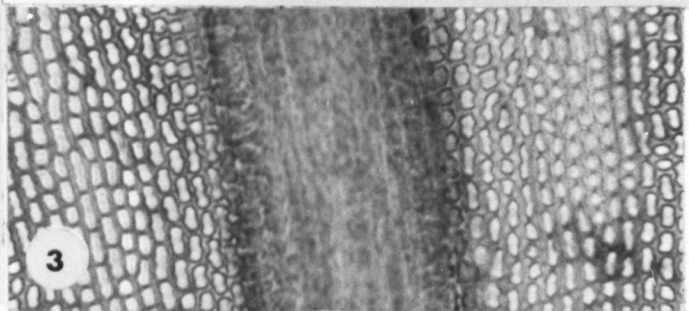
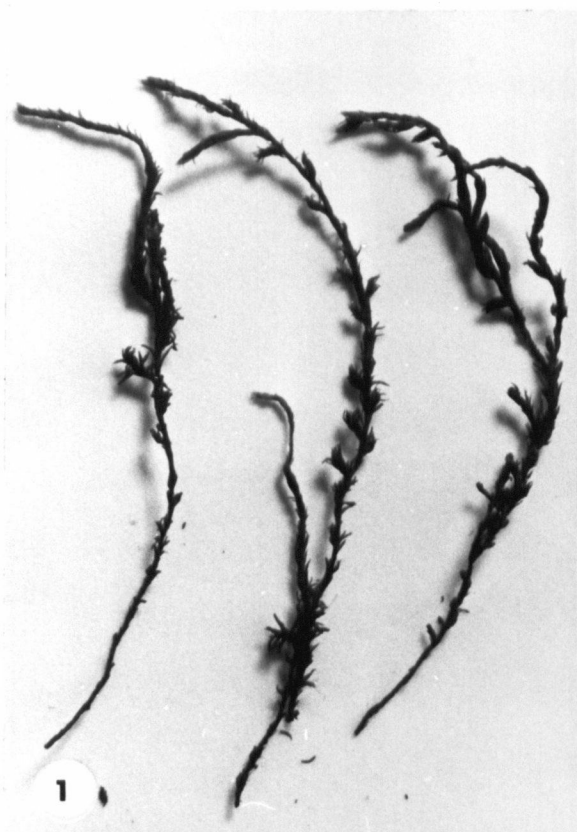


PLATE V

R. heterostichum

Figure 1 - Cross section from upper part of leaf, just below hyaline point (X 280)

Figure 2 - Cross section from near base of leaf (X 280)

Figure 3 - Cross section from bottom edge of upper 1/3 of leaf (X 280)

Figure 4 - Cross section from upper edge of lower 1/3 of leaf (X 280)

Figure 5 - Operculum (X 110)

Figure 6 - Sporophytes (X 5)

Figure 7 - Spores (X 1120).

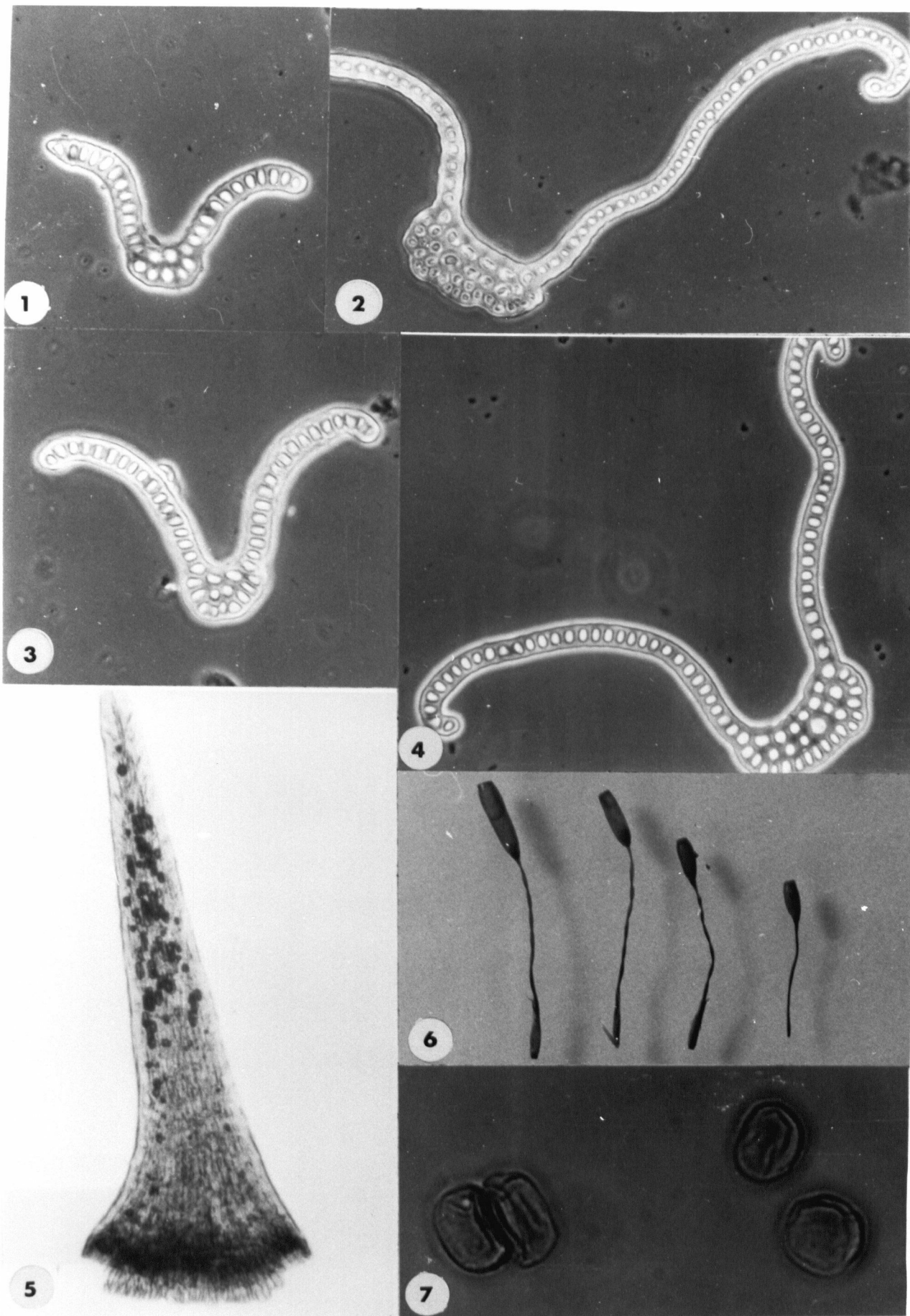


PLATE VI

R. heterostichum

Figure 1 - Peristome teeth (X 280)

Figure 2 - Sporophytes of R. heterostichum var. affine
(X 5)

Figure 3 - Peristome teeth showing papillosity (X 1120)

Figure 4 - Exothecial cells from middle of capsule (X 280)

Figure 5 - Cross section from upper portion of leaf just
below hyaline point (X 280)

Figure 6 - Stomate (X 1120)

Figure 7 - Portion of annulus (X 280).

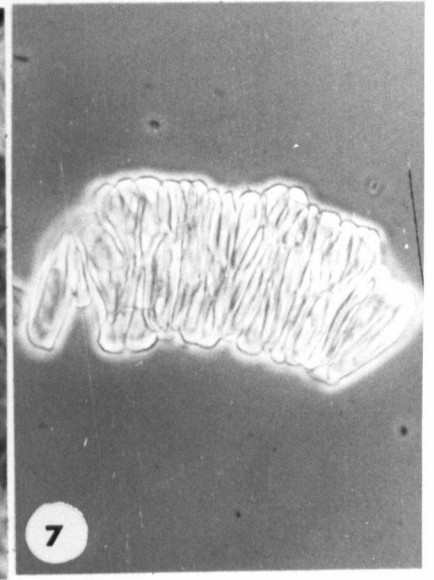
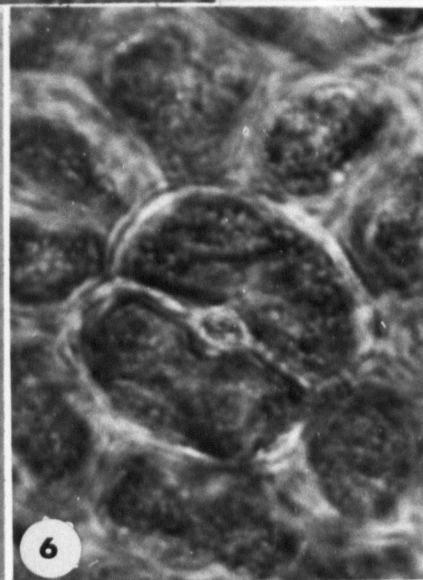
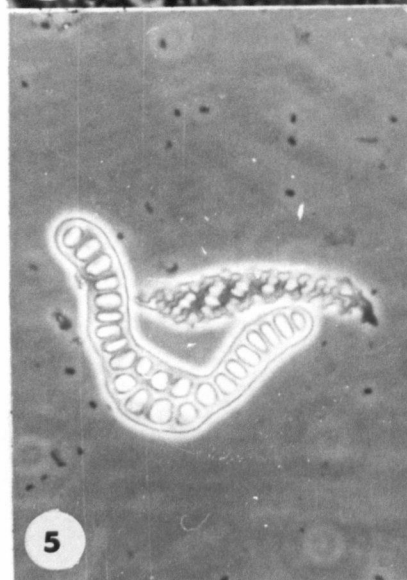
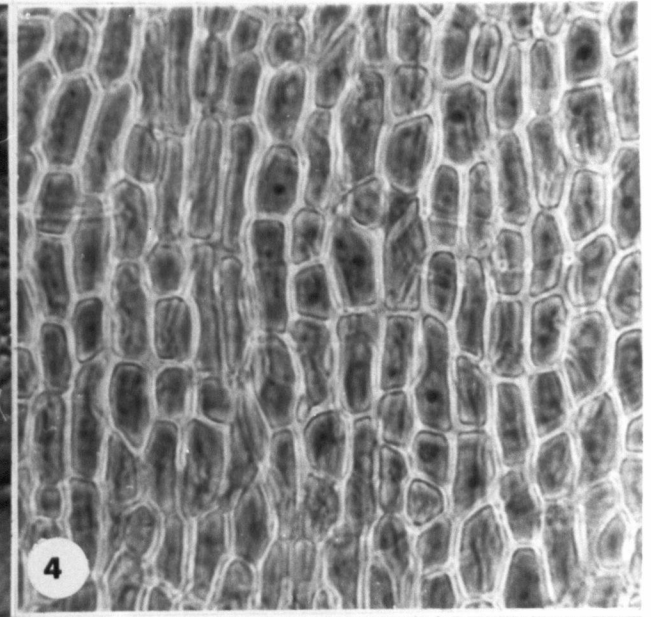
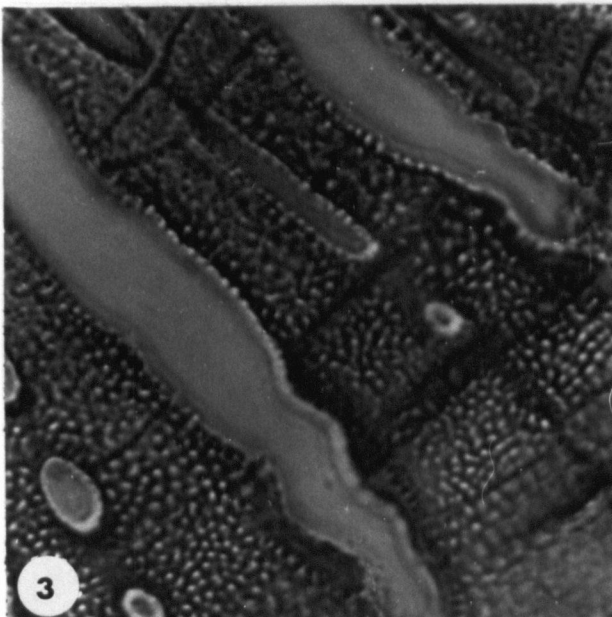
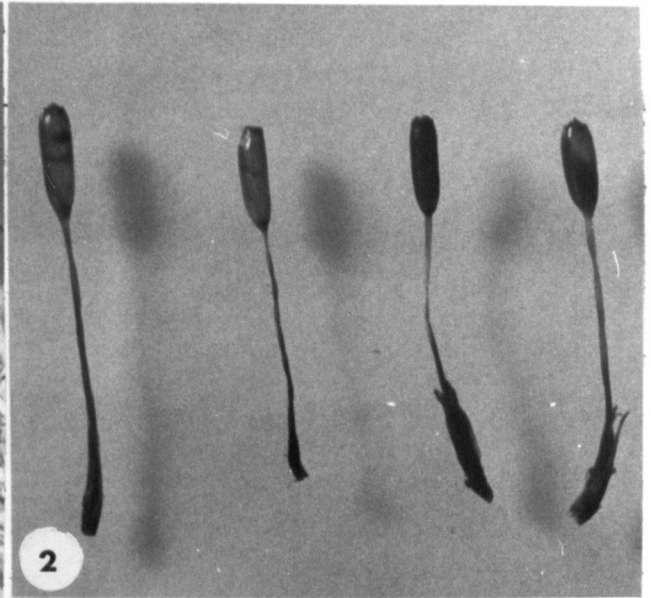
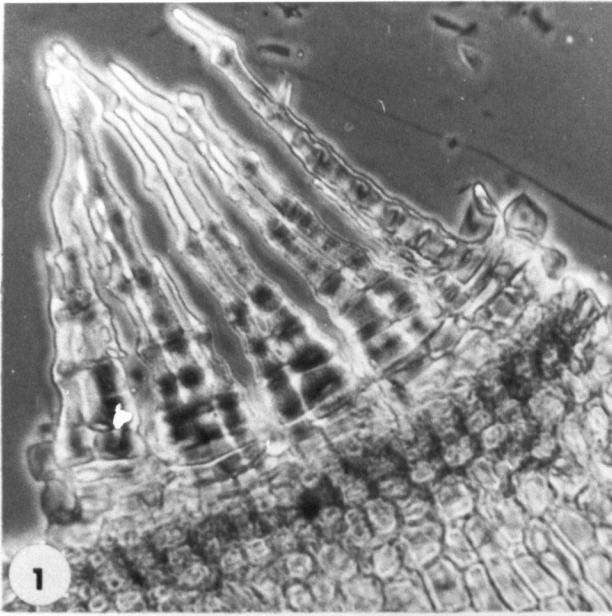


