A MONOGRAPH OF THE GENUS HYGROHYPNUM LINDB. (MUSCI)

by

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ABSTRACT

The genus *Hygrohypnum* Lindb. (Musci) is monographed for the world for the first time. Thirty-nine species and a large number of subspecific taxa recognised at the inception of this study were investigated using traditional tools of herbarium taxonomy, extensive field work throughout North America and the experimental cultivation of ten North American species in a uniform environment.

These studies show that *Hygrohypnum* is a Northern Hemisphere genus, in which the important taxonomic characters are: stem anatomy, shape of the leaf and its apex, leaf concavity, costa structure, alar cell differentiation, length of the marginal leaf cells, sexuality, structure of the perichaetial leaves and the annulus. Based on these characters the following 16 species are recognised: *H. alpinum* (Lindb.) Loesk., *H. duriusculum* (De Not.) nov. comb., *H. smithii* (Sw. in Lilj.) Broth., *H. bestii* (Ren. et Card.) Holz., *H. cochlearifolium* (Vent. in De Not.) Broth., *H. norvegicum* (Schimp.) Amann, *H. molle* (Hedw.) Loesk., *H. styriacum* (Limpr.) Broth., *H. luridum* (Hedw.) Jenn., *H. alpestre* (Hedw.) Loesk., *H. polare* (Lindb.) Loesk., *H. ochraceum* (Wils. ex Turn.) Loesk., *H. eugyrium* (Schmip.) Broth., *H. subeugyrium* (Ren. et Card.) Grout, *H. montanum* (Lindb.) Broth., and *H. closteri* (Aust.) Grout. *Hygrohypnum alpinum* and *H. styriacum* are new in Western North America and *H. bestii*, known previously as a Western North American endemic, is now shown to be on the Upper Peninsula of Michigan and around the Gulf of St. Lawrence.

The taxonomic treatment presents a generic description and keys to the species and provides each species with a description, a discussion of
variability and taxonomic matters, illustrations and a distribution map.

The status of each excluded taxon is discussed.

The generic concept and the possible relationships among the recognised species are examined by comparing the author's opinion with information derived from an ordination and two cluster analyses.
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INTRODUCTION

Hygrohypnum is a genus of semi-aquatic pleurocarpous mosses that is currently treated in the family Amblystegiaceae, itself a group of taxa of predominantly aquatic or otherwise damp environments. Certain taxa presently treated within the genus can be traced to Hedwig's (1801) Species Muscorum, but the original concept of the genus dates from Schimper (1853) in Bryologia Europaea. Schimper named the genus Limnobium Schimp. and distinguished it from Hypnum on the basis of the broadly ovate-lanceolate to almost orbicular leaves and the nature of the alar cells which were said to be hardly differentiated from other basal leaf cells and little or not at all inflated or excavated. Of the habitat in which the genus grew, Schimper noted only that the name, Limnobium, reflected the habitat of the five original species.

The manifold systematic problems in the genus Hygrohypnum have their origin in the habitat in which the genus occurs and the absence of a sound, modern generic concept.

Hygrohypnum normally occurs on rocks or stones between the high and low water levels; or, in or beside small, cold, swiftly running mountain streams. Like other plants of similar environments various real and alleged species of Hygrohypnum have responded to the fluctuating water levels by assuming a myriad of forms which have blurred species limits. It is to be expected then, that the species concepts held by many workers have been badly confused and that among the most variable species numerous subspecific taxa have been recognized.

Renauld (1883) revised the European species and presented a more precise generic circumscription and Brotherus (1909 and 1925) provided keys to the species or certain groups of species known to those times. The genus has been
treated in numerous regional floras (Braithwaite, 1898; Limpricht 1904; Roth, 1905; Dixon, 1896 and 1924; Brotherus, 1923; Monkemeyer, 1927; Grout, 1931; Nyholm, 1965 and others), but it has never been revised on a world wide basis. As a result of this neglect many taxa have been described under different names, while others of diverse and questionable affinities have been included within the genus, apparently for the sole reason that the plants occured on rocks in streams. This generic heterogeneity prompted Loeske (1910) to refer to Hygrohypnum as a "biologische Mischgattung."

The objectives of this monograph have been to: 1. assess all of the described species to circumscribe a more natural genus, 2. discern stable morphological characters with which to distinguish species, 3. provide keys to and descriptions, illustrations and maps of all the recognized species and 4. put into usable descriptive form an assessment of the variation that may be encountered in each species.

To accomplish these goals Hygrohypnum has been investigated in three ways. 1. Field work was conducted throughout North America in order to assess the ecological amplitude of the genus and to gain field experience to assess natural variability in the recognized taxa. 2. Ten species from diverse localities from throughout North America were grown under uniform environment to determine the stability of certain morphological characters. 3. More than 2,200 herbarium specimens were dissected and made into microscope slide preparations for critical study. Subsequently more than 13,000 specimens were examined and annotated.
Many Darwinian systematists have expressed the view that a classification system should reflect phylogeny. This is a very desirable goal, but unfortunately an understanding of phylogeny depends on the existence of a fossil record, which all too often is fragmentary at best. In the absence of a fossil record the relationships among extant species may be inferred or occasionally established from data on karyology, breeding systems, development, chemistry, ecology and phytogeography. However, when the only available data are derived from external, adult morphology it is very difficult, if not impossible to truly understand the biological relationships among a group of species. As a consequence I have not speculated on the phylogeny of *Hygrohypnum*.

The sequence in which the species of *Hygrohypnum* are presented in this work represents a series of overlapping patterns of morphological variation. The design of this sequence serves only to elucidate trends in adult morphology. The sequence of species is graphically represented in fig. 81 on page 400. The most important morphological trends are as follows;

1. Leaves very broad to narrow.
2. Leaves exclusively straight to straight and/or falcate.
3. Alar cells mostly undifferentiated to variously differentiated.
4. Stem anatomy exhibiting a cortex of small, thick-walled cells, a medulla of larger, thinner-walled cells and a central strand to a more variable pattern of differentiation.
5. Plants mostly autoicous to plants with a more variable sexuality.
THE TAXONOMIC HISTORY OF HYGROHYPNUM

Progress in the study of mosses has been dependent upon technical advances in microscopy. The inability to observe microscopic features caused early workers to employ very broad generic concepts. As a consequence, pleurocarpous mosses, exclusive of *Fontinalis*, were originally treated in the all inclusive genus *Hypnum*. Hedwig (1801) was the first to use microscopic features in classifying mosses and with his work commenced the gradual subdivision of the genus *Hypnum sensu latu* into many smaller, more natural genera.

In the following discussion the taxonomic history of *Hygrohypnum* is traced to three Hedwigian species and is then followed through the description of additional species and their subsequent treatment in various sectional and subgeneric groupings of *Hypnum* or in such segregate genera as *Limnobium*, *Stereodon*, *Amblystegium*, *Calliergon* and ultimately *Hygrohypnum*. In the following discussion it should be understood that the classifications ascribed to each cited author have been edited so as to deal only with those taxa that are considered to be modern species of *Hygrohypnum* or a synonym thereof.

The origins of the genus can be traced to three species treated by Hedwig within the broadly conceived genus *Hypnum* Hedw. In his *Species Muscorum* Hedwig (1801) subdivided *Hypnum* into eight numbered groups to which he gave neither formal nor hierarchical ranking. As criteria for delimiting his eight groups Hedwig emphasized leaf symmetry and the various attitudes the leaves exhibited along the stems. Branching patterns were also used, but were subordinate to leaf characters. By modern standards, the taxa included in these early groupings are of diverse relationships. However, in terms of the characters used, Hedwig's groups were reasonably
sound. Hedwig recognized and classified Hypnum alpestre, H. molle and H. luridum as follows:

Group III, Foliis rectis, aequaliter et arcte imbricatis, (ramis teretibus). Hypnum alpestre Sw. ex Hedw.


Group VIII, Foliis secundis, incurvis. Hypnum luridum Hedw.

Bridel (1801) recognized Hypnum palustre Huds. ex Brid., and H. molle Dicks., but did not treat H. alpestre Sw. Like Hedwig, Bridel subdivided Hypnum into eight groups, but he applied to them formal names apparently of sectional rank. In direct contrast to Hedwig, Bridel placed greater weight on branching pattern in delimiting his groups and relegated leaf form and orientation upon the stems to subordinate roles. Bridel's classification of currently recognized species of Hygrohypnum is as follows:

Group V, section Scuiroidea, Surculo confertim ramoso.

subgroup 2, foliis secundis reflexis contorsive. Hypnum palustre Huds. ex Brid.

Group VIII, section Polymorpha, Surculo vage ramoso, foliis directione aequali.

subgroup 4, Amphibia Hypnum molle, Dicks.

Bridel (1812) modified his earlier classification system along the lines of Hedwig's and subdivided Hypnum into nine groups. These groups and a number of their subdivisions were given formal names at sectional rank. Through a typographical error the number 2 was used twice in denoting the groups and consequently the nine groups numbered only eight. In the new system Bridel placed greater value on leaf characters and relegated branch-
ing features to a lesser role. Bridel's classification as applied to

*Hygrohypnum* is given below:

1

Group 2

Section Illecebra, foliis imbricatis appressa vel appresso patentiusculus, ramis pinnatis vel subpinnatis, ramulis teretibus obtusis. *Hypnum alpestre* Sw. and *Hypnum molle* Dicks.

Section Cuspidata, foliis imbricatis appressa vel appresso patentiusculus, ramis pinnatis vel subpinnato, ramulis compressisculus acutis. *Hypnum neglectum* Brid.

Group 7, foliis secundis circinnato-falcatis

Section Lurida, caulibus confertim ramosus.

*Hypnum luridum* Hedw. and

*Hypnum subsphaericarpon* Brid.

It seems apparent here that Bridel recognized the similarities of Hedwig's treatment of *Hypnum alpestre* Sw. and Hedwig's and his own treatment of *Hypnum molle* for he included them both in section Illecebra.

The classification presented by Bridel (1827) was essentially unchanged from the system of 1812. He did correct the error in the group numberings and he excluded *Hypnum neglectum* Brid. The most significant change occurred in the division of *Hypnum* into two subgenera based on endostomial characters.

Subgenus *Hypnum*, peristome interioris ciliis perforatis.

Subgenus *Stereodon*, peristome interioris ciliis imperforatis.

*Hypnum molle*, *H. alpestre*, *H. palustris* and *H. subsphaericarpon* were all included in the subgenus *Stereodon*.

1 Indicates the second and erroneously numbered group 2
Sprengel (1827) subdivided Hypnum into three groups, each of which was subdivided into a number of smaller groups. Like Hedwig and Bridel, Sprengel used leaf symmetry and leaf attitude upon the stem as characters of primary importance. However, he appears to have been the first to employ costa structure, smoothness or papillosity of the leaf cells and toothing of the leaf margin as classificatory criteria. Using these features, Sprengel divided Hypnum into three numbered groups of unspecified rank.

Group 2, Foliis secundis,

* nervo fffis. Hypnum sphaericarpon Spreng.

** Foliis secundis enervis. Hypnum palustre (no authority designated)

Group 3, Foliis directione varius

* Foliis directione variis erecto-palulis, Nervo evanido,
  Foliis integerrimus, Foliis fetisque laevibus.
  Hypnum molle Dicks. and
  Hypnum neglectum Brid.

Hypnum sphaericarpon was an obvious misspelling of Hypnum subsphaericarpon Brid. It is worth noting that where Bridel recognized sufficient similarity between Hypnum molle Dicks. and H. alpestre Sw. to include them within the same grouping, Sprengel united the two under H. molle Dicks.

Hübner (1833) divided Hypnum into several sections, for which he provided elaborate descriptions. His treatment is unique for within section Alpestria he included only taxa that have since been included within Hygrohypnum. His treatment is as follows:

Section Alpestria

Caule fasciculatim ramoso, ramis confertis erectis simplicibus
turgido-teretibus, foliis dense imbricatis basinervibus, setis laevibus.

- Hypnum molle Dicks.
- Hypnum alpestre Sw.,
- Hypnum palustre Linn.
- Hypnum sphaericarpon Spreng.

Hampe (1837) divided Hypnum into two apparent subgenera which he called Isothecium Brid. and Stereodon et Hypnum Brid. These two groups were subdivided further, but Hampe did not indicate the criteria he used. His treatment is unique for he treated Hypnum luridum Hedw. and H. sphaericarpon Brid. as varieties of Hypnum palustre Linn. and placed Hypnum alpestre Sw. as a variety of H. molle Dicks.

De Notaris (1838) provided a treatment similar to that of Hübner. In his Hypnum sect. Palustria De Notaris clearly included taxa that have all become recognized species of Hygrohypnum or synonyms of recognized species. De Notaris' system is given below:

- Hypnum sect. Palustria De Not.

Caule repentes confertim ramosi, fôlia imbricata plerumque secunda, subfalcative concaviscula, tenuieve seta laevi.

- Hypnum palustre Brid.
- Hypnum subsphaericarpon Brid.
- Hypnum molle Dicks.

Schimper (1853, in Bruch, Schimper and Gümbel) presented the first conceptual synthesis of the modern genus Hygrohypnum. Schimper extracted Hypnum luridum Hedw., H. molle Hedw. and H. alpestre Hedw. from Hypnum and placed them in the new genus Limnobium Schimp. Hypnum subsphaericarpon Brid. and H. neglectum Brid. were shown to be variants of H. luridum Hedw. and united
with it. Simultaneously, he described *Limnobium norvegicum* Schimp. and *L. arcticum* Schimp. Schimper (1855) added *Limnobium eugyrium* Schimp. and *L. ochraceum* (Turn. ex Wils.) Schimp. In so doing, Schimper brought together a group of species exhibiting such a diversity of form as to have widely spaced to crowded branches, straight, loosely appressed to spreading or falcate-secund leaves, pointed or obtuse branch tips and short and double or single costae. However, Schimper determined that these taxa shared a similar areolation, a seldom excavated region of poorly defined alar cells, a broadly ovate-lanceolate or orbicular leaf shape and a common habitat in and around streams.

Wilson (1855) retained a more conservative view and treated present day species of *Hygrohypnum* as *Hypnum*. He divided *Hypnum* into three groups based upon leaf symmetry and leaf attitude upon the stem. He treated various species of *Hypnum* as follows:

**Section I, leaves + spreading in everyway.**

**Section Alpestria**

**A.** Stems creeping, irregularly branched; or occasionally arched pinnate, ***Leaves roundish, rather obtuse, entire, two nerved, nerveless.**

*Hypnum molle* Dicks.

*Hypnum palustre* Dill., Linn.

*Hypnum arcticum* Sommerf.

**Section II, leaves secund.**

**Section Cuppressiformia**

**B.** Stem procumbent, + entire, fructifications near the base; leave falcate-secund, entire or serrulate, nerveless or two nerved at the base, *Leaves acuminate.*
Commmencing with Sullivant (1856) the genus Limnobium Schimp. was subjected to a variety of interpretations. Sullivant (1856) and Schimper (1860 and 1876) interpreted the taxon as a subgenus of Hypnum. Renauld (1883), Boulay (1884), Husnot (1894) and Dixon (1896 and 1924) treated Limnobium as a section of Hypnum. Mitten (1864) differed slightly treating section Limnobium within Stereodon Brid.

Renauld (1883) critically revised the European species as Hypnum section Limnobium. In so doing he offered some significant insight into the section. He observed that the section could be subdivided into two groups based on leaf morphology. He characterized the groups as follows:

Group 1. Les feuilles sont élargies ovales ou suborbiculaire, souvent contractées à la base, arrondes ou sommet ou brièvement et obtusément apiculées.

- Hypnum dilatatum Wis.
- Hypnum molle Dicks.
- Hypnum alpinum Sch.
- H. arcticum Sommerf.
- H. goulardii Sch.
- H. obtusifolium Hook.

Group 2. Les feuilles sont oblongues ou oblongues-lancéolées, plus ou moins rétrécies-acuminées.

- Hypnum palustre L.
- H. polare Lindb.
- H. alpestræ Sw.
- H. eugyrium B.S.G.
- H. lusitanicum Sch.
H. micans Wils.

De Bat (1885) presented a reclassification of the genus *Hypnum* within which modern species of *Hygrohypnum* were treated in two sections. His systems paralleled that of Renauld (1883) emphasizing groups of species exhibiting straight, orbicular leaves which he called section *Eu-Limnobium* and those species bearing straight or falcate, more or less lanceolate leaves, which he placed in section *Hetero-Limnobium*. De Bat's system is as follows:

**Eu-Hypnum**

a. Rectifolia

1ère Section, a ramification irreguliere (correspond aux simplicia)

**SECTION Eu-Limnobium**

A. Feuilles circulaires ou ovales-circulaires ou avec obtus (correspondant aux obtusifolia)

- H. alpinum
- H. goulardii
- H. alpestre
- H. dilatatum
- H. molle
- H. norvegicum
- H. deflexifolium (= Scorpiurium)

B. Feuilles ovales-acuminées peu ou âprement homotropes

- H. lusitanicum
- H. polare
- H. micans
B. Curvifolia - Feuilles ovaes-oblongues ou ovaes lanceolées, nettement homotropes ou incurvées.

SECTION Hetero-Limnobia

H. ochraceum
H. subenerve
H. eugyrium
H. palustre

Lindberg (1872) observed that Limnobium Schimp. was a later homonym of Limnobium Rich., a genus of the Hydrocharitaceae. As a substitute for Limnobium Schimp. Lindberg coined the name Hygrohypnum Lindb. Later, Lindberg (1879) reduced Hygrohypnum Lindb. to subgeneric status under Amblystegium Schimp. Braithwaite (1898) treated Hygrohypnum Lindb. as a section of Amblystegium and Limpricht (1904) placed Hygrohypnum Lindb. as subgenus in Hypnum.

Kindberg (1894) continued to use Limnobium for certain currently recognized species of Hygrohypnum and at the same time elevated Hynum subg. Calliergon Sull. to genus. In Calliergon Kindberg treated species now referred to Calliergon and Hygrohypnum. Kindberg (1897) elaborated his concept of Calliergon and described a number of subgenera and sections which included species of modern Calliergon, Drepanoclados, Smorpidium, Sematophyllum and Hygrohypnum. Modern species of Hygrohypnum were distributed in Kindberg's treatment of Calliergon as follows:

Calliergon subg. Limnobium

A. Capsule not annulate, Leaves entire, II. Leaves of stem not falcate, those of the branches falcate, alar cells not large, costa abbreviate sometimes double or indistinct. Pedicel of capsule shortish. Stems creeping or pinnate.
Calliergon palustre (L.) Kindb.


B. Capsule annulate, Leaves sometimes denticulate, b. stems not pinnate, sometimes radiculose, alar cells generally distinct.

Section Badiiformia Kindb.

Leaves not decurrent, those of branches often falcate.
Dioicous and very r. fruiting.

'Calliergon polare (Lindb.)' Kindb.

Section Ochraceiformia Kindb.

bb. Costa generally short and indistinct, 2. Leaves entire or nearly so, decurrent and distant, those of branches often falcate, stems eradiculose, dioicous rarely fruiting.

Calliergon ochraceum (Turn. ex Wils.) Kindb.

C. torrentis Kindb.

C. goulardii (Schimp.) Kindb.

Section Molliformia Kindb.

bb. Costa generally short and indistinct, 3. Leaves not or indistinctly decurrent, sometimes denticulate, generally crowded and not falcate, Stem not creeping vs. radiculose.
Often monoicous.

Calliergon eugyrium (B.S.G.) Kindb.

C. arcticum (Sommerf.) Kindb.

C. molle (Dicks.) Kindb.

C. alpestre (Sw.) Kindb.

C. columbico-palustre C.M. et Kindb.
C. circulifolium C.M. et Kindb.
C. submolle Kindb.

Section Montaniforme Kindb.
Leaves small, sometimes decurrent, usually denticulate, those of the branches often falcate. Stems creeping vs. monoecious.

Calliergon pseudo-arcticum Kindb.
C. montanum (Lindb.) Kindb.
C. pseudo-montanum Kindb.
C. viridulum (Hartm.) Kindb.

Paris (1905) and Roth (1905) used Limnobium Schimp. in their publications. Loeske (1903) recognized the priority of Hygrohypnum Lindb., but it was not until Brotherus (1909) published volume 1 of Die Naturlichen Pflanzenfamilien that Hygrohypnum came into general usage. Brotherus also determined that the affinities of Hygrohypnum were not with Hypnum, but with his new hypnaceous subfamily, the Amblystegiae. Brotherus (1923) elevated the subfamily to the rank of family.

Grout (1931) also used the subfamily Amblystegiae. More importantly, he determined that Hygrohypnum could be subdivided into four groups. These groups were given formal names, but no taxonomic rank. His groups were distinguished as follows:

Group I, Palustreformes
Leaves more than twice as long as broad, very concave with the upper margins infolded, entire or slightly serrulate above, alar cells numerous.

Group II, Arctici
Leaves less than twice as long as wide, often nearly circular in outline, more or less concave, entire or slightly serrulate at apex, margins usually plane.
Group III, Montani

Stems without a central strand, leaves acuminate to apiculate, distinctly serrulate above, slightly decurrent, lower margins reflexed.

Group IV, Ochracei

An outer layer of stem cells enlarged and hyaline, forming a hyaline sheath.

Wijk, Margadant and Florschutz (1962) presented a list of all published species and the subspecific taxa of Hygrohypnum. Wijk et al. (1969) emended that list as follows:

Hygrohypnum alpestre (Hedw.) Loesk.

H. alpinum (Lindb.) Loesk.
  var. viriscens Amann
  var. tsurugizanicum (Card.) Nog.

H. aureum Herz.

H. brasiliense Herz.

H. caussequi (Ren. et Card.) Card.

H. circinatum Herz.

H. closteri (Aust.) Grout

H. cordifolium Okam.

H. coreanum Card.

H. dilatatum (Wils.) Loesk.
  var. callineurum Amann
  var. duriusculum (Limpr.) Amann

H. doi Sak.
  var. simplex Sak.

H. ellipticum Ther.

H. entodontoides (Broth. et Par.) Broth.
H. eugyrium (Schimp.) Broth.
  ssp. subeugyrium (Ren. et Card.) Grout
  var. mackayi (Schimp.). Broth.
  var. miquelonense (Ren. et Card.) Grout
  var. nervosum (Roell) Podp.
  var. occidentale (Card. et Ther.) Grout

H. fontinaloides Chen

H. glaciale Warnst.

H. hedbergii P. Vard.

H. liukiuense Sak.

H. luridium (Hedw.) Jenn.
  ssp. pseudomontanum (Kindb.) Wijk et Marg.
  var. crassinervium (Baur.).Podp.
  var. ehlei (Arn.) Wijk et Marg.
  var. malacocaulon (Herz.) Podp.
  var. obtusatum Podp. * nom. nud.
  var. pseudochraceum (Roth) Podp.
  var. subsphaericarpon (Brid.) C. Jans. in Podp.
  var. tenellum (Schimp.) Podp.

H. lusitanicum (Schimp.) Corb.

H. mizushimae Sak.

H. molendinarium (Lam. et Cand.) Wijk et Marg.

H. molle (Hedw.) Losek.
  ssp. bestii (Ren. et Card.) Grout
  var. bestii (Ren. et Card.) Hab.
  var. japonicum Sak.
  var. pyrenaicum (Ren.) Podp.
  var. schimperianum (Lor.) Loesk.