PLATE VII

R. heterostichum var. affine

- Figure 1 - Habit showing branching pattern (X 1.5)
- Figures 2 & 4 - Cross section from upper portion of leaf
(X 280)
- Figure 3 - Cross section from near base of leaf (X 280)
- Figures 5 & 6 - Cross section from middle portion of leaf
(X 280).

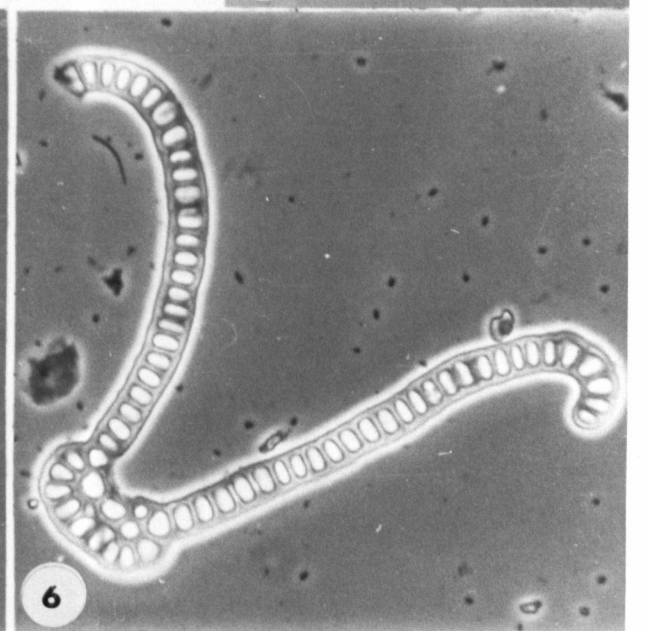
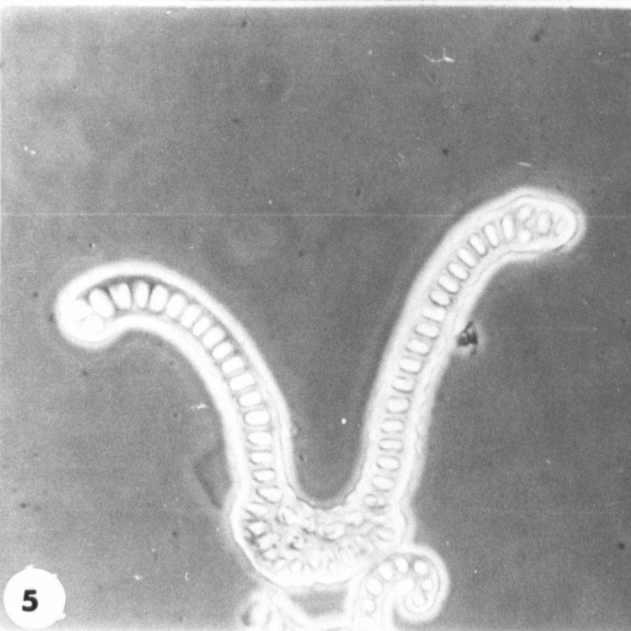
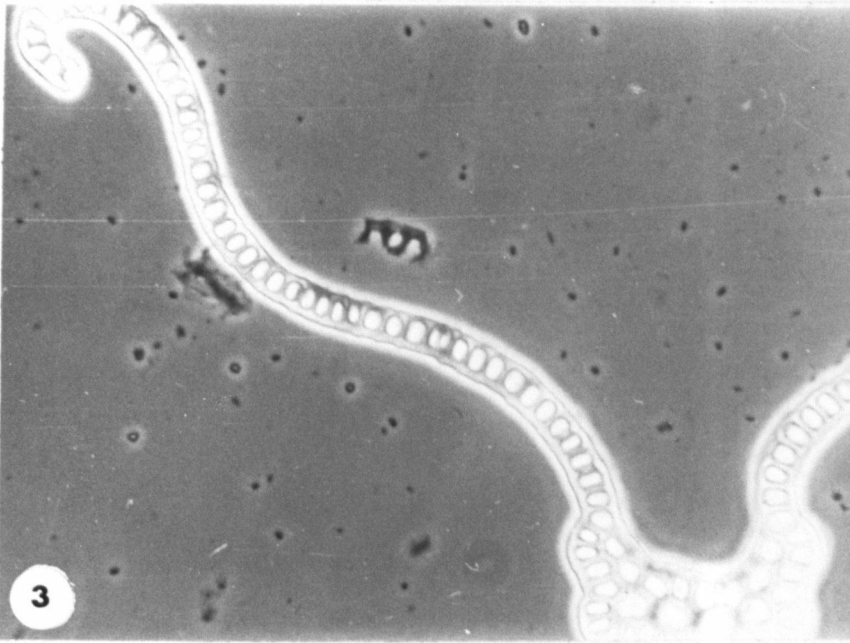
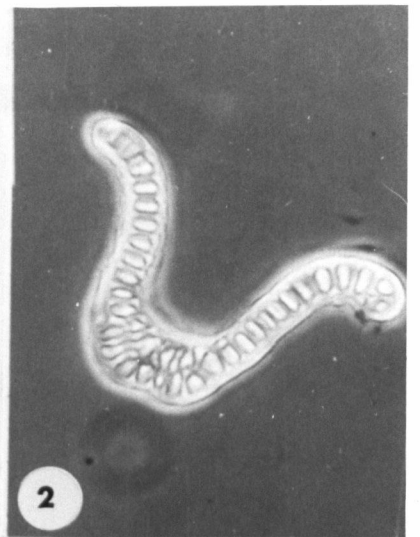
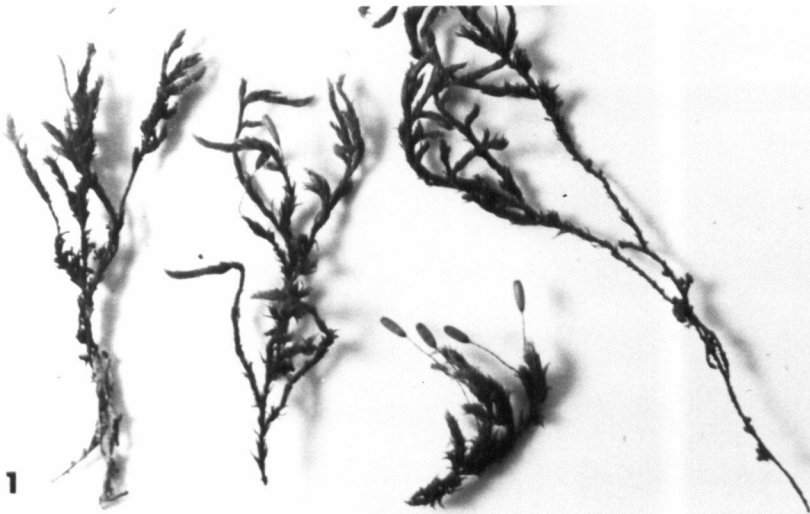


PLATE VIII

R. sudeticum

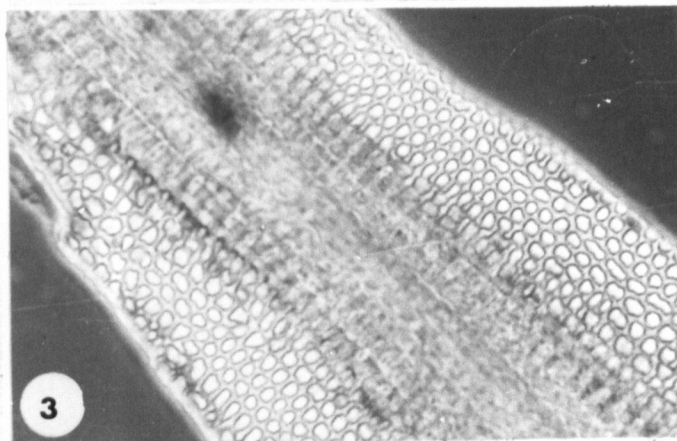
- Figures 1 & 2 - Habit showing branching pattern (X 1.5)
- Figure 3 - Cells from upper portion of leaf (X 280)
- Figure 4 - Cells from middle portion of leaf (X 280)
- Figure 5 - Cells from lower 1/3 of leaf (X 280)
- Figure 6 - Hyaline point of leaf showing denticulation both on the margin and on the surface (X 280).



1



2



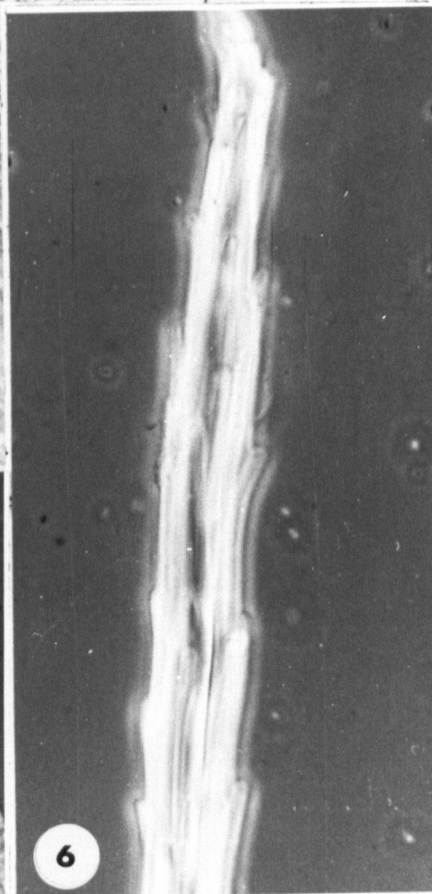
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5



6

PLATE IX

R. sudeticum

- Figure 1 - Cross section from upper portion of leaf just below hyaline point (X 280)
- Figure 2 - Cross section from lower edge of upper 1/5 of leaf (X 280)
- Figure 3 - Cross section from lower edge of upper 1/3 of leaf (X 280)
- Figure 4 - Cross section from near base of leaf (the lower section). (X 280)
- Figure 5 - Sporophytes (X 5)
- Figure 6 - Peristome teeth (X 280)
- Figure 7 - Portion of annulus (X 280)
- Figure 8 - Spores (X 1120)
- Figure 9 - Peristome teeth showing papillosity (X 1120).

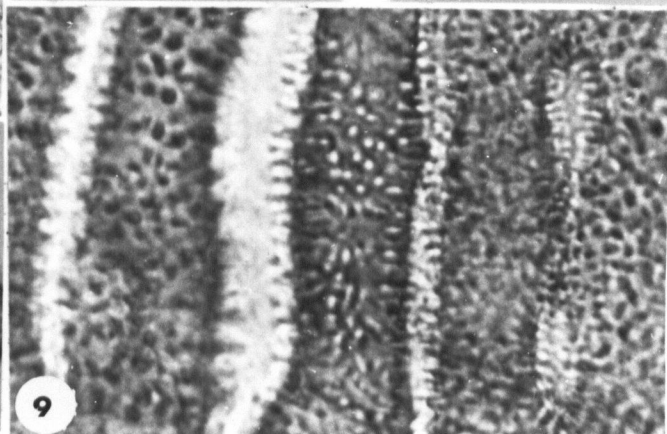
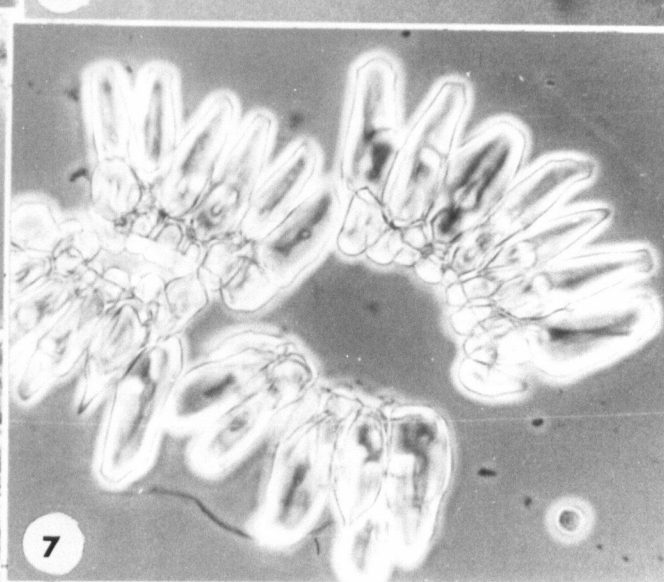
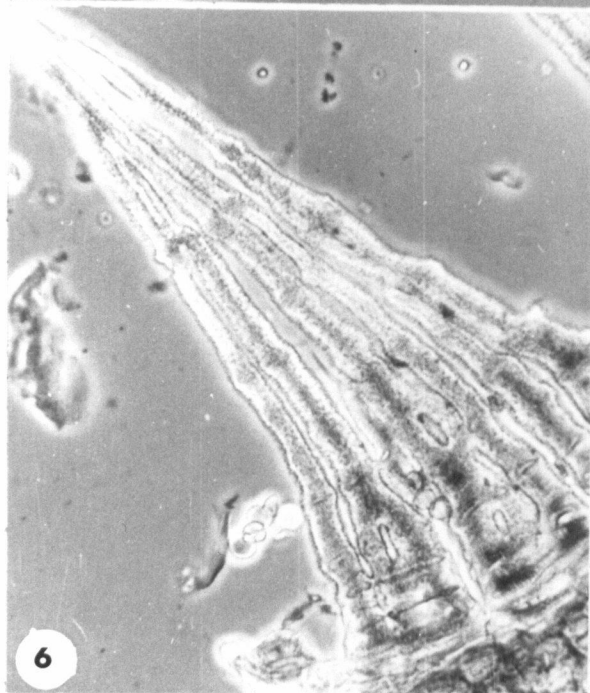
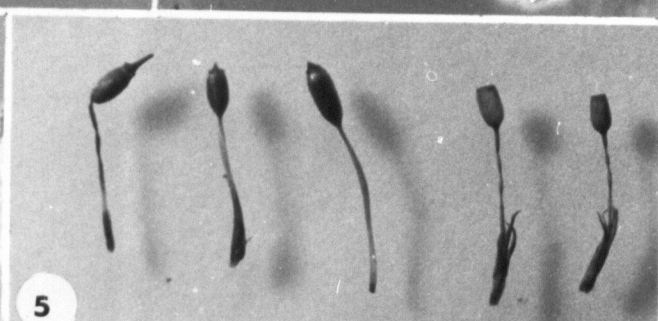
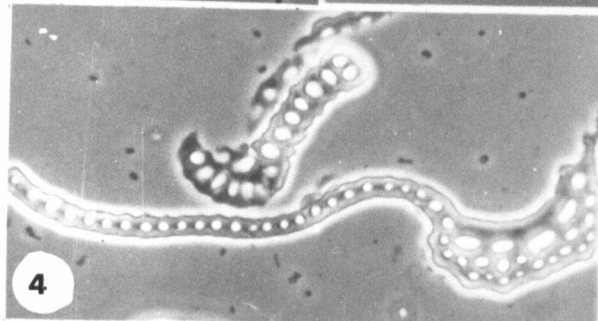
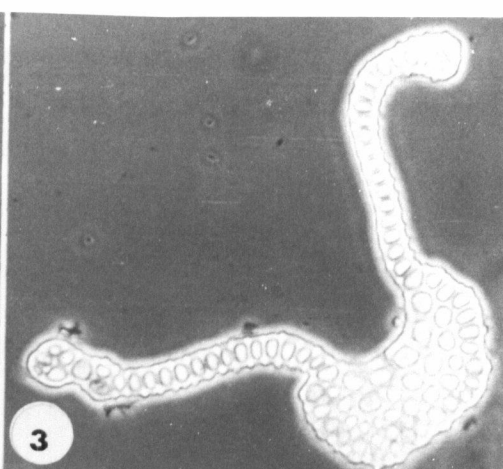
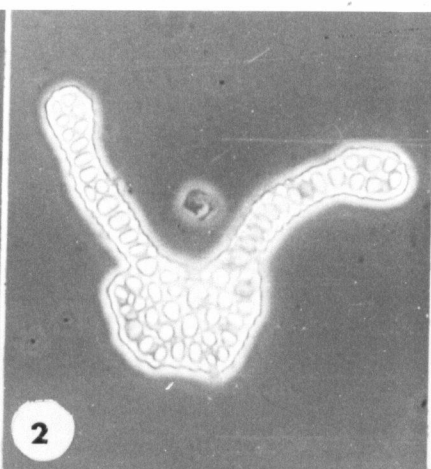
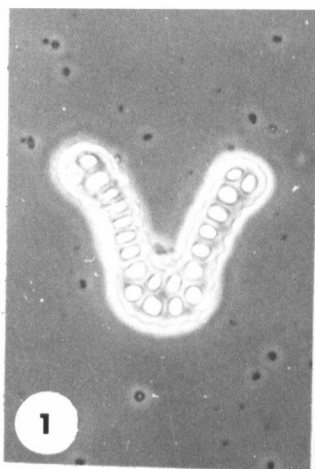


PLATE X

R. sudeticum var. macounii

- Figures 1 & 2 - Habit showing branching pattern (X 1.5)
- Figure 3 - Upper portion of leaf showing leaf cells and short hyaline point (X 280)
- Figure 4 - Sporophytes (X 5)
- Figure 5 - Cells from middle portion of leaf (X 280)
- Figure 6 - Leaf apex showing absence of hyaline point (X 1120)
- Figure 7 - Cells of leaf base (X 280)
- Figure 8 - Operculum of R. sudeticum (X 110).

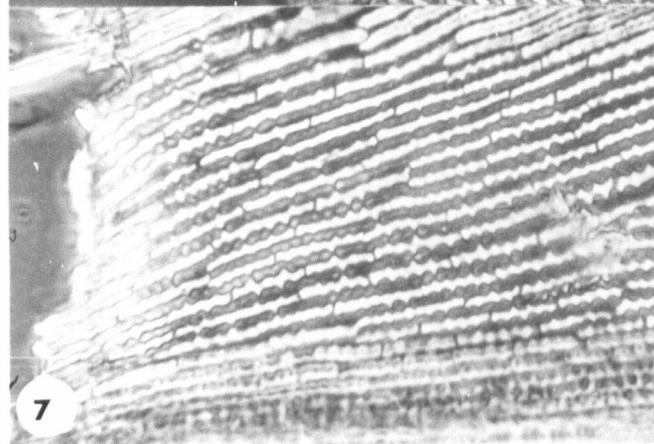
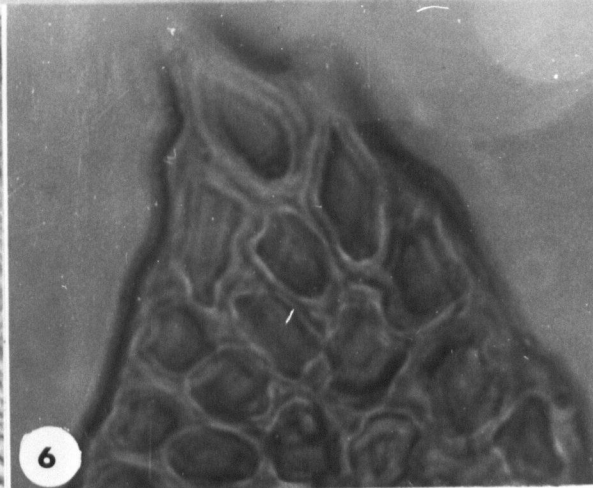
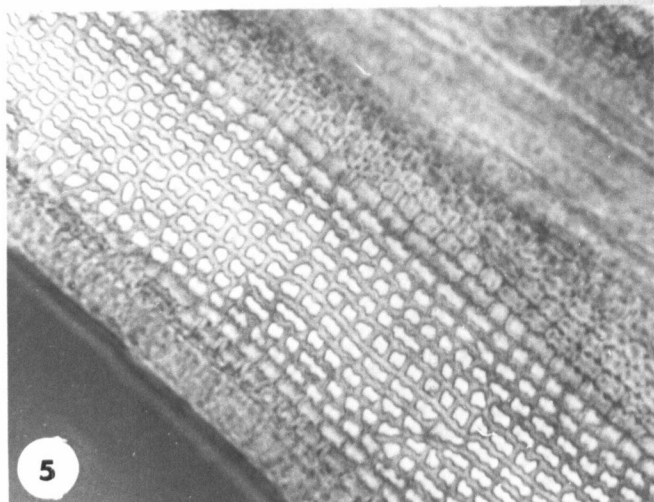
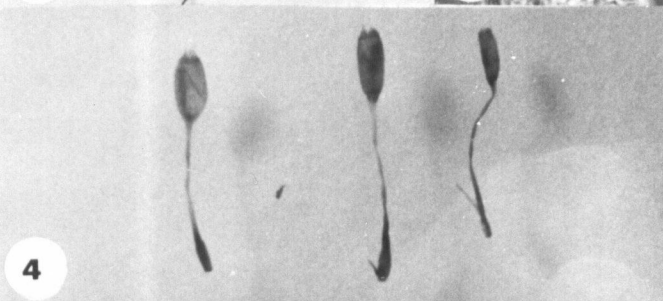
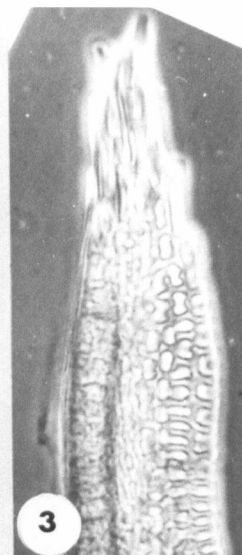
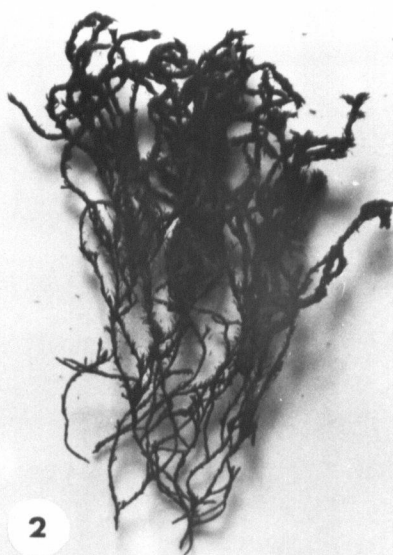