H. montanum (Lindb.) Broth.

H. nicholsii Grout

H. norvegicum (Schimp.) Amann

H. novae-caesarae (Aust.) Grout

H. ochraceum (Wils.) Loesk.
H. pelichiense Williams
H. peruviense Williams
H. poecilophyllum Dix.
H. polare (Lindb.) Loesk.
    var. pseudostramineum (Lindb.) Podp.
H. purpurascens Broth.
H. smithii (Sw. in Lilj.) Broth.
    var. goulardii (Schimp.) Wijk et Marg.
H. styriacum (Limpr.) Broth.
H. szaferi Szaf.
H. tenquendamense Herz.
H. validum Herz.

Bartram (1965) added the most recently described species, a South American plant which he called *Hygrohypnum falcifolium* Bart.
METHODS OF THE MORPHOLOGICAL ANALYSIS

The apparent inadequacy of those characters traditionally employed is distinguishing species of *Hygrohypnum* indicated the need for a complete reassessment of all potential morphological characters. Table 1 presents a list of eighty-six morphological characters which were examined during this study. The assessment of the taxonomic value of these features was conducted by 1. the traditional examination of herbarium specimens and by 2. cultivating living specimens under conditions of uniform environment. In those cases where material collected in the field bore mature sporophytes or where cultivated material produced sporophytes, the spores so derived were germinated and allowed to produce leafy gametophores. Thus, in some cases it was possible to compare gametophores grown from spores, gametophores derived from new vegetative growth from adult plants and the control herbarium specimens.
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METHODS OF CULTIVATION

All cultured plants, except those grown from spores, were maintained in a refrigerated growth room held between 6° and 9° C. All plants were grown on 4 layers of paper towel disks and moistened with a 50% solution of Hoagland's culture medium (Hoagland and Arnold, 1938). Most plants were grown in 90 mm X 19 mm plastic petri dishes, while certain larger specimens were grown in 155 mm X 65 mm covered plastic dishes. The cultures were illuminated by 6 banks of 60 inch long cool white fluorescent bulbs. Each bank bore 4 bulbs held at 38 inches above the plants. Additional illumination was provided by twelve 60 watt incandescent bulbs placed equidistant among the banks of fluorescent lights. The total illumination was 530 foot-candles in a 16/8 photoperiod.

Cultures grown on paper toweling were frequently contaminated by unicellular green algae and/or Oscillatoria. Such contamination was controlled by periodically washing the plants with tap water and gently scrubbing them with a stiff artist's brush. When necessary several washed stems were transferred to new culture dishes.

Experimental plants grown from spores were maintained in 90 mm X 20 mm glass petri dishes in 50% Hoagland's medium in 2% Difco Bacto-Agar. They were maintained in a growth room at 10° C on a 12/12 photoperiod.

METHODS OF PREPARATION OF MATERIAL FOR MICROSCOPE EXAMINATION

All materials were examined utilizing microscope slide preparations employing Hoyer's mounting medium. The Hoyer's was modified from Anderson (1954) so as to use 50 cc of gum arabic.
RESULTS OF THE MORPHOLOGICAL ANALYSIS

Stem Anatomy

The structure of the stem, as seen in cross-section, is extremely important in assessing both similarities and differences among the various species.

The stem is usually differentiated into three histological regions, but there may only be two or as many as four. Usually the epidermal cells and several concentric rows of cells inside the epidermis are small, thick-walled and yellow – to red-brown in color. This zone of cells is called the cortex (Fig. 1 a - b). Inside the cortex there is a broad region of large, thin-walled, usually hyaline cells called the medulla (Fig. 1 a - f). This medullary region may discolor with age. At the very centre of the stem cross-section a group of small cells may be abruptly differentiated from the medulla. These cells are called the central strand (Fig. 1 a - f) and it is regularly present in most species. *Hygrohypnum bestii* and *H. subeugyrium* are unusual for in them the central strand is only weakly developed or absent. *Hygrohypnum montanum* is remarkable because it lacks a central strand entirely.

In *Hygrohypnum ochraceum*, *H. polare* and *H. eugyrium* the epidermis of the stem is differentiated from the adjacent cortex and is called a hyalodermis. In *H. ochraceum* the hyalodermis is abruptly enlarged and thin-walled (Fig. 1 c). In older plants the thin outer wall is usually worn away leaving only the cavity created by the inner tangential wall and the radial walls of each cell. The hyalodermis of *H. polare* is similar to that of *H. ochraceum*, but the enlarged cells usually do not completely encompass the stem (Fig. 1 d & e), in which case the hyalodermis is referred to as incomplete. A hyalodermis is most poorly differentiated in *H. eugyrium*
and is evident only because the outer tangential wall of the epidermis is slightly thinner and less pigmented than the radial and inner tangential cells walls (Fig. 1a-e).
Fig. 1 a–f. Variation in stem anatomy.

a. H. duriusculum  
b. H. luridum  
c. H. ochraceum  
d. and e. H. polare  
f. H. eugyrium  

Scale: [100um]
Leaf Shape and Symmetry

Leaf shape is a very important character in distinguishing species of *Hygrohypnum*. In the past, the use of leaf shape as a taxonomic criterion has been beset with two serious problems. In some species leaf shape and leaf symmetry are variable. A natural consequence of that variability is that the variability in leaf shape and symmetry of one species can overlap with that of another. It is understandable, then, that many people have confused many species by placing too much reliance on this single character. A second problem is the employment of leaf shape as a taxonomic criterion derives from the frequently ambiguous application of the terms used to describe leaf shape.

The various attempts to standardize and quantify the description of leaf shape seem to have yielded little agreement among botanists. Much of the problem seems to involve the extent to which the nature of the leaf apex affects the leaf shape. No attempt has been made here to resolve this problem. For the purposes of this study, Figure 2 illustrates the usage of the various descriptive terms as applied to leaf shape in *Hygrohypnum*.

The examination of numerous herbarium specimens has shown that leaf shape within a species varies within broadly definable limits. It is very significant that those species that have been available for experimental study exhibit the same basic variation in leaf shape when grown in culture as they do under natural conditions. Based on data from herbarium material, Figures 3 - 6 directly compare the variability in leaf shape of several frequently confused species. An asterisk at the base of a leaf indicates the most or one of the most frequently encountered leaf shapes for a given species. The leaves of species grown under natural and experimental conditions are compared in Figures 7 - 9.
Lodge (1959, 1960) showed that in *Drepanocladus* leaf falcation was environmentally induced. Zales (1973) also established the variability of leaf curvature in *Philonotis*. Similarly, culture studies on *Hygrohypnum* have shown leaf falcation to be highly variable and invalid as a taxonomic criterion. However, those species frequently producing falcate leaves exhibit variable responses to experimental culture. Under natural conditions *Hygrohypnum eugyrium* may produce straight or falcate leaves on the same stem or on different, but contiguous stems. *Hygrohypnum montanum* produces straight and falcate leaves on the same stem, but in very specific locations. In culture, both *H. eugyrium* and *H. montanum* produce exclusively straight leaves. Under both natural and experimental conditions *Hygrohypnum styriacum* produces both straight and falcate leaves. Certain specimens of *Hygrohypnum ochraceum* which produce exclusively circinate-canaliculate leaves in nature, respond to experimental conditions by producing both circinate-canaliculate leaves and straight and plane ones. Herbarium specimens reveal that *Hygrohypnum luridum* can produce specimens with straight and/or falcate leaves on different plants, on different but contiguous stems or in alternating sequences along the same stem. Experimental data on *H. luridum* are less clear because there is limited material available for study. It has been shown that in one collection non-contiguous stems, which bore straight or falcate leaves in nature uniformly produced straight leaves in culture.

The variability in leaf shape and the obscuring effect of falcation upon leaf shape dictate certain procedures for evaluating leaf shape. In all cases the leaves should be observed under a coverslip with their adaxial side down. The leaf shape exhibited by a particular specimen must be arrived at through the subjective assessment of at least twenty-
five leaves dissected from healthy stems. The leaf shape in plants bearing falcate leaves may be assessed in several ways. Frequently, the leaves borne dorsally or ventrally on prostrate stems are straight or less falcate than those laterally placed. When only falcate leaves are available one must attempt to place the falcate leaf adaxial side down under a coverslip and extrapolate the theoretical shape from the less asymmetrical side of the leaf.
Fig. 2 a - g. Terminology of Leaf Shape

a. Orbicular
b. Oblong-Elliptic
c. Broadly ovate
d. Ovate
e. Oblong
f. Oblong-lanceolate
g. Lanceolate
Fig. 3 a–v. Comparison of leaf-shape variation within and between species.

a–e. H. alpinum
f–i. H. duriusculum
j–n. H. smithii
o–r. H. bestii
s–v. H. molle

Scale:

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Fig. 4 a–x. Comparison of leaf-shape variation within and between species.

a–c. *H. norvegicum*

d–f. *H. cochlearifolium*

g–j. *H. styriacum*

k–s. *H. luridum*

t–x. *H. alpestre*

Scale:

- a–c; [0.5 mm]
- d–j, t–x; [1 mm]
- k–s; [1 mm]
Fig. 5 a - u. Comparison of leaf-shape variation within and between species.

a - d. H. polare

e - l. H. ochraceum

m - u. H. eugyrium

Scale: ______ 1mm ______.
Fig. 6 a - n. Comparison of leaf-shape variation within and between species.

a - c. *H. subeugyrium* from North America and Europe.
d - f. *H. subeugyrium* from Japan.
g - i. *H. closteri*
j - n. *H. montanum*

Scale:

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a - f;  1mm

g - n;  0.5mm
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Fig. 7 a - t. Comparison of leaf-shape in naturally growing plants of *Hygrohypnum* and their response to artificial culture.

**H. alpinum**
- a - b. Natural plants; c - d. Cultivated plants

**H. duriusculum**
- e - f and i - j. Natural plants
- g - h and k - l. Cultivated plants

**H. molle**
- m - n. Natural plants
- o - p. Cultivated plants

**H. bestii**
- q - r. Natural plants
- s - t. Cultivated plants

Scale: [1 mm]
Fig. 8 a - t. Comparison of leaf-shape in naturally growing plants of *Hygrohypnum* and their response to artificial culture.

**H. smithii**
- a - b. Natural plants
- c - e. Cultivated plants

**H. styriacum**
- f - g. Natural plants
- h - j. Cultivated plants

**H. luridum**
- k - m. Natural plants
- n - p. Cultivated plants

**H. luridum**
- q. Natural plants
- r. Leaf derived from growth of vegetative plants.
- s - t. Leaves derived from gametophores grown from spores.

Scale: [1 mm]
Fig. 9 a - t. Comparison of leaf-shape in naturally growing plants of *Hygrohypnum* and their response to artificial culture.

**H. ochraceum**
- a - f. Natural plants
- g - j. Cultivated plants

**H. eugyrium**
- k - m. Natural plants
- n - p. Cultivated plants

**H. montanum**
- q - r. Natural plants
- s - t. Cultivated plants

Scale:
- a - p; [ ] 1mm
- q - t; [ ] 0.5mm
Leaf Apex

The shape of the leaf apex, like that of the complete leaf, is quite variable in some species and less so in others. In some species the shape of the leaf apex often overlaps with the shape exhibited by other species. However, toothing and curvature of the margin and concavity modify the character of the leaf apex so that if often can be used as an effective character.

The description of the shape of the leaf apex has been subjected to the same terminological ambiguity as has leaf shape. For the purposes of this study Fig. 10 illustrates the application to Hygrohypnum of the terms describing the shape of the leaf apex.

Figure 11 b illustrates the abruptly acuminate leaf apex of Hygrohypnum styriacum. Both Hygrohypnum luridum and H. eugyrium have acute leaf apices whose margins are often inrolled imparting a weakly apiculate appearance. The fine teeth at the leaf tips of H. eugyrium (Fig. 11 c & d) differ from the habitually entire leaf tips of H. luridum (Fig. 11 a).

Hygrohypnum norvegicum and H. cochlearifolium have long been confused with each other. The sharply acute leaf apex of H. norvegicum differs from the rounded, obtuse apex of H. cochlearifolium (Fig. 12 a & b).