PLATE XI

R. brevipes

- Figures 1 & 2 - Habit showing branching pattern (X 1.5)
- Figure 3 - Leaf apex showing strongly denticulate hyaline point (X 280)
- Figure 4 - Cells from lower 1/3 of leaf (X 280)
- Figure 5 - Cells from upper 1/3 of leaf (X 280)
- Figure 6 - Cells from near middle of leaf (X 280).

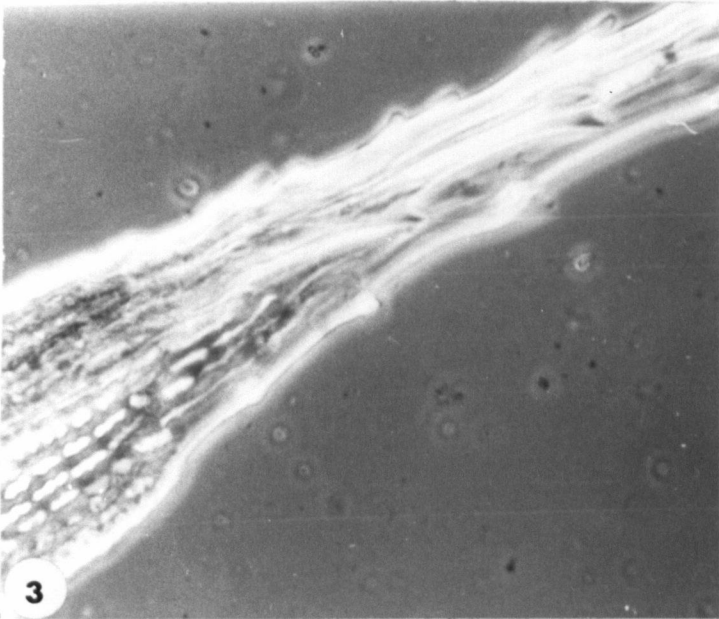
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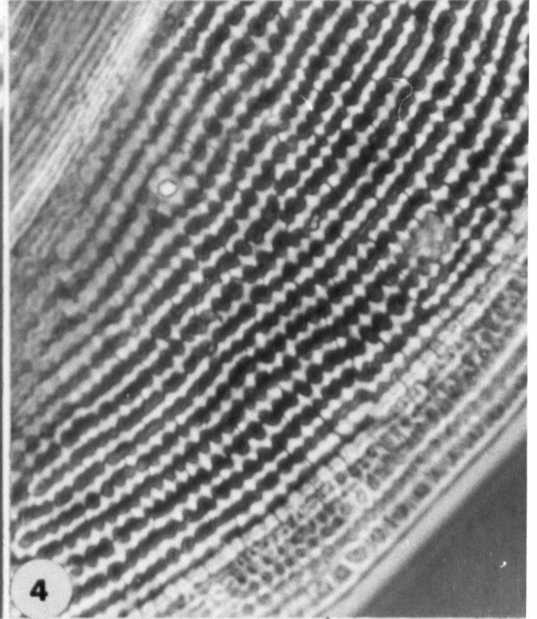
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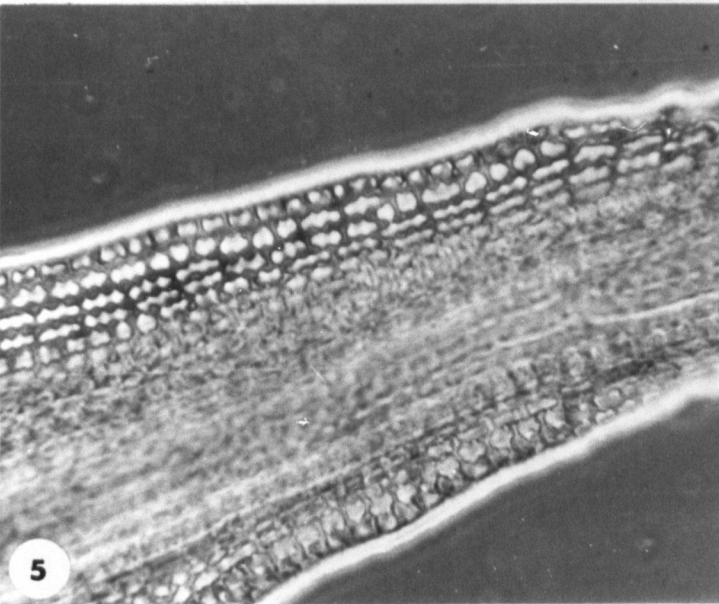
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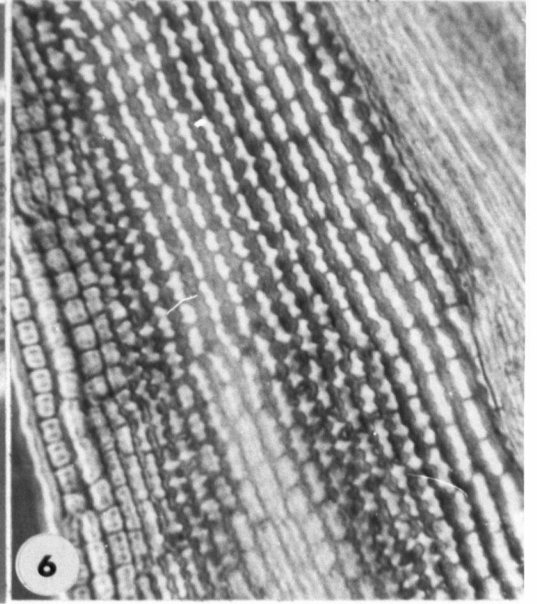


PLATE XII

R. brevipes

- Figure 1 - Sporophytes (X 5)
- Figure 2 - Cross section from near base of leaf showing costa (X 280)
- Figures 3 & 5 - Cross section from upper 1/3 of leaf (X 280)
- Figure 4 - Cross section from near base of leaf showing margin (X 280)
- Figure 6 - Cross section from middle portion of leaf (X 280)
- Figure 7 - Operculum (X 160).

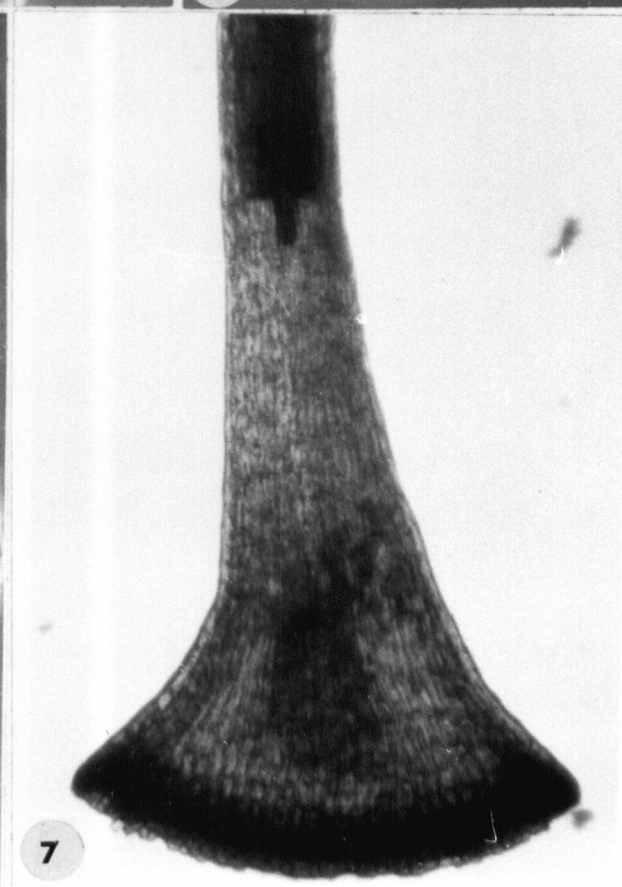
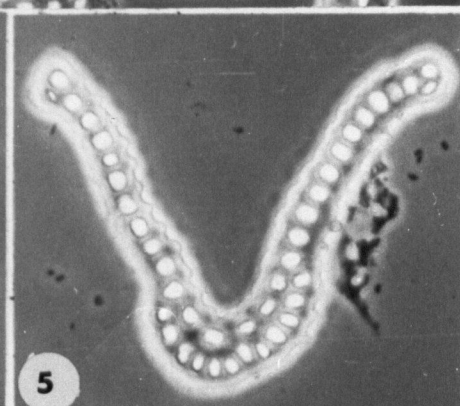
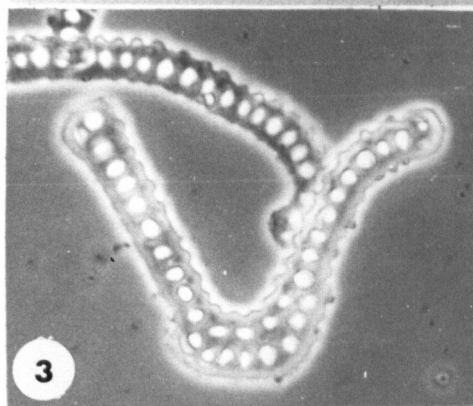
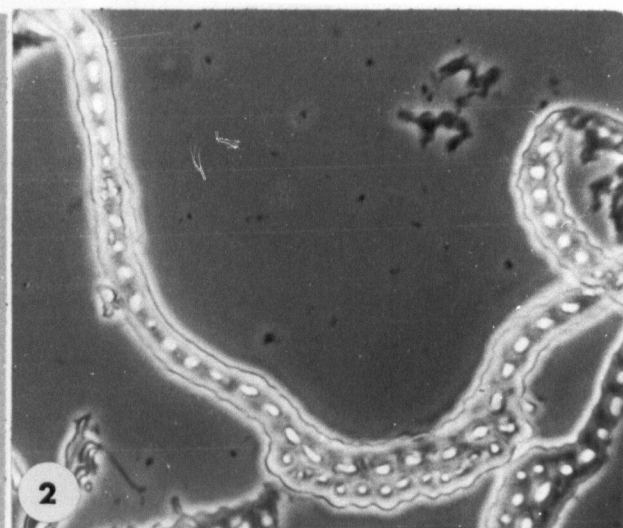
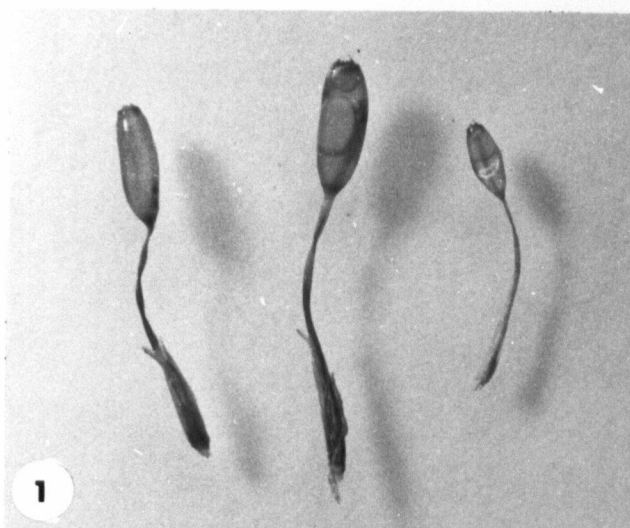