The deep concavity of the leaf apex and its tiny squarrose apiculus make Hygrohypnum alpestre unique in the genus (Fig. 12 f). The acute, but blunt and denticulate leaf apices which are regularly observed in H. subeugyrium are also unique to this species (Fig. 11 e & f).

Hygrohypnum molle has been confused regularly with H. duriusculum. The leaf apex of the former is usually gradually tapered and acute with a slightly blunted point (Fig. 12 c). The apex of H. duriusculum is rarely acute, but normally it is rounded obtuse or rounded obtuse and
sometimes slightly, but bluntly apiculate (Fig. 12 d).

_Hygrohypnum styriacum_ and _H. luridum_ are often confused with each other. The abruptly acuminate apex of the former (Fig. 11 b) differs from the acute apex of the latter (Fig. 11 a).
Fig. 10 a - h. Descriptive terminology for the shape of the leaf apex.

a - b. Rounded

c. Obtuse

d. Broadly acute

e. Acute

f. Acuminate

g - h. Apiculate
Fig. 11 a - f. Variation in the shape of the leaf apex.

a. H. luridum

b. H. styriacum

c - d. H. eugyrium

e - f. H. subeugyrium

Scale: 100um
Fig. 12 a - f. Variation in the shape of the leaf apex.

a. *H. norvegicum*
b. *H. cochlearifolium*
c. *H. molle*
d. *H. duriusculum*
e. *H. montanum*
f. *H. alpestre*

Scale:

a - e; | 100um |
f; | 0.5mm |
Costa

The costa of *Hygrohypnum* is variable and thus of limited taxonomic value. The costa is usually short and double, but may also be long and double or short and/or long and single or single and forked. Each species, at some time, exhibits a single costa. However, the frequency of occurrence of a single costa is so low in such species as *Hygrohypnum eugyrium*, *H. montanum* and *H. molle* that the costa can be considered as only short and double. *Hygrohypnum polare* is unique in the genus since its costa is exclusively single, stout and percurrent or ending just a few cells below the apex. A short, double costa predominates in *Hygrohypnum duriusculum*, but a slender, single costa occurs regularly in a few leaves. The costa of *Hygrohypnum smithii* is always stout and although it is both short and double or single, a single costa predominates. *Hygrohypnum luridum* is equally unique for within the species the costa varies continuously throughout its complete range of variation as exhibited in the entire genus.
Leaf Concavity

Leaf concavity is readily apparent in almost all species of *Hygrohypnum* and is one of the several features which unify the genus. However, it is useful in distinguishing species only in cases where it can be described as deeply concave. Deep concavity is defined here not in quantitative terms, but in terms of what can be seen in a microscope slide preparation when the leaf has been placed adaxial side facing downward. If the concavity is such that the weight of the coverslip will impart a curved fold that is nearly parallel to the leaf margin, as in Fig. 13 b & d, or such that a series of irregular or linear folds form throughout the leaf, as in Fig. 13 d, then the leaf is interpreted as deeply concave. Figures 13 a & c illustrate the normal configuration of these same leaves.

The asymmetrical curvature of falcate leaves imparts a channelled or caniculate concavity to the leaves. The differences shown in such concavity among falcate-leaved species is not significant.
Fig. 13 a - d. The nature of leaf concavity.

H. alpestre

a. A leaf as seen with a dissecting microscope.

b. The same leaf as seen in a microscope slide preparation.

H. cochlearifolium

c. A leaf as seen with a dissecting microscope.

d. The same leaf as seen in a microscope slide preparation.
Median Leaf Cells

The broad variation in the dimensions of the median leaf cells within individual species and between different species renders these cells of little taxonomic usefulness. In most cases the extremes of median leaf cell length vary independent of leaf size in a given species. Only rarely will a comparison of the average cell lengths of two species be helpful in distinguishing them from each other. All leaf cell dimensions were measured from middle lamella to middle lamella.

Marginal Leaf Cells

The length of the median marginal leaf cells is extremely useful in one case. Hygrohypnum bestii has often been mistaken for H. molle or H. duriusculum. The median marginal leaf cells of H. bestii vary from 60 to 250 um long, while those of H. molle or H. duriusculum are rarely more than 55 um. Equally rarely one or two marginal cells in H. eugyrium and H. subeugyrium are from 65 to 70 um. The marginal cells of H. ochraceum are very plastic, ranging from 45 to 250 um. The marginal leaf cells of all other species are under 50 um.

Figures 14 and 15 illustrate some variation observed in the marginal leaf cells.
Fig. 14 a – g. Variation in marginal leaf cells.

a – b. \textit{H. alpinum}

c – d. \textit{H. duriusculum}

e – f. \textit{H. bestii}

g – h. \textit{H. molle}

Scale: \[50\mu m\]
Fig. 15 a - f. Variation in marginal leaf cells.

- a - b. *H. ochraceum*
- c - d. *H. eugyrium*
- e - f. *H. subeugyrium*

Scale: [scale bar 50μm]
Alar Cells

The alar cells are one of the most important taxonomic criteria in the genus. Yet, many of the problems within the genus can be traced to the fact that the alar cells have not been carefully examined. This may be due, in part, to the comments of Schimper (1853). He said that the alar cells are "wenig oder gar nicht ausgeholt und das Zellnetz deselben kaum von der ubrigen Blattbasis verschieden." His observation may have resulted from the frequent occlusion of the alar cell lumens by dark cytoplasmic contents which obscure any observable differentiation.

It is true that the alar cells of Hygrohypnum are not as dramatically distinct as those of some species of Calliergon or Hypnum. However, it is also true that there is sufficient alar differentiation in some species of Hygrohypnum, such that when they are cleared, these cells reveal several readily observable patterns of differentiation.

Two prerequisites are absolutely essential for the effective assessment of the alar cells. First, ten to twenty-five clean leaves must be carefully removed from a mature stem or primary branch segment. Secondly, the leaves should be placed adaxial side downward in a drop of clearing agent such as Hoyer's, lacto-phenol or KOH.

Several different expressions of alar differentiation are evident in the genus. Each expression is the result of a combination of 1. cell shape, 2. cell size, 3. relative numbers of cells, 4. wall thickness, 5. excavation and 6. discoloration.

Quadrate, short rectangular or irregular shapes are those most frequently encountered among the alar cells of Hygrohypnum. Cells of such shapes differ markedly from the rhomboid, fusiform or linear flexuose
shapes of median leaf cells. However, the recognition of a discernible group of alar cells depends upon the relative numbers of quadrate or short rectangular cells and a subjective assessment of how abruptly they differ from surrounding cells. A few isolated quadrate to short rectangular cells may occur in Hygrohypnum molle (Fig. 16 a), but the bulk of the cells are similar to the linear or long rectangular basal or lower median leaf cells. Such a condition is interpreted here as exhibiting no alar differentiation. Figures 16 b, c & d illustrate respectively the alar regions of H. cochlearifolium, H. norvegicum and H. closteri. In these species there are several quadrate to short rectangular cells in the alar region. However, the transition from the surrounding linear or fusiform cells is so gradual that a distinct group of cells is not apparent. This condition differs markedly from that of H. molle, but all of these taxa are interpreted as lacking any alar differentiation. In addition, Hygrohypnum bestii, H. smithii, H. styriacum and H. montanum are similarly interpreted as exhibiting no alar differentiation.

A clearly discernible group of numerous quadrate to short rectangular alar cells occurs in Hygrohypnum polare (Fig. 17 a) and H. luridum (Fig. 17 c). Figure 18 a illustrates a similar situation in H. duriusculum, which differs in the more frequent occurrence of irregular cells and thicker walls. The alar cells of H. polare are very constant, but those of H. luridum and H. duriusculum are variable. While H. luridum varies little in the relative numbers of alar cells, H. duriusculum may exhibit as few as 3 vertical, parallel rows of alar cells, including the leaf margins (Fig. 18 b). This contrasts with the situation seen in Fig. 18 a. In Hygrohypnum duriusculum this variation occurs in both robust and depauperate plants, particularly those from Western North America. It is this variability that has no doubt contributed to the confusion between H. duriusculum
and *H. molle* and emphasizes the need to observe numerous leaves before making a judgement. The alar cells of *H. luridum* and *H. duriusculum* vary further in cell wall thickness, excavation (Fig. 17 d & 18 c) and cell wall discoloration.

Abrupt cell enlargement or inflation is another frequently encountered mode of alar differentiation. An abrupt increase in cell size is interpreted here to mean at least a two fold increase in length and/or width relative to the adjacent cells. This condition is apparent in *Hygrohypnum eugyrium* (Fig. 19 a) and *H. alpinum* (Fig. 19 b).

In rare instances a recognizable group of alar cells may occur as a gradual transition in cell shape and size from the surrounding median and basal cells. Figure 19 d illustrates a small group of such cells, while Figure 19 c illustrates a larger group. These two states represent opposite ends of the spectrum of alar differentiation in *Hygrohypnum ochraceum*.

Another expression of alar differentiation may not be conveniently referred to a general pattern. Figure 18 d illustrates a situation in which 1 or 2 rows of enlarged, incrassate, discolored cells extend across the leaf base at the line of insertion. Just above this basal row and along the leaf margin is a variable number of quadrate or irregular cells. This alar cell configuration is typical of *Hygrohypnum subeugyrium*. 
Fig. 16 a – d. Variation in alar cell differentiation.

a. *H. molle*

b. *H. cochlearifolium*

c. *H. norvegicum*

d. *H. closteri*

Scale: 100um
Fig. 17 a - d. Variation in alar cell differentiation.

a - b. *H. polare*

c - d. *H. luridum*

Scale: [100um]
Fig. 18 a - d. Variation in alar cell differentiation.

a - c. *H. duriusculum*

d. *H. subeugyrium*

Scale: 100um
Fig. 19 a – d. Variation in alar cell differentiation.

a. H. eugyrium
b. H. alpinum
c. - d. H. ochraceum

Scale: [100um]
Response to Drying

Upon drying the leaves of most species exhibit little change in overall appearance or in their attitude upon the stem. A few, however, undergo very dramatic changes, which when used with other characters can be useful in distinguishing certain taxa. Figures 20 & 21 compares the moist and dry conditions in some of these plants.

Shrinkage in leaf width is the most common response to drying and results in several recognizable patterns of leaf convolution. Figure 20 b illustrates two such patterns. One pattern where the leaf margins inroll can be seen in a leaf near the middle of the figure. The second pattern can be seen in the upper half of the same figure. Here the leaves have responded by twisting about their midline. A third pattern can be seen in the upper half of Fig. 20 d. In this case the margins in the lower half of the leaf become squarrose. These drying responses characterize *Hygrohypnum duriusculum*.

Figures 21 b & 21 e illustrate the drying response of *Hygrohypnum bestii*. Here severe leaf contortion does not accompany shrinkage. Instead, the leaves remain nearly plane or are slightly twisted. In such cases the reduction in apparent leaf surface area is more evident.

*Hygrohypnum molle* has long been confused with *H. duriusculum* and *H. bestii*. However, *H. molle* undergoes very little change in appearance upon drying (Fig. 21 c). A slight amount of shrinkage and twisting is evident, but the leaves tend to retain their imbricate to slightly spreading attitude.

For all its remarkable polymorphism, *Hygrohypnum luridum* shows little change in appearance upon drying.

An entirely different response to drying is seen in Fig. 62 e. Here the leaves are falcate and folded along their midline into a caniculate
channel. Shrinkage in leaf width is negligible, but the leaf apex undergoes a characteristic twisting to resemble a filiform leaf tip. This is a common response in *Hygrohypnum ochraceum*.

The leaves of *Hygrohypnum closteri* are widely spaced along their stems. In the moist condition the leaves are spreading (Fig. 76 d). Upon drying the leaves shrink and twist and accentuate the distant spacing by becoming almost squarrose (Fig. 76 c).
Fig. 20 a – h. Variation in alteration in habit from wet to dry conditions in morphologically different shoots.