PLATE XIII

R. brevipes

- Figure 1 - Peristome teeth (X 280)
- Figure 2 - Lower portion of capsule showing stomates (X 280)
- Figure 3 - Exothecial cells near mouth of capsule (X 280)
- Figure 4 - Portion of annulus (X 280)
- Figure 5 - Operculum (X 110)
- Figure 6 - Upper portion of Calyptra (X 110)
- Figure 7 - Sporophytes of R. brevipes var.
"microcarpiiformis" (X 4).

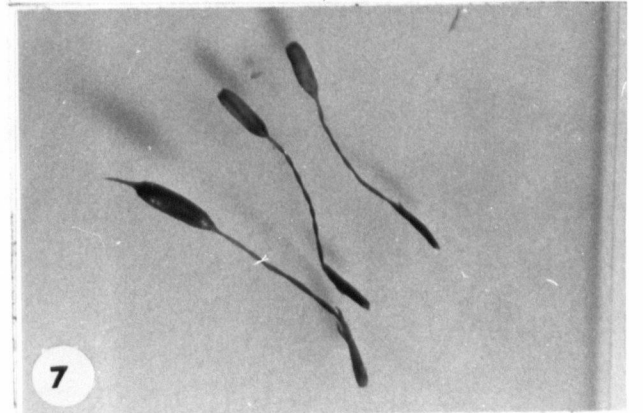
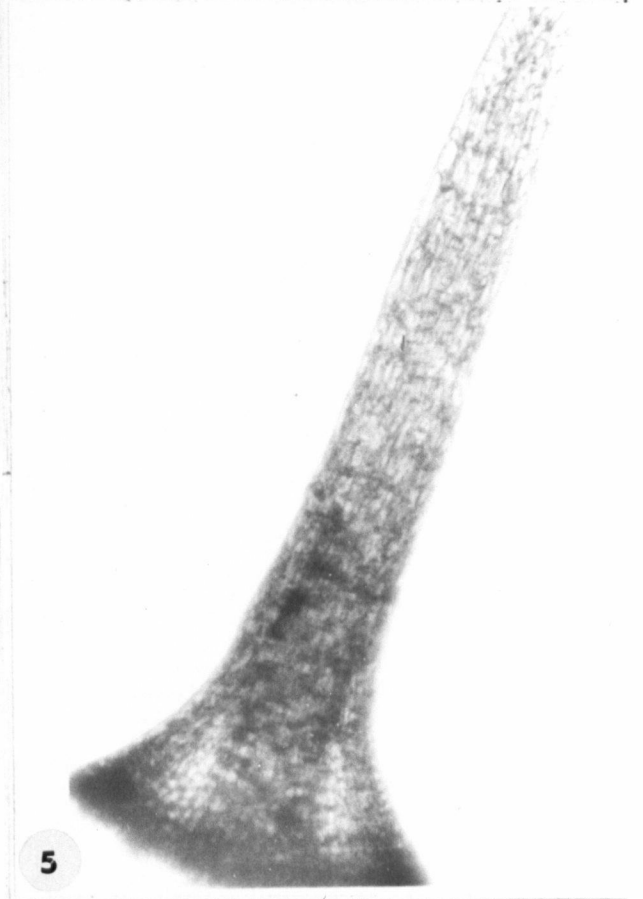
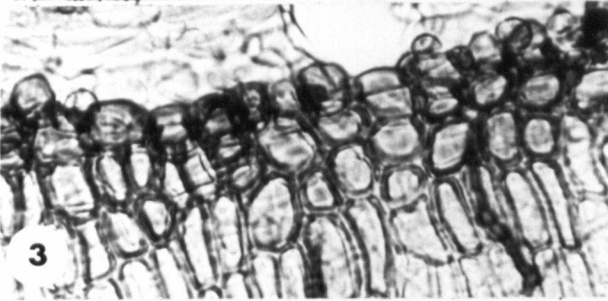
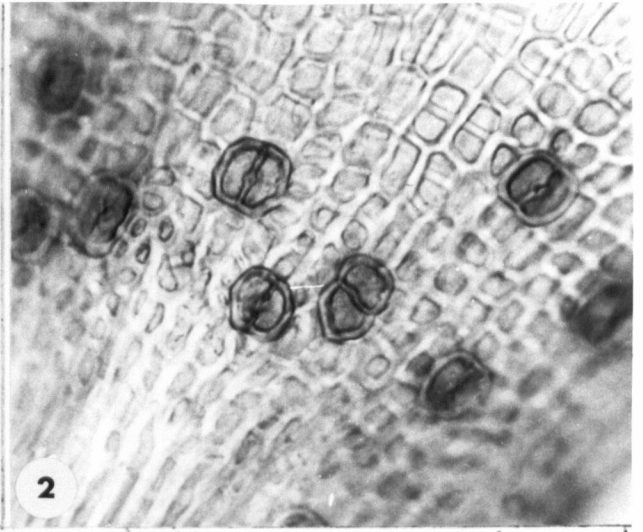
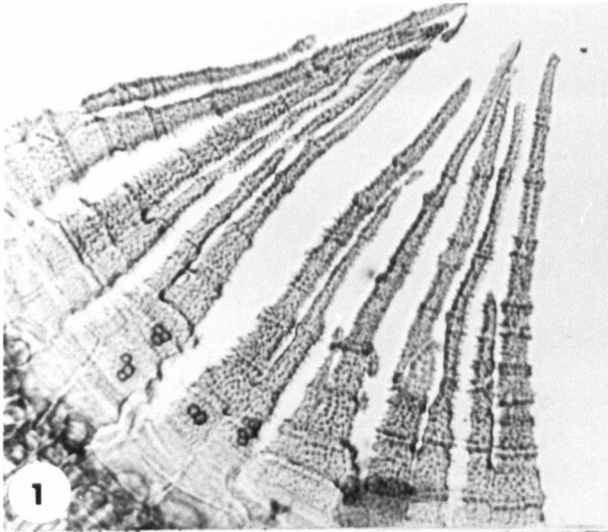


PLATE XIV

R. brevipes var. "laevis"

Figure 1 - Habit showing branching pattern (X 1.5)

Figures 2 & 5 - Cross section from lower 1/3 of leaf
 (X 280)

Figures 3,4 & 6 - Cross section from middle portion of
 leaf (X 280).

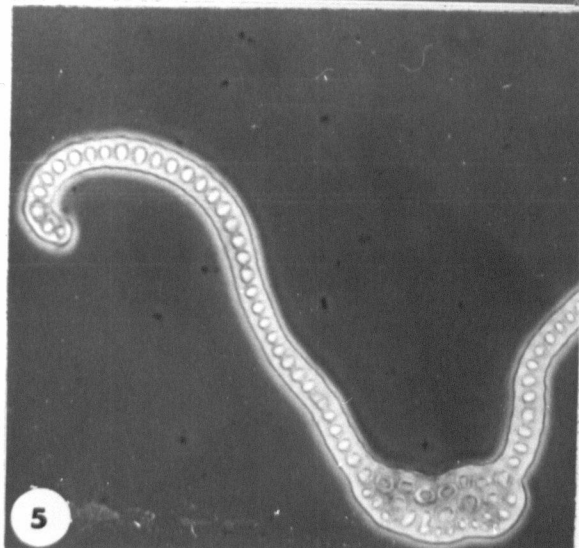
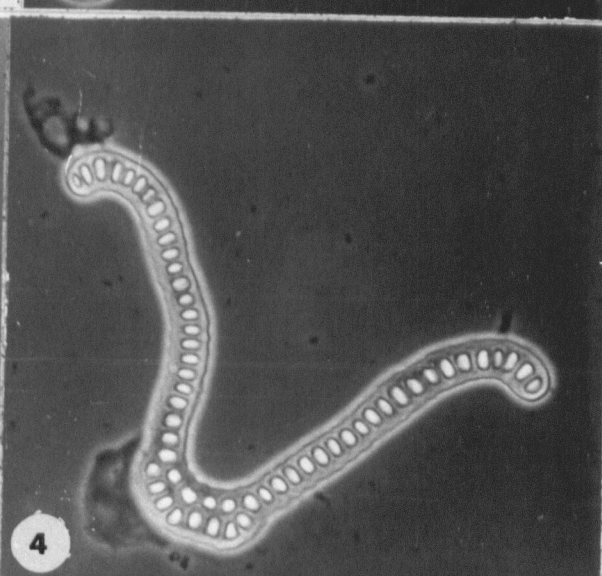
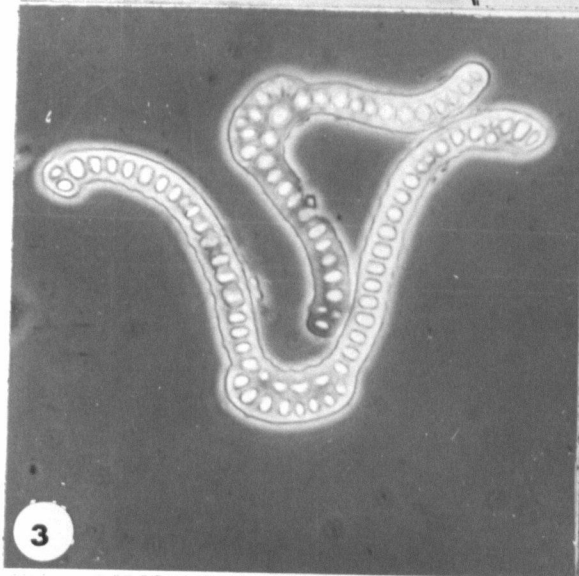
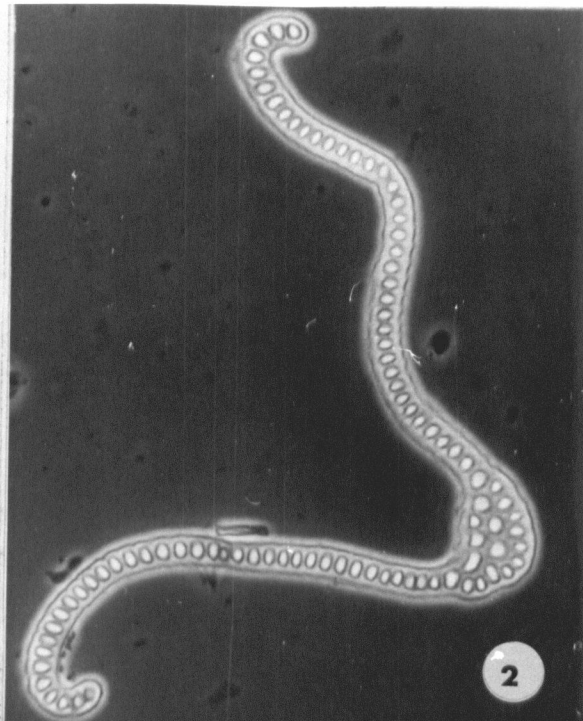


PLATE. XV

R. brevipes var. "eramulosum"

Figure 1 - Habit showing branching pattern (X 1.5)

Figure 2 - Sporophytes (X 5)

R. brevipes var. "microcarpiformis"

Figure 3 - Cells from just below hyaline point of leaf
(X 280)

Figure 4 - Habit showing branching pattern (X 1.5)

Figure 5 - Cells from middle portion of leaf (X 1120)

Figure 6 - Cells from lower portion of leaf (X 1120).