H. duriusculum

a. Moist; b. Dry

c. Moist; d. Dry

e. Moist; f. Dry

g. Moist; h. Dry
Fig. 21 a - e. Variation in alteration in habit from wet to dry conditions in morphologically different shoots.

**H. bestii**

a. Moist; b. Dry

d. Moist; e. Dry

**H. molle**

c. Moist; unchanged in the dry condition.
Sexuality

The problems imposed on bryophyte taxonomy by the infrequency of sexual plants is well known. However, in *Hygrohypnum*, the sexual condition provides clear discontinuities between certain species or correlates with discontinuities evident from other characters.

All but four species of *Hygrohypnum* are autoicous. *Hygrohypnum bestii*, *H. ochraceum* and *H. polare* are dioicous. The male and female plants of *H. bestii* and *H. polare* are similar in appearance. The male plants of *H. ochraceum* are more slender and their leaves more widely spaced than in the females.

*Hygrohypnum styriacum* exhibits the most unusual sexual condition in the genus. This species has a single perigonium subtended by 2 to 3 perichaetia which in turn are subtended by 1 to 3 small, scale like bracts (Fig. 13 a & b). This complete cluster of sexual inflorescences is borne in the axil of a foliage leaf. The perigonium may have as many as four leaves or as few as one. When only one perigonial leaf is present the antheridia directly abut the outer perichaetial leaf immediately adjacent. In those cases where the antheridia are enclosed by 2 to 4 perigonial leaves the overall disposition of the sexual inflorescences differs from typical autoiccy only in immediate proximity to one another. When only 1 perigonial leaf is present, however, the situation is reminiscent of paroicy. The term pseudo-paroicy is offered to describe this situation.
Fig. 22 a - b. The pseudo-paroicous inflorescence of *Hygrohypnum styriacum*.

a. The inflorescence as it appears naturally.

b. A diagrammatic representation of the inflorescence.
Perichaetial Leaves

The perichaetial leaves exhibit a number of useful characters that strengthen the discontinuities between certain taxa.

*Hygrohypnum alpinum* and *H. molle* stand apart from other species by the papillae they exhibit on the abaxial surface of some apical cells of the inner perichaetial leaves (Fig. 23 a & b). These papillae are formed by the overriding of the distal end walls. Occasionally one or two papillae have been observed in the same position of the inner perichaetial leaves of *H. cochlearifolium*. All other species of *Hygrohypnum* have smooth inner perichaetial leaf cells.

*Hygrohypnum closteri* and *H. montanum* similarly stand apart from the bulk of the genus. Their inner perichaetial leaves are either plane or very weakly plicate. The perichaetial leaves of all other species have 2 to 4 strong plicae. (See Fig. 25 f, g & h)

A plane inner perichaetial leaf margin is the general condition in the genus. *Hygrohypnum cochlearifolium* and *H. smithii* differ dramatically from this in the exhibition of strongly recurved margins (Fig. 24 d, e & f).

The costa is variable in the inner perichaetial leaves of most species of *Hygrohypnum*. However, the inner perichaetial leaves of *H. polare*, like the vegetative leaves, exhibit a strong, single percurrent costa (Fig. 25 c). The vegetative leaves of *H. closteri* are usually singly costate, but a few short and double costae do occur. Its inner perichaetial leaves are unusual for the costa is exclusively single (Fig. 25 h).

The shape of the apex of the inner perichaetial leaf apex is variable. However, it may be of some value in certain cases. The most common shape of the inner perichaetial leaf apex is acute. The acuteness varies from abrupt in *Hygrohypnum alpinum* and *H. cochlearifolium* (Fig. 24 a & f) to
gradually so in most species. *Hydrohypnum smithii* differs by being rounded or obtuse (Fig. 23 c & 24 d). Reflecting the shape of the apex of its vegetative leaves, *H. styriacum* has a slightly acuminate inner perichaetial leaf apex (Fig. 25 d). The inner perichaetial leaves of *H. closteri* are also slightly acuminate (Fig. 25 h), a striking departure from the acute, but blunt apex in the vegetative leaves.

The toothing along the margin and in the apex of the inner perichaetial leaves tends to reflect the situation in the vegetative leaves, but is generally too variable to be useful.
Fig. 23 a – c. Variation in the perichaetial leaf apex.

a. *H. molle*

b. *H. alpinum*

 c. *H. smithii*

Scale: | 100um |
Fig. 24 a - f. Variation in the perichaetial leaves.

a. *H. alpinum*

b. *H. duriusculum*

c. *H. molle*

d. *H. smithii*

e - f. *H. cochlearifolium*
Fig. 25 a – g. Variation in the perichaetial leaves.

a – b. *H. luridum*

c. *H. polare*

d – e. *H. styriacum*

f – g. *H. montanum*

h. *H. closteri*
Sporophyte

The sporophyte offers few characters that are of value in distinguishing species of *Hygrohypnum*. The sporophytes are not uniform, but the differences they exhibit are in such variable features as capsule and seta length or color. However, the annulus and the endostomial cilia are useful in certain cases.

All *Hygrohypnum* species except *H. luridum* have a well developed annulus. The absence of the annulus in *H. luridum* provides a sharp contrast with *H. styriacum*, a species with which *H. luridum* is often confused.

*Hygrohypnum duriusculum* has 1 to 3 well developed cilia between adjacent endostomial segments, while in *H. alpinum* and *H. molle* the cilia are rudimentary or wanting. *Hygrohypnum cochlearifolium* also differs from *H. molle* by its 2 to 3 well developed cilia, which unfortunately fall away very early.
TAXONOMIC TREATMENT


Calliergon (Sull.) Kindb. in part, Canad. Rec. Sci. 6(2):72. 1894.


Names treated as synonyms elsewhere, but for which the literature was unavailable for assessment during this study.

_Hypnum_ Hedw. subsect. Palustrië (Ne Not) Rabenh., Deutsch.

Krypt. Fl. 2(3):270. 1848.

_Hypnum_ Hedw. subg. Hygrohypnum (Lindb.) Schiffn., Lotos Prag.

55:211. 1907.


1896.

A Generic Description of _Hygrohypnum_

Plants usually growing on irrigated rock and stones in and beside small, cold, swiftly running mountain streams or rivulets, sometimes in large rivers, rarely at low elevations in temperate zones, rarely on wood, or submerged in still water or on damp, shaded cliff ledges; plants variously forming loosely to very tightly woven, appressed mats or ascending patches, mats or rarely turfs; color variable, dirty-yellow, yellow-brown, yellow-green, bright or dark, dull-green, olivaceous-green, blackish-green, most species exhibiting a rusty mottling or variegation, rarely one or two species exhibit a bright metallic red or bronze pigmentation, all species becoming yellow-brown, brown, reddish-brown or blackish-brown with age; stems
usually 1 to 15 cm long, rarely to 20 cm, procumbent or ascending at the tips, leafy throughout or becoming denuded in the oldest extremities; branching irregular, arising from the axils of lateral or ventral leaves, procumbent, ascending, rarely erect or fastigate; Stem cross-sections usually revealing 2 to 4, sometimes 5 rows of small, thick-walled, yellowish-brown, brown or reddish-brown cortical cells, rarely exhibiting an incompletely differentiated or well-developed row of slightly less thick or inflated, thin-walled outer cortical cells, medullary cells larger, usually hyaline and thinner walled, often becoming discolored and thicker walled with age; central strand poorly to well developed, rarely entirely absent; rhizoids reddish-brown, arising from the base of ventral stem leaves or the ventral side of the perichaetia.

Leaves variable, usually orbicular, broadly elliptic, broadly ovate or ovate, ovate-lanceolate, oblong or oblong-lanceolate, rarely lanceolate; usually straight, often falcate and/or secund, sometimes squarrose recurved; apex broadly rounded or obtuse to acute, rarely slightly acuminate or broadly rounded and/or obtuse with an apiculus, apical margins usually entire or finely denticulate, sometimes serrulate, rarely a few fine teeth at the apex or rarely coarsely denticulate, apical margins usually plane, sometimes inrolled so as to appear apiculate, rarely recurved or reflexed as an apiculus; margins of the lamina usually entire or finely and irregularly denticulate, rarely serrulate throughout, usually plane, sometimes infolded as wing along one or both sides of the leaf, rarely narrowly recurved; concavity variable, usually shallow to deeply so, rarely almost plane; costa variable, usually short and double with one or both arms ending below midleaf, sometimes long and double with one or both arms extending beyond midleaf, or single, slender or stout, usually ending between 1/2 to 3/4 of the leaf length, rarely pre-
current, sometimes forked one or twice, nearly all the costal variation may be observed within a single plant; leaves abruptly narrowed at the insertion, sometimes clasping the stem when the alar cells are excavated; leaves crowded to distant; attitude upon the stem when wet variable, usually appressed imbricate or tumid julaceous, or spreading or rarely wide spreading, upon drying the leaves may change little in attitude or undergo varying degrees of lateral shrinkage and contortion.

Aceolation variable, all cells smooth, median leaf cells short rhombic or fusiform to long, linear-flexuose, usually linear flexuose, cells usually or uniform width; sometimes unusually wide cells are irregularly interspersed, walls usually thin, rarely thickened; toward the leaf apex the cells generally become shorter, fusiform rhombic or oval, sometimes changing little from the median cells; marginal leaf cells usually less than 60 μm long, rarely exceeding 60 μm, but when doing so often regularly exceeding 100 μm; basal cells variable, becoming gradually wider, longer or shorter than the median cells or changing little, becoming thicker walled or changing little, pitted or unpitted, hyaline or variously pigmented particularly when thick-walled, yellow-brown, reddish-yellow, brown or reddish-brown; alar cells variable, undifferentiated or variously forming small and irregular to large groups of quadrate, short rectangular or irregular cells or variable groups or enlarged and thin-walled to inflated cells, plane or excavated, hyaline or yellow-brown, brown, reddish-brown, rarely bright red.

Plants autoicous, dioicous or pseudo-paroicous; perigonial leaves ovate, laminal cells smooth, ecostate, margins entire or weakly serrulate, concave-imbricate enclosing 4 to 10 oblong-elliptic antheridia and several hyaline, uniseriate periphyses; outer and middle perichaetial leaves var-
iable, ovate to ovate-lanceolate, costa absent, short and double or
single to midleaf, squarrose-reflexed in the upper half, laminal cells
smooth; inner perichaetal leaves erect, broadly, long linear or tri-
angular lanceolate, usually 2 to 4 deep plicae, rarely plane or nearly
so, costa variable, absent, short and double, long and double or single
and/or forked, faint or stout, margins usually plane, rarely recurved,
entire or finely to coarsely serrulate, especially in the apex, apex
obtusely acute to long tapering acute, laminal cells smooth, rarely a
few cells in the leaf apex are papillose on the abaxial leaf surface by
means of distally overlapping endwalls.

Seta 6 to 31 mm long, usually 10 to 20 mm, erect or slightly inclined
when moist, smooth, color variable, yellowish-orange, yellowish-red,
reddish-brown, dark bright red; cross sections revealing 2 to several rows
of small, thick-walled cells, medullary cells slightly larger, thin-walled,
becoming thicker walled with age; central strand broad, well developed;
upon drying the seta twists in various directions.

Capsules 1 to 3 mm long, ovoid to oblong-cylindrical, erect and symmetri-
cal or inclined and slightly to strongly arcuate; color variable, yellow-
brown, brown, or reddish-brown; exothecial cells variable, rounded, quadrate,
short rectangular, irregular, thick or thin walled; differentiated neck
present or absent, stomates superficial on the neck and lower capsule,
variable in number, 7 to 30; annulus usually of 2 to 3 rows of cells, some-
times 4, rarely absent; operculum conic or conic apiculate; calyptra
cucullate; capsule response to drying variable, generally shrinking, remain-
ing erect or becoming strongly arcuate cylindric, the neck when differentiated
becoming wrinkled upon drying, capsule strongly contracted beneath the mouth
or sometimes hardly at all.

Peristome double, exostome of 16 teeth, pale yellow, yellow-brown, or
light reddish-brown below, hyaline in the upper half, each segment is horizontally striate in the lower 1/2 to 1/3, finely papillose in the upper 1/3 to 1/2; endostome of 16 hyaline to pale yellow teeth, finely papillose to almost smooth, frequently cracked along the keel, especially in the lower half; 1 to 3 rudimentary to well developed cilia between adjacent segments, basal membrane 2 to 4 tiers in height.

Spores usually dusky yellow or yellow-green, finely papillose.
Key to the species of *Hygrohypnum*

1. Stem cross-section revealing an epidermis of small thick-walled cells which are similar to the subadjacent cortical cells...........4

1. Stem cross-section revealing an epidermis in which some or all of the cells are enlarged and thin-walled relative to the sub-adjacent cortical cells or some cells have a slightly thinner and less pigmented outer tangential cell wall compared with the other epidermal cells walls and the subadjacent cortical cells.....2

2. Costa uniformly strong and single, percurrent..................H. polar

2. Costa short and double, double to midleaf or if single and/or forking, then ending well before the apex.........................3

3. Alar cells inflated, forming a distinct group of cells, often becoming red or reddish-brown with age; leaf apex acute...H. eugyrium

3. Alar cells wider and shorter than adjacent cells, but neither inflated nor abruptly different from them, marginal alar cells increasing in length distally from the point of insertion, hyaline or yellowish; never red; leaf apex blunt....................H. ochraceum

4. Leaves all straight; sometimes secund..........................5

4. Leaves falcate or some leaves on the same or different stems within the same specimen falcate and/or straight...................18

5. Leaves broadly ovate to orbicular...............................6

5. Leaves ovate to oblong-ovate or ovate-lanceolate................11

6. Median marginal leaf cells 60 um or longer...............H. bestii

6. Median marginal leaf cells rarely longer than 55 um...........7

7. Alar cells clearly differentiated, either thin-walled or incrassate..........................................................8

7. Alar cells undifferentiated or a few quadrate or short rectangular cells which are incrassate or thin-walled...................9

8. Alar cells thin-walled, usually hyaline, enlarged, rounded rectangular, forming a rectangular group whose long axis parallels the leaf margins; inner perichaetial leaves papillose on the abaxial surface near the apex...............................H. alpinum

8. Alar cells incrassate, clearly pigmented in older leaves, quadrate, short rectangular or irregular, forming an irregular group; inner perichaetial leaves smooth...............................H. duriusculum
9. Costa usually single, stout, to midleaf or slightly beyond, sometimes forked and/or stout, short and double; plants very coarse and rigid..................................H. smithii

9. Costa almost exclusively short and double, if single, then the costa is slender and the plants are soft.................................10

10. Leaves deeply concave to cochleariform, usually 0.8 to 1.2 mm long, apex obtuse or broadly rounded, inner perichaetial leaf margins entire and recurved; endostomal cilia 2 to 3............H. cochlearifolium

10. Leaves concave, but never cochleariform, usually 1.0 to 1.7 mm long, apex tapering to an acute, but blunt point; inner perichaetial leaf margins coarsely denticulate and plane; endostomal cilia rudimentary or wanting.................................H. molle

11. Alar cells clearly differentiated, either inflated and mostly thin-walled or smaller, incrassate and quadrate to short rectangular........12

11. Alar cells undifferentiated or with but a few quadrate to short rectangular cells which do not form a recognizable group............14

12. Leaf apex narrowly recurved along the margin and reflexed as a small apiculus, especially in leaves at or near stem or branch tips; leaves deeply concave, especially near the apex........H. alpestre

12. Margins of leaf apices plane or variously inrolled, never recurved, apex never forming a reflexed apiculus..........................13

13. Leaf apices always acute and entire......................H. luridum

13. Some leaf apices with a few fine teeth or obtuse and distinctly denticulate..................................................H. subeugyrium

14. Leaf apex abruptly acuminate, tapering to a slender tip; plants pseudo-paroicous.................................................H. styriacum

14. Leaf apex obtuse or acute, with or without a blunt tip........15

15. Costa predominantly single to midleaf or beyond, sometimes short and double.........................................................16

15. Costa usually short and double, rarely single to midleaf........17

16. Leaf apex obtuse; plants coarse; inner perichaetial leaves plicate, margins recurved....................................H. smithii

16. Leaf apex acute with a blunt tip; plants coarse; inner perichaetial leaves never plicate, margins plane..........................H. closteri

17. Leaf apex entire; leaves usually 0.5 to 0.8 mm long...........H. norvegicum
17. Margin of the leaf apex uneven to denticulate; leaves usually 1.0 to 1.7 mm long......................................................H. molle

18. Leaves exclusively falcate.................................................19

18. Falcate and straight leaves occurring simultaneously on the same stem or on different stems within the same specimen.........................23

19. Alar cells undifferentiated from adjacent cells......................20

19. Alar cells well developed; small, numerous, quadrate to short-rectangular, incrassate or inflated; plane or excavated.........................21

20. Leaf margin finely to coarsely serrulate, especially in the apex, and narrowly recurved, particularly in the lower half of the leaf.................................................................H. montanum

20. Leaf margin always entire and plane.................................H. styriacum

21. Alar cells inflated..........................................................H. eugyrium

21. Alar cells small, quadrate to short rectangular, incrassate........22

22. Leaf apex always acute, the margin entire.........................H. luridum

22. Some leaf apices: obtuse and distinctly denticulate or acute with a few fine teeth..........................................................H. subeugyrium

23. Leaf apex always entire.....................................................24

23. Leaf apices bearing a few fine teeth....................................25

24. Leaf apex acute; alar cells numerous, quadrate to short rectangular; annulus absent; plants autoicous...............................H. luridum

24. Leaf apex abruptly acuminate; alar cells undifferentiated or just a few quadrate cells; annulus present; plants pseudo-paroicous.....H. styriacum

25. Alar cells inflated, thin-walled, leaf apex always acute; stem epidermis differentiated as an ill-defined hyalodermis..H. eugyrium

25. Alar cells quadrate to slightly enlarged, incrassate; some leaf apices obtuse and denticulate; stem epidermis similar to cortical stem cells.........................................................H. subeugyrium
Hygrohypnum alpinum (Lindb.) Loesk., Hedwigia 43:194. 1904.

Neotype: Norway, Gudbrandsdalen; Blytt as Hypnum molle. (S-PA).


Amblystegium molle var. alpinum Lindb., Musci Scand. 33. 1879.

Hygnum dilatatum var. alpinum (Lindb.) Ren., Rev. Bryol. 10:51. 1883.

Hygnum molle var. alpinum (Lindb.) Boul., Muscin. France 24. 1884.


Hygnum dilatatum var. alpinum (Lindb.) Husn., Musc. Gall. 413. 1894.


Names of taxa for which study material was unavailable and available literature was inadequate for evaluating the taxon.


Names of taxa for which the literature was unavailable for this study.


Plants usually soft and pliable when moist or dry, less often somewhat stiff and brittle when dry, especially in North American material, generally forming small loosely woven patches or less often larger more tightly woven mats, both of which easily fragment. Color variable, pale yellow, silty yellow-brown, brownish-yellow-green or bright yellow-green, sometimes exhibiting a translucent sheen. Stems to about 5 cm long, leafy throughout; stems and stem leaves generally obscured within the mat or patch. Branching variable, branches 1 - 2 (3.5) cm long, characteristically ascending to erect
in one plane. Stem cross-section exposing 2 to 3 (4) rows of small, thick-walled, yellow or organe-brown cortical cells; medullary cells larger, thin-walled, hyaline with little evidence of wall thickening and discoloration with age; central strand present, hyaline or brownish. Rhizoids abundant, dark reddish-brown, smooth walled, arising at the base of ventral stem leaves.

Leaves variable; closely spaced or distant, differing little from the wet to dry condition, though leaf shrinkage is readily evident upon drying; closely spaced leaves are loosely appressed-imbricate and either essentially plane or ruffled-contorted; distant leaves are spreading to erect-spreading and variously contorted by marginal inrolling or ruffling. Leaves (1) 1.3 - 1.7 (2) mm long X (0.9) 1.2 - 1.6 (1.7) mm wide; shape variable, usually oblong elliptic to orbicular, but varying from ovate to transverse; margins usually entire, less often finely serrate to serrulate, especially in the apex, varying among leaves on the same stem, usually plane throughout, occasionally slightly recurved at the base. Leaves variously plane or ruffled or less often weakly concave. Leaf base narrowly decurrent or transverse. Costa usually double with slender arms, often very faint, one or both arms may reach midleaf, rarely slender and single and/or forked with the main axis reaching slightly above midleaf.

Areolation variable; median leaf cells short fusiform to linear flexuose, moderately thin-walled, (25) 35 - 55 (75) um long X (4) 6 - 7 (9) um wide; apical cells shortening gradually, variously oval, quadrate or short fusiform; marginal leaf cells in the upper half of the leaf little different from the median cells, usually 25 to 50 um long, rarely longer; toward the leaf base cells variously become longer or shorter in length or slightly wider or changing very little from the median cells; basal cells thicker
walled, hyaline or sometimes becoming yellowish or brown with age, pits few to none; alar cells usually forming a well defined rectangular group of thin-walled, sometimes slightly inflated and/or excavated, irregular to rectangular cells, normally hyaline, sometimes becoming brownish with age.

Plants autoicous; perigonial leaves ovate, 0.5 to 0.8 mm long, ecostate, entire, except for 2 to 4 teeth at the sharply acute apex; outer perichaetial leaves ovate to ovate lanceolate, ecostate, squarrose in the upper half; inner perichaetial leaves linear to linear-lanceolate, up to 4 mm long, ecostate or faintly single or double ecostate, 0, 2, or 4 deep plicae; margins of the middle and inner perichaetial leaves characteristically coarsely serrate at the apex with certain cells in the apex coarsely papillose on the abaxial leaf surface by overriding distal endwalls.

Seta 8 to 20 mm long, usually 9 to 16 mm, color variously yellowish-red, orangish-red or red, smooth, straight when wet, variously twisted when dry; capsule as per the genus.

Outer peristome typical for the genus; inner peristome teeth finely papillose, cilia absent or very rudimentary; spores dusky yellow or smoky grey, finely to coarsely papillose, 13 to 22 um in diameter, usually 14 to 18 um.

*Hygrohypnum alpinum* is a well defined species and can be recognized readily by its broadly ovate to orbicular leaves which exhibit a group of thin-walled, usually hyaline and irregular to rectangular alar cells. The long axis of the rectangular group of alar cells is parallel to the leaf margin (Fig. 27 g & h). Certain cells in the apex of the inner perichaetial leaves are papillose on the abaxial surface by means of overriding distal
endwalls (Fig. 27 a). This useful feature was first observed by Amann and Meylan (1912), but seems to have gone unnoticed since then.

The species concepts of *Hygrohypnum alpinum* and *H. dilatatum* (Wils. ex Schimp.) Loesk. have been intimately involved with a number of misconceptions of *H. molle* (Hedw.) Loesk. and *H. alpestre* (Hedw.) Loesk.