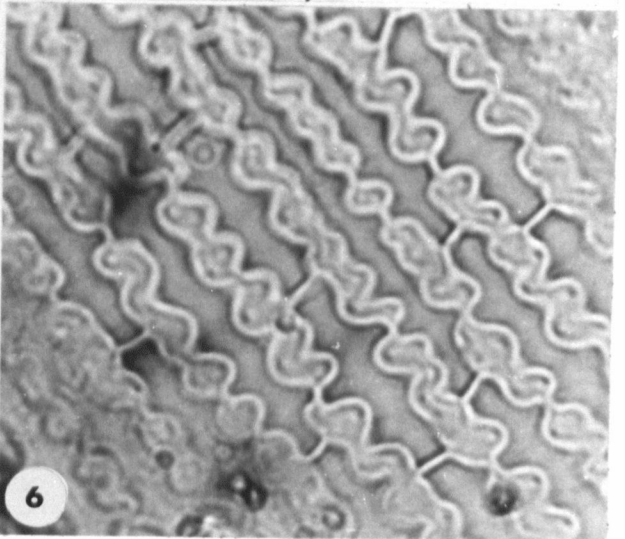
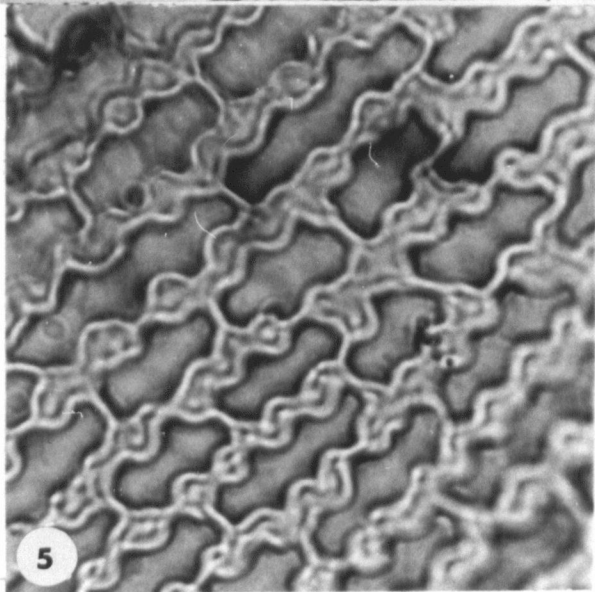
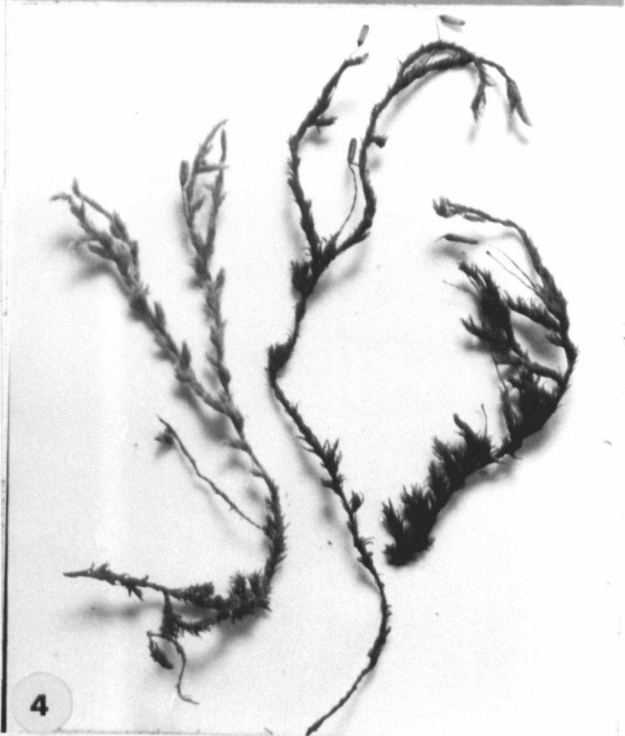
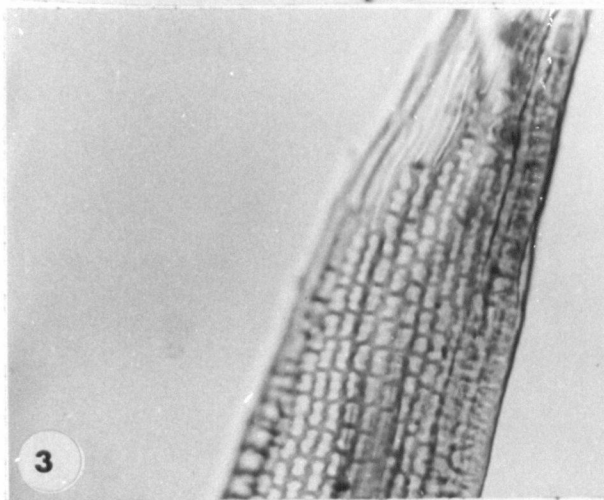
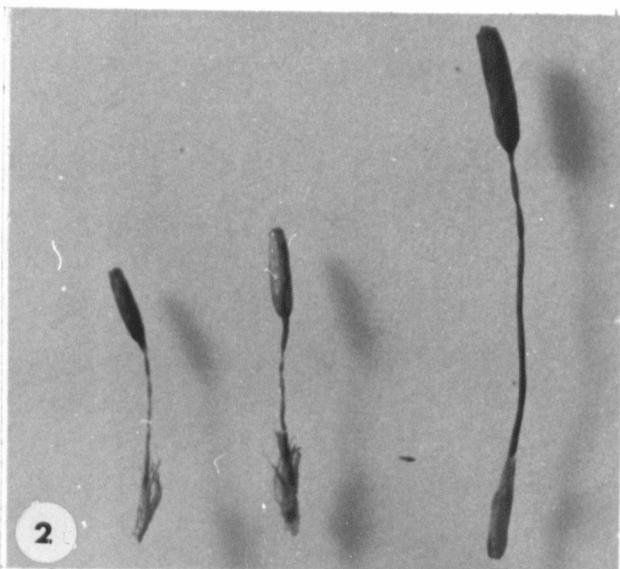


PLATE XVI

R. brevipes var. "microcarpiformis"

- Figure 1 - Cross section from lower edge of upper
1/3 of leaf (X 280)
- Figures 2 & 4 - Cross section from middle portion of
leaf (X 280)
- Figure 3 - Cross section from lower 1/3 of leaf
(X 280)
- Figure 5 - Exothecial cells from middle of capsule
wall (X 280)
- Figure 6 - Spores (X 1120).