Hedwig (1801) described *Hypnum molle* and *H. alpestre* based on the earlier concepts of Dickson (1790) and Swartz (1799) respectively. Except for Bridel (1812, 1827), several subsequent workers treated *Hypnum alpestre* Sw. as synonymous with *Hypnum molle* Dicks. (Sprengel, 1827; De Notaris, 1838) or relegated *Hypnum alpestre* Sw. to varietal status with *Hypnum molle* Dicks. (Hampe, 1837). Schimper (1853) partially clarified the situation, but a broad and somewhat mistaken concept of certain species served only to cloud the issue. Like Hedwig, Schimper based his concept of *Limnobium molle* on that of Dickson. Schimper also observed that although Swartz (1799) accurately described *Hypnum alpestre*, he represented the species with an illustration that Schimper felt to be *Hypnum molle* sensu Dickson. This is emphasized in Schimper's treatment of *Limnobium alpestre* where he listed *Hypnum alpestre* as the basionym, but specifically excluded Swartz' illustration, Tab. VI, referring it to *Limnobium molle*. Obviously, Schimper noted that *Hypnum Stereodon alpestris* Brid, from *Bryologia Universa* II is synonymous with *Hypnum molle* Dicks. and similarly *Hypnum Stereodon mollis* Brid. was synonymous with *Hypnum alpestre* Sw. However, Bridel (1827) clearly

Evidence to be presented later has established that the name *Hypnum duriusculum* De Not. has priority over *Hypnum dilatatum* Wils. in Schimp. However, for the sake of clarity *Hypnum dilatatum* will be employed in the present discussion.
indicated that H. S. alpestris was based on Hypnum alpestre Sw. and H. S. mollis was based on Hypnum molle Dicks.

The concept of Limnobium molle Schimp. seems to have been a very broad one. Schimper (1853) illustrated the species with two plates: Tab. III, Fig. 1 - 14, pg. 576 and Tab. IV, Fig. 2 - 6, pg. 577. Schimper (1860) extracted and described Hypnum alpinum Schimp. and H. dilatatum Wils. in Schimp. from the 1853 concept of Limnobium molle. To illustrate these two new taxa Schimper cited Tab. III, Fig. 1 - 14, pg. 576 to represent Hypnum alpinum and Tab. IV, Fig. 2 - 6, pg. 577 to represent Hypnum dilatatum. Further, Schimper (1860) cited no illustration for his more restricted treatment of Hypnum molle, but clearly based it on Dickson's concept. An examination of the few available Schimper specimens indicates that he held a sound concept of Hypnum molle, H. dilatatum, H. alpinum and H. alpestre. It is, therefore, remarkable that: 1. the illustration cited to represent Limnobium alpestre in Bryologia Europaea and redesignated in Syn. ed I is clearly Hygrohypnum molle (Hedw.) Loesk. and, 2. that in Syn. ed. I, he clearly ascribes the Swartz illustration of Hypnum alpestre to Hypnum alpinum Schimp.

As presently understood Hygrohypnum molle (Hedw.) Loesk., H. dilatatum (Wils. in Schimp.) Loesk., H. alpinum (Lindb.) Loesk, and H. alpestre (Hedw.) Loesk. are very clearly defined species. Of the illustrations in Bryologia Europaea, Tab. III, Fig. 1 - 14, pg. 576 are referable to Hygrohypnum alpinum, Tab. IV, Fig. 2 - 6, pg. 577 are referable to H. dilatatum and Tab. IV, Fig. 1, 1b and 7 - 21, pg. 577 are referable to H. molle.

It is worth noting that Hedwig's (1801) Tab. LXIV. Fig. 2 for Hypnum alpestre is misleading. It erroneously shows a single costa in the leaves. The costa of Hygrohypnum alpestre is usually short and double or long and
double. Similarly, Tab. IV, Fig. 7, pg. 577 from Bryologia Europaea shows a falcate leaf with a single costa, a character combination that is unknown in Hygrohypnum molle.

As late as 1927 Monkemeyer erroneously represented Hygrohypnum dilatatum with an illustration obviously of H. molle (Fig. 168 b). The similarity of H. alpinum and H. dilatatum led Lawton (1971) to employ a leaf of H. alpinum to represent H. dilatatum (Plate 156, Fig. 1).

As there has been considerable confusion over several taxa in the "Hygrohypnum molle complex", so too has there been confusion concerning the nomenclatorial status of Hygrohypnum alpinum. Schimper (1876) described Hypnum alpinum Schimp. as a segregate from Limnobium molle Schimp. Unfortunately, Hypnum alpinum Schimp. is a later homonym of Hypnum alpinum (With.) Web. et Mohr. The first name to be validly and legally applied to Schimper's taxon was Amblystegium molle var. alpinum in Lindberg (1879). Lindberg clearly indicated that the variety was based on Schimper's original concept. Schimper (1876) based the species on 5 cited specimens, but designated no holotype.

Of the five specimens two are important. Schimper cited a Blytt specimen from the Norwegian Dovrefjeld and a specimen collected by Thedenius from Nedalen in the Harjedalen region of Sweden. That Nedalen is now a part of Norway is of little import. These two specimens have not been seen. However, a Blytt specimen called Hypnum molle from Gudbrandsdalen, Norway, a site not far from the Dovrefjeld, and a Thedenius specimen called Hypnum dilatatum from Tannas in the Harjedalen district of Sweden and again a site not far from Hedalen, are present at S-PA. Both of these specimens are valid examples of Hygrohypnum alpinum. The Blytt specimen is in the better condition of the two. In the absence of any proven Schimper material of Hygrohypnum alpinum, the Blytt specimen is selected as the neotype.
Hygrohypnum alpinum exhibits some variation in leaf shape, costa structure, the nature of the leaf margin and the attitude of the leaves upon the stem. Leaf shape varies from broadly ovate to orbicular (Fig. 26 a - e). The leaf apex may be broadly acute or rounded with a small, abrupt apiculus (Fig. 26 a - e). The costa is usually slender and double, but rarely one may encounter a slender, single and/or forked costa reaching mid-leaf (Fig. 26 a - e). Schimper's (1876) description noted the finely serrulate margin at the leaf apex. The present study has shown the margin to the leaf apex to vary from entire to finely serrulate between leaves on the same or different plants. One of the most remarkable features of H. alpinum is the disposition of its leaves along the stems. Virtually all the leaves of North American specimens and a significant number of European specimens exhibit leaves that are convolute or ruffled parallel to their longitudinal axis (Fig. 26 f, g & h). Other European specimens exhibit leaves that are essentially plane or slightly concave (Fig. 26 i & j).

Hygrohypnum alpinum is most easily confused with H. duriusculum. The following table of characters will help to separate them.

<table>
<thead>
<tr>
<th>H. alpinum</th>
<th>H. duriusculum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alar cells thin-walled, more or less rectangular, and hyaline.</td>
<td>Alar cells thick-walled, quadrate to irregular, usually discolored.</td>
</tr>
<tr>
<td>Apical perichaetal leaf cells papillose by anteriorly over- riding end walls.</td>
<td>Perichaetal leaf cells smooth.</td>
</tr>
<tr>
<td>Endostomial cilia absent or very rudimentary.</td>
<td>One or two well to poorly developed cilia between the endostomial teeth.</td>
</tr>
<tr>
<td>Stem branches usually less than 2 cm long, more or less ascending to erect.</td>
<td>Stem branches of variable length, usually prostrate or ascending.</td>
</tr>
</tbody>
</table>
Older stems generally retaining their leaves. Older stems generally denuded of leaves.

In Europe *Hygrohypnum alpinum* and *H. duriusculum* can be fairly easily separated by field observable characters. *Hygrohypnum alpinum* normally forms soft, easily fragmenting patches of tightly woven, stoloniferous stems, from which arise numerous short, ascending to erect branches. The stoloniferous stems are generally foliose throughout and densely clothed in rhizoids ventrally. *Hygrohypnum duriusculum* is rigid to the touch and the prostrate, irregularly branched stems are regularly denuded in the older extremities. Rhizoids are sparse or absent. Branches of irregular position and variable length usually lie parallel to the stem and are prostrate to slightly ascending at the tips. The patches or tufts do not fragment easily.

In Western North America one must initially rely on microscopic characters to separate *H. alpinum* and *H. duriusculum*. In this region *H. duriusculum* often assumes a habit similar to that of *H. alpinum*, i.e. densely foliose, and densely rhizoidal stoloniferous stems which bear numerous short, erect or ascending branches. With increased field experience one can employ the ruffled appearance of the leaves *H. alpinum* (Fig. 26 g & h) to separate it from *H. duriusculum* whose leaves are generally less crowded and more symmetrical, plano-concave (Fig. 29 c).

My own field experience with *Hygrohypnum alpinum* in Western North America has been confined to southern British Columbia. In that region the species occurs exclusively on large boulders on the banks of or in the middle of small, swiftly running mountain streams. The only time that this species occurs in a submerged situation for any length of time is during spring runoff. Otherwise, it occurs on emergent rocks that are subjected to spray from turbulent water.
Fig. 26 a - j. Variation in the leaf shape and the habit of the shoots of *Hygrohypnum alpinum*.

a - e. Variation in foliage leaves.

f. A moist shoot of a specimen with ruffled leaves from Western North America.

g - h. Comparison between the moist (g) and dry (h) shoot of a ruffled leafed specimen from western North America.

i - j. Comparison between the moist (i) and dry (j) shoot of a plane to concave leafed specimen from Europe and North America.

Scale:

a - e; 1 mm

f - j; Each stem is approximately 1 cm long.
Fig. 27 a - h. Cellular detail of the perichaetial and foliage leaves of *Hygrohypnum alpinum*.

a. Perichaetial leaf apex.
b - c. Foliage leaf apicies.
d. Median cells of foliage leaves.
e - f. Marginal cells of foliage leaves.
g - h. Alar cells of foliage leaves.

Scale:

a: [100um]

b - c, g - h: [100um]

d - f: [100um]
Fig. 28. *Hygrohypnum alpinum*
Exsiccati Examined

Macoun, Canadian Musci

- # 357 as H. dilatatum. (TRTC)
- # 396 as H. alpestre, but in part H. luridum. (USA, NY, MO)
- # 900 as H. dilatatum. (USA)

Canadian Mosses, # 490 as H. dilatatum. (USA, NY)
Grout, North American Musci Pleurocarpi, # 427 as H. dilatatum.
(MIN, MO, NY, TENN, UC, USA)
Bauer, Musci europ. et amer. axsiccati, # 2089. (BRNM, NY S-PA)
Rabenhorst, Bryotheca europaea, # 1348. (NY, S-PA)
Husnot, Musci Galliae, # 593 as H. palustre var. julaceum. (S-PA)
Verdoorn, Musci Selecti et Critici, series VI, # 270. (MICH, NY, LE, TENN)

Selected Specimens Examined

Canada

British Columbia
Garibaldi Provincial Park, Sentinel Glacier Area; Schofield 32953 as H. alpestre. (CAMN, DUKE, TENN)
North Vancouver, Lynn Canyon; Schofield 35292 as H. dilatatum.
(UBC)
Caribou District, end of Long Lake; Boas 688 as H. dilatatum.
(CAN, UBC)
Glacier; Macoun as H. dilatatum IN Canadian Musci # 900 (USA)
Kamloops Lake District, Skuian Creek; Brinkman 259 as H. dilatatum.
(CAN, MICH)
Lake Lindeman; Williams 6 May 1896 as H. dilatatum. (NY)
Salmo, Sheep Creek; Jamieson 5551. (UBC)

United States

Alaska
St. ?acrous Bay; Howell 18 Aug 1895 as H. dilatatum in
Howell's Alaska Pacific Coast Plants # 1818. (NY)
Short Bay; Howell 8 Aug 1895 as H. molle. (MIN)

Washington
Cascades Mtns, Copper Creek; Allen, June 1905 as H. dilatatum
in North American Musci Pleurocarpi # 427. (MICH, NY, TENN, WTU, MO, UC, USA)
Snohomish Co., Monte Cristo; Schofield 20085 as H. dilatatum
(CAN, S-PA)
Clallam Co, Olympic National Park, Olympic Hotsprings;
Svilha 758 as H. dilatatum. (WTU; F)
Mount Rainier Region, Paradise Valley; Frye 11 Aug 1904 as
H. dilatatum. (WTU)
Chelan Co., Transen Creek; Sharp 2112. (TENN)

Idaho
Bonner Co., Priest Lake; Ireland 8565 as H. dilatatum. (ALTA, UBC)
Lemhi Indian Reservation, Mill Creek; Henderson 3979 as H. dilatatum.
(USA)