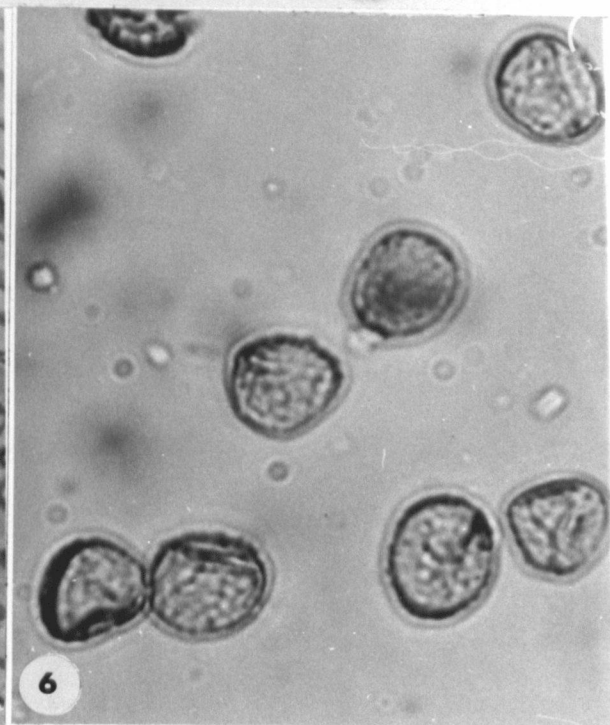
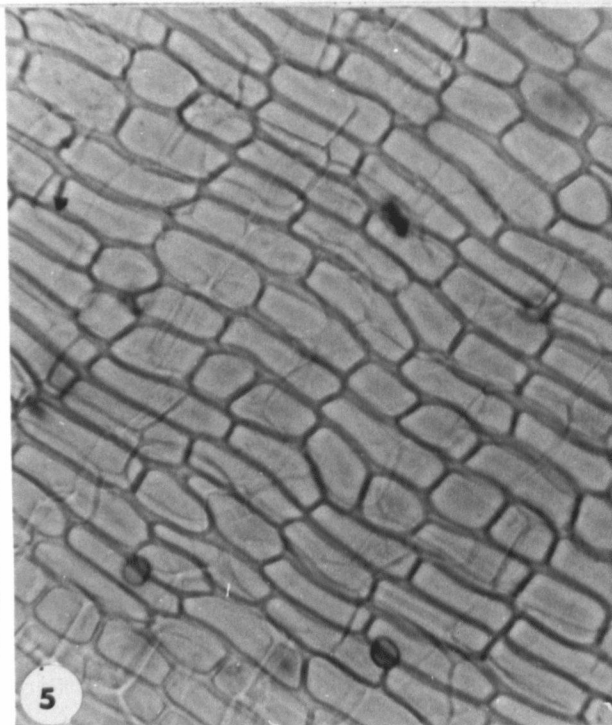
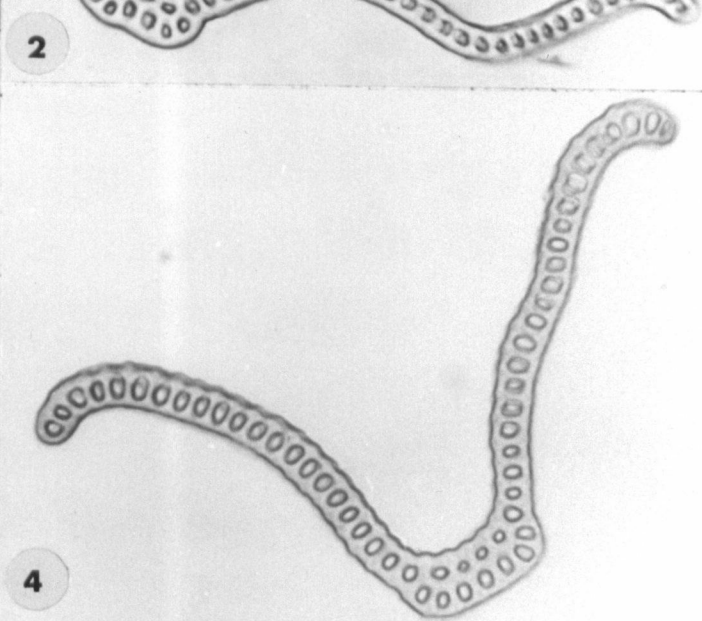
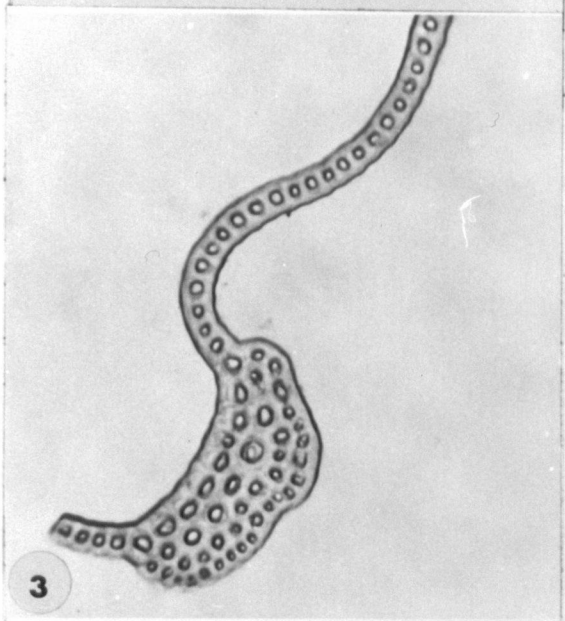
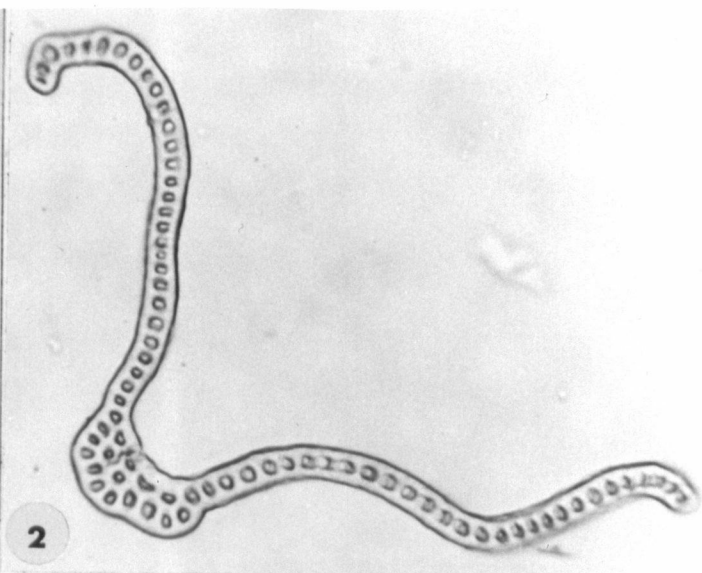
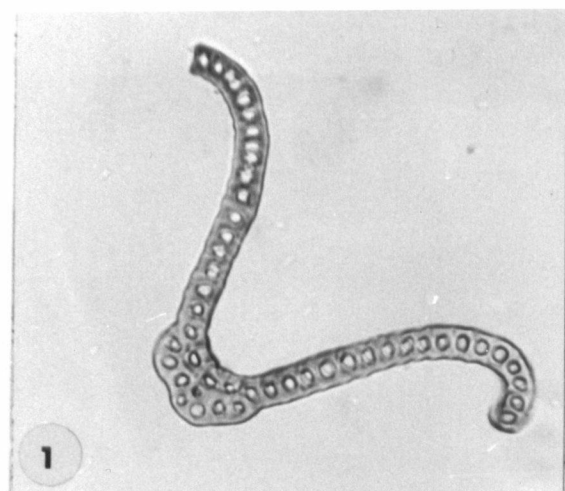


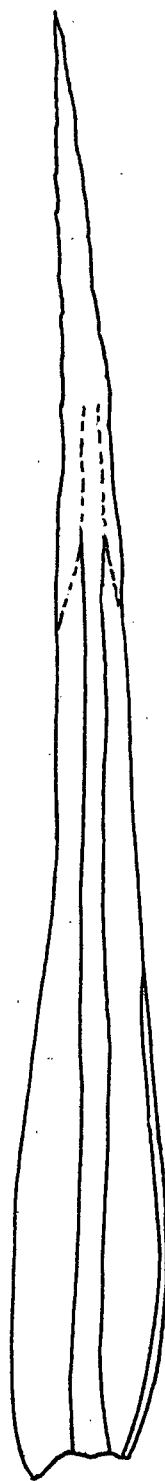
PLATE XVII

Figures 1 - 4 - Leaves of R. "laxum" (X 48)

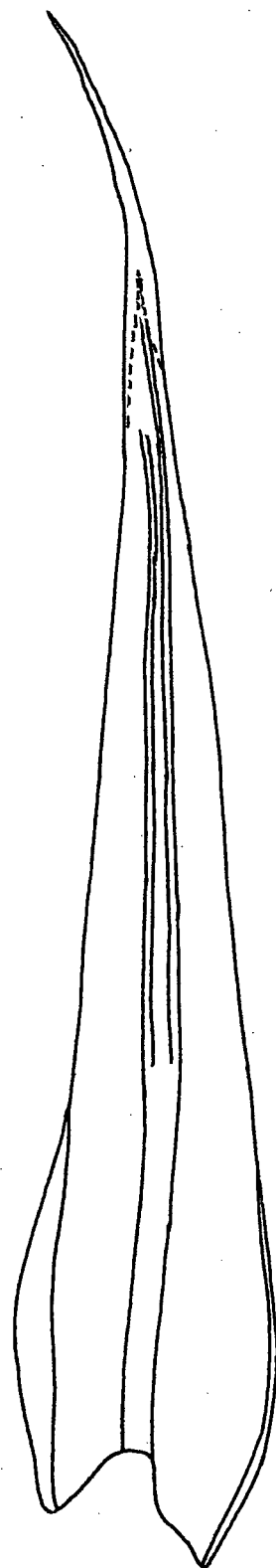


2

1



3

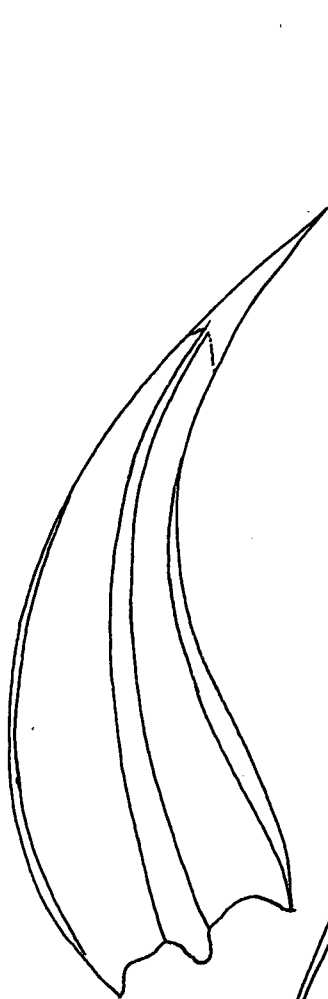


4

PLATE XVIII

Figures 1 & 3 -Leaves of R. heterostichum (X 48)

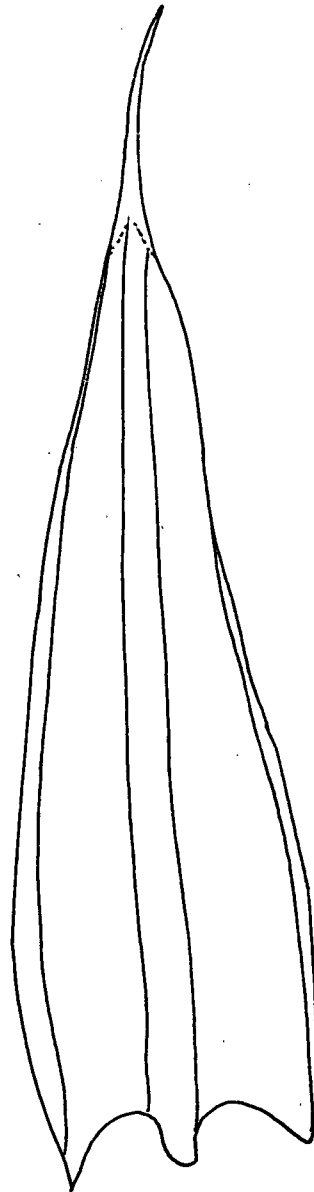
Figure 4 -Leaf of R. heterostichum var. affine (X 48).



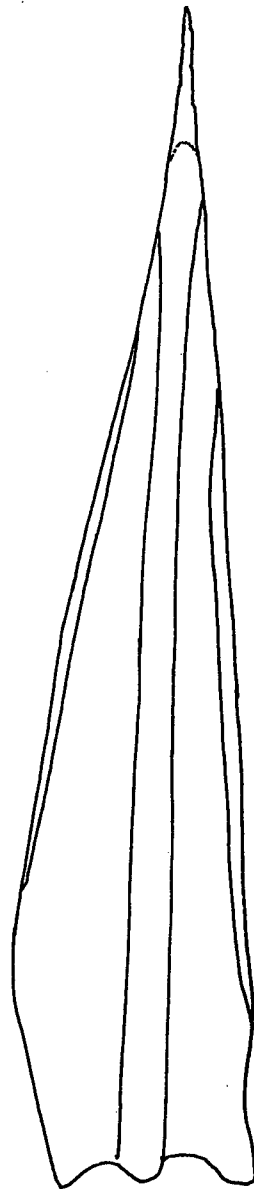
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2



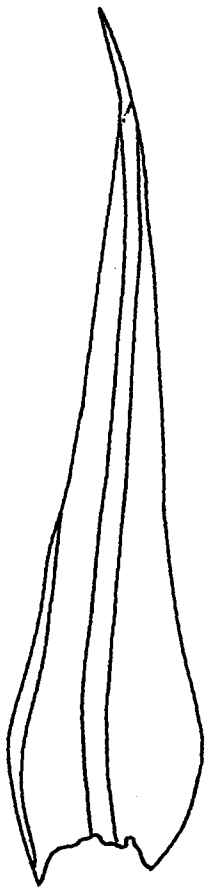
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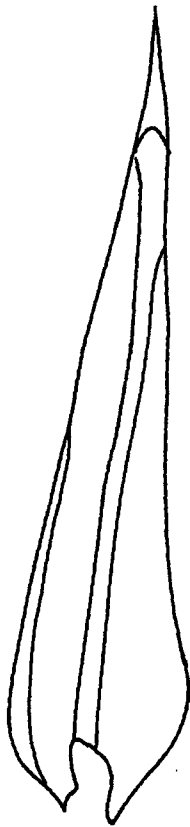
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PLATE XIX

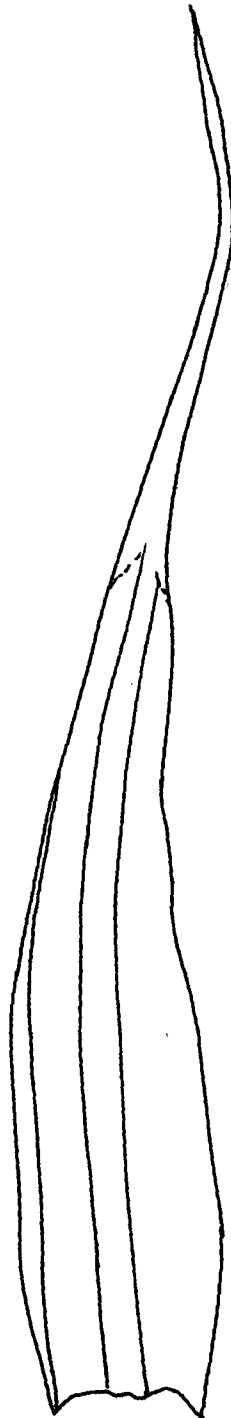
Figures 1 - 4 - Leaves of R. sudeticum (X 48)



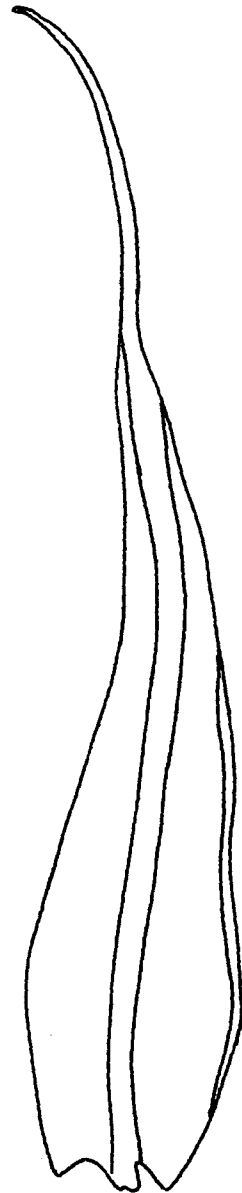
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2



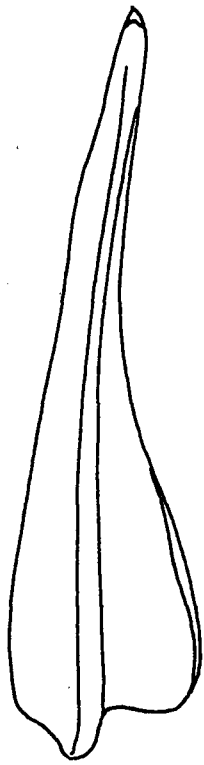
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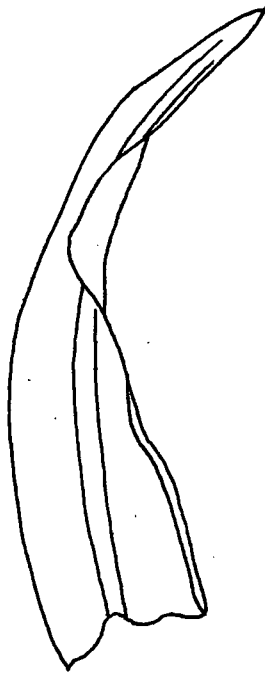
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PLATE XX

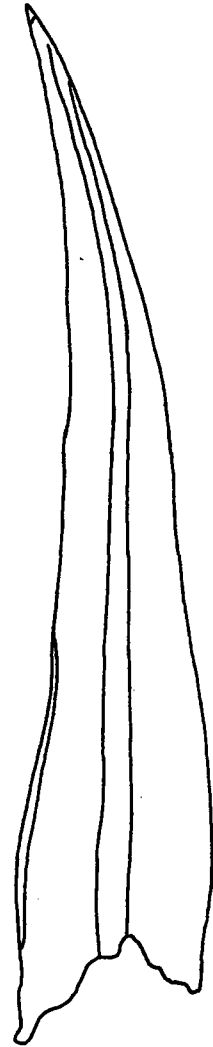
Figures 1 - 3 - Leaves of R. sudeticum var. macounii (X 48)



1



2

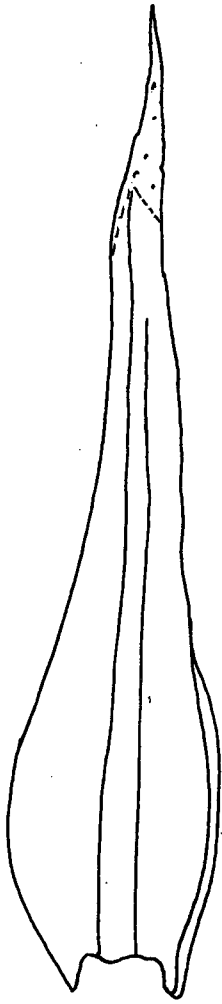


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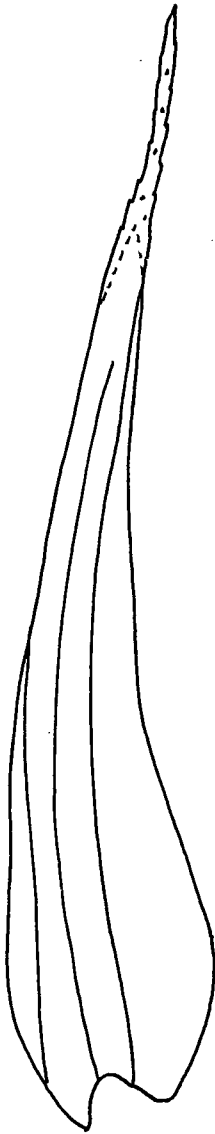
PLATE XXI

Figures 1 & 2 - Leaves of R. brevipes (X 48)

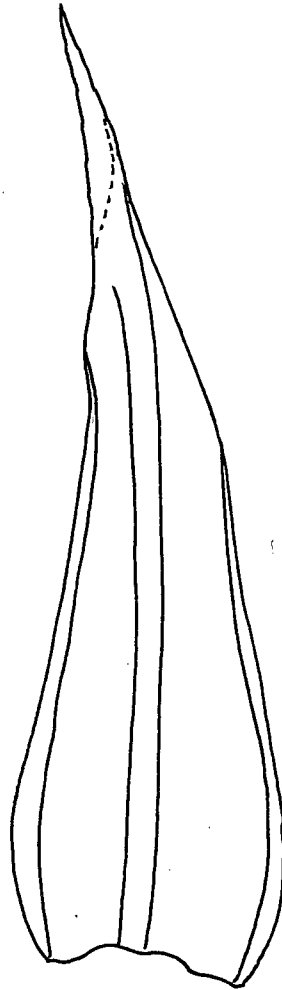
Figures 3 & 4 - Leaves of R. brevipes var. "laevis" (X 48)



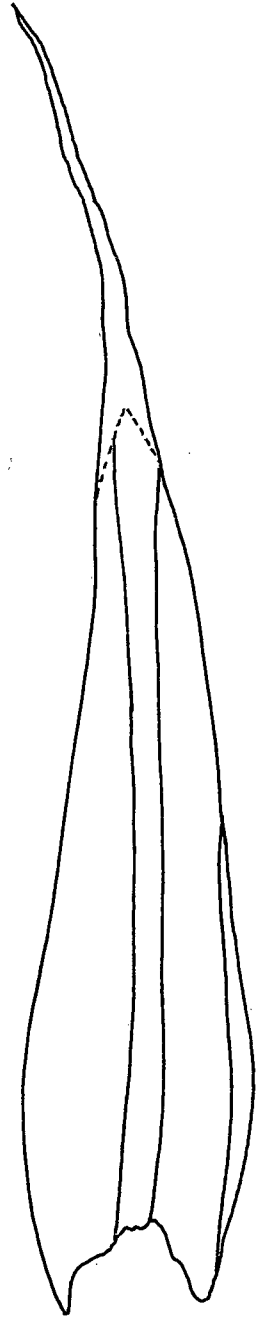
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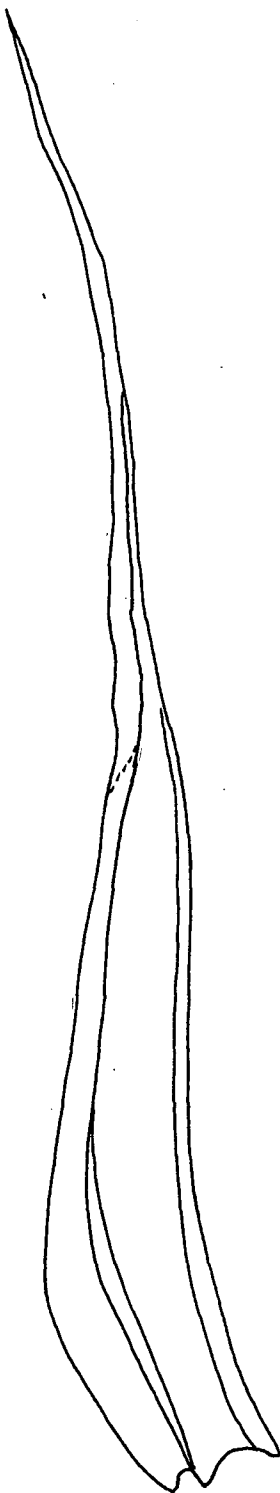
PLATE XXII

Figure 1 - Leaves of R. brevipes var. "eramulosum"
(X 48)

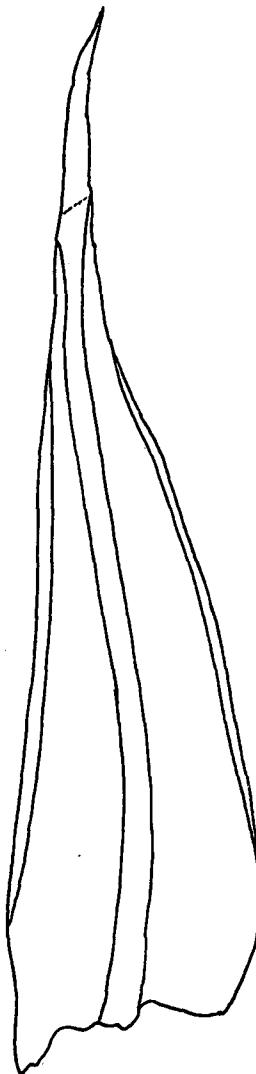
Figures 2 - 4 - Leaves of R. brevipes var. "microcarpiformis"



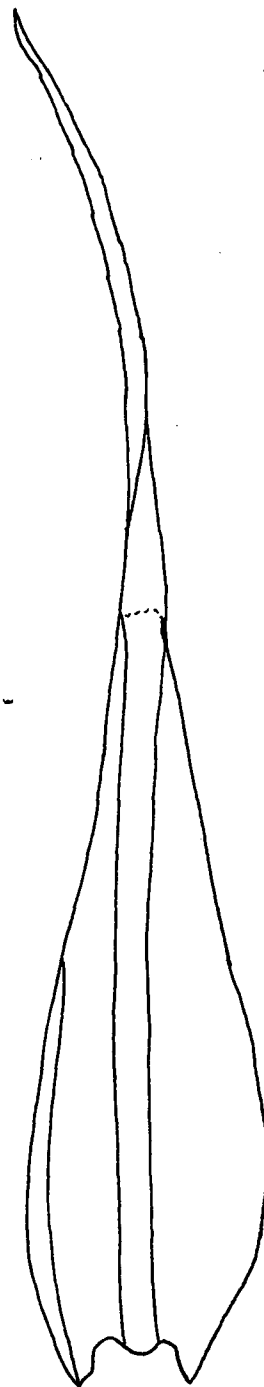
1



2



3



4