Montana
Glacier National Park, Lake MacDonald; Standley 18388 as
H. alpinum. (USA)
Missoula Co. Rattlesnake Campground; Sharp & Clebsch
M-16. (TENN)
Belt Mountains; Williams 19 Sept 1891 as H. *arcticum*,
admixture of H. *bestii* and H. *dilatatum*. (MIN)
California
Siskiyou Co., Duck Lake Creek; Norris 23300 as H. *dilatatum*.
(HSC)

France
Dep. de l'Isere, Vallon des Etages; Culmann 2 Sept 1927 in
Musci europ. et amer. exsiccati # 2089. (S-PA, TENN, NY, BRNM)
Haute Savoie, Mt. Blanc; Payot, in Musci Galliae # 593. (S-PA)

Switzerland
Valais, Mattmark; Nicholson & Dixon 7 July 1913. (BM)
Berner, Oberlander, Handegg; Culmann Sept 1911 in Musci Selecti
et Critici, series VI, # 270. (MICH, NY, TENN)
Tessin, Ticino, Compolungopass; Traumann 8 June 1908, (S-PA)
Uri, Alpetti; Culmann 7 Aug 1882. (S-PA)

Austria
Tirol, Otzaler Alpen; Berner July 1931. (S-PA)
Vorarlberg, Arlberg; Eggler. (S-PA)
Salzburg, Kresmuler; Loeske 2 Aug 1903. (S-PA)
Karnten, Malta; Breidler 1885. (S-PA)

Italy
Macuguaga, Val Anyasca; Nicholson & Dixon 10 July 1913. (BM)

Iceland
N. V. Dynjauvi; Hesselbo 26 June 1912. (NY)

Norway
Opdal, Driva; Kaurin Okt 1881. (S-PA)
Gausta; Jäderholm July 1895. (S-PA)
Mordaland, Hardanger; Kotilainen 2 Sept 1931. (S-PA)
Gudbrandsdalen; Blytt as H. *molle*. NEOTYPE. (S-PA)
Troms, Lyngen, Kjosen; T. Ulvinen 20 Sept 1968. (LE)

Sweden
Harjedalen, Storsjo; Thedenius July 1842. (S-PA)
Jamtland, Frostvikens; Nyman 6 Aug 1947. (S-PA)
Asele Lappmark, Marsfjallet, Jikelminia; Hulphers 14 June 1943.
(S-PA)
Lycksele Lappmark, Storfjallet back vid Vallintjakko; Normann
15 Aug 1945. (S-PA)
Pite Lappmark, Arjeplogs; Moller 30 July 1918. (S-PA)
Lule Lappmark, Kamajokk; Nyman Aug 1893. (S-PA)
Torne Lappmark, Karevaggejokk; Nicholson & Dixon 26 Aug 1907. (BM)
Hygrohypnum duriusculum (De Not.) Jamieson nov. comb.

Lectotype: Erbar. Crittog. Ital, ser. II, no. 204. (§)


Amblystegium dilatatum (Wils.) Lindb. Musci Scand. 33. 1879.


Hypnum circulifolium C. M. & Kindb. in Macoun, Cat. Canad. Pl. 6:242. 1892.


Hypnum eugyrium var. dilatatum (Wils. in Schimp.) Grout, Mosses Handls. Mics. 345. 1903.

Hypnum dilatatum var. duriusculum (De Not.) Limpr., Laubm. Deutsch. 3:353. 1904.
Limnobium dilatatum var. duriusculum (De Not.) Roth, Eur. Laub. 2:645. 1905.


Hygrohypnum dilatatum var. duriusculum (De Not.) Amann, Fl. Mouss. Suisse 2:361. 1912.


Names of taxa for which neither the appropriate literature nor any specimens were available during this study.


Plants usually coarse and stiff to the touch, rarely soft and flexible, forming loosely to tightly woven mats or patches, rarely deep cushions or tufts. Color variable, bright yellow-green with rusty mottling, dull olive-green with rusty mottling, dirty yellow to yellow-brown with or without rusty mottling, all colors grading into one another at various times. Stems (1) 2 - 7 (9) cm long, foliose throughout or denuded from the base to more than half the length of the stem. Branching irregular, usually ascending from prostrate stems; often the only leafy part of the plant, but sometimes denuded at the base. Stem cross-sections revealing 3 to 4 rows of small, thick-walled yellowish to reddish-brown cortical cells; medullary cells larger, thin-walled, sometimes becoming thicker walled and discolored with age; central strand well developed, often discolored. Rhizoids variable, infrequent or densely clothing the ventral surface of prostrate stems, arising
from the bases of ventral stem or branch leaves.

Leaves variable, closely spaced to widely distinct, differing in appearance within and between the wet and dry conditions. Wet condition, leaves appressed imbricate or spreading and somewhat contorted, some closely spaced appressed imbricate leaves are often secund, other closely spaced leaves are spreading to erect spreading and variously contorted, while still other closely spaced leaves simply appressed imbricate; widely spaced leaves when wet, variously loosely appressed imbricate or spreading. Upon drying, all leaves whether loosely spaced or distant, appressed-imbricate, secund or spreading, undergo varying degrees of shrinkage in width, spreading and contortion; the contortion may involve twisting, usually toward the stem and to the left or inrolling on the margins with concomitant twisting. Leaves may vary from closely to widely spaced from one region of the stem to another; Leaves straight when wet, contorted when dry, sometimes appearing falcate from the shrinkage, never truly falcate when moist. Leaves (0.7) 1.25 - 1.8 (2.3) mm long X (0.6) 1.0 - 1.4 (1.8) mm wide; shape usually oblong-elliptic to broadly ovate, less often orbicular or ovate; margins usually entire, often uneven or undulating, rarely clearly serrulate, often narrowly reflexed in the alar region; plane or shallowly concave; apex variously acute, obtuse, obtuse with a small apiculus or rounded; leaf base often narrowly decurrent at the point of insertion and sometimes clasping the stem with a narrow collar; costa variable, usually short and double with slender forks reaching to midleaf, often short and double and very faint, short and single, or single and/or bi- or trifurcate reaching well above the middle.

Areolation extremely variable; Median leaf cells short fusiform to long linear flexuose, rarely long rhombic, variously thin to moderately thick-
walled; (26) 45 - 70 (104) μm long x (3) 5 - 6 (8) μm wide, cell dimensions variable between leaves on the same stem and often differing from one side to the other of the same leaf; cells shortening gradually toward the apex, apical cells shape variable, fusiform, short rhombic, rounded rectangular to rounded quadrate; marginal cells usually shorter than adjacent laminal cells, 25 to 50 μm long, a few isolated cells may rarely exceed 60 μm, especially in large European specimens; cells usually increasing in length, width and wall thickness toward the leaf base, shape differing little from median cells; basal cells thick-walled, pits few to none, becoming discolored with age, yellowish to reddish-brown discoloration sometimes creating a weak sunburst effect across the base; alar cells forming a well defined group of thick-walled, quadrate to short rectangular cells, or irregular, plane to deeply excavated, reaching 3 to 5 rows from the margin and 4 to 5 cells up the margin from the leaf base.

Plants autoicous; perigonial leaves ovate lanceolate, 0.6 to 0.75 mm long, ecostate, entire or slightly serrate at the apex, deeply concave; outer perichaetial leaves ovate lanceolate, weakly ecostate to ecostate, squarrose from above the middle; inner perichaetial leaves linear lanceolate, up to 3 mm long, ecostate or with a very faint, long single or forked costa reaching to 3/4 of the leaf length, 2 to 4 long plicae, margins entire or sometimes slightly serrate in the apex, leaf cells all smooth.

Seta 9 to 27 mm long, usually 12 to 20, color variously yellowish-red, red or maroon, smooth, straight when wet, variously twisted when dry. Capsule typical for the genus, annulus of 2 to 3 rows of deciduous cells.

Peristome characteristic of the genus; endostome usually with 1 to 3 well defined cilia, sometimes rudimentary; spores smoky brown, finely papillose, (11) 15 - 19 (23) μm in diameter.
Hygrohypnum duriusculum is a highly variable species and is only slightly less complex than H. luridum. Under the microscope, the species can be recognized best by its usually oblong-elliptic to broadly ovate leaves (Fig. 30 a - c) and the well defined group of thick-walled, usually discolored, quadrate, short rectangular or slightly irregular alar cells (Fig. 31 c, e - h).

Coarseness and rigidity of habit and defoliation of the older parts of the stems have long been used as field criteria characterizing H. duriusculum. Though useful characters, they should be used with discretion. Certain specimens from the Austrian and Swiss Alps and the Norwegian mountains are very soft to the touch and could be confused with H. molle. In North America H. duriusculum, H. bestii and H. smithii are coarse, stiff and have defoliated older stems. Furthermore, H. duriusculum is sometimes foliose throughout.

The attitude of the leaves on the stems allows one to recognize several growth forms, which often intergrade. These forms can be roughly correlated geographically. Hygrohypnum duriusculum most commonly forms low appressed mats or patches on rocks in streams. In Europe and Eastern North America it is common for the leaves to be rather distant along the stems (Fig. 29 a - d). When dry, the leaves of European specimens are conspicuously shrunken (Fig. 29 f). In the shrunken condition the leaves become variously contorted, twisting in various directions or spreading-squarrose. There appears to be no regularity in the contortion or spreading of the leaves. Leaf shrinkage upon drying sometimes give the suggestion of falcation, but this is lost upon rewetting. Leaf shrinkage is less pronounced in Eastern North American material with distant leaves. The pattern of contortion is more regular. The dry leaves of specimens from Eastern North America are predominantly widely to erect.
spreading, sometimes almost squarrose (Fig. 29 d). The leaves are further contorted; either twisted upon themselves or with their margins inrolled to form a channel and then twisted. Plants of this form are most common in the New England States, New York, the northern Appalachian mountains, Quebec and the Maritime provinces. Some specimens from Europe and Eastern North America bearing distant leaves have the leaves loosely appressed imbricated. Their leaves are not so obviously shrunken.

Another form common to Europe and Eastern North America, which may also reach into Western North America bears its leaves rather close together (Fig. 30 h). The leaves are not as conspicuously shrunken and are loosely apressed imbricate. Though this form and the previous ones are sometimes remarkable distinct, they do intergrade. This would imply that the forms are responses to some environmental phenomenon. Certain specimens can be found in both Europe and North America which bear distinct, more or less spreading leaves in the lower part of the stem and more or less closely spaced appressed imbricate leaves at or near the stem apex or vice versa.

A variation of these plants with closely spaced, loosely appressed imbricate leaves, occurring erratically throughout the entire range of the species, is one in which the appressed imbricate leaves are often swept to one side of the stem creating a secund appearance (Fig. 29 g & h). Certain European material of this type has leaves that are slightly more shrunken than those from Scandinavia or North America. This form, too, grades imperceptibly into other forms.

In Western North America habit variation exhibits another pattern. The plants tend to form low, prostrate, densely woven mats of denuded or foliose stems bearing numerous ascending to erect, densely foliated braches, which seldom exceed 1.5 cm in length. Leaves in this form are usually distant,
though they may vary from spreading contorted or secund.

Growth forms in Europe and North America that have widely spaced leaves usually form loosely woven mats. In these plants it is often difficult to distinguish branches from stems as both may be leafy. More important is the fact that the stems or branches are usually much longer than the 1.5 cm long branches of Western North American material.

If herbarium material can be taken as a measure of the habit diversity and the quality of growth reached in different localities and under different environmental conditions, then it can be said that Hygrohypnum duriusculum reaches its most favorable growth potential in the high Alps of Austria, Switzerland and adjacent Italy. Numerous specimens collected by Breidler, Glowacki, Ganders et al., in the last century show that, in the aforementioned areas H. duriusculum forms large, thick cushions or almost turf-like mats. Only rarely does material from other areas approach the size attained in the high Alps.

In North America and extra-alpine areas of Europe, Hygrohypnum duriusculum occurs more frequently as the well known, easily fragmenting mat or patch of stiff, naked stems bearing many fewer leafy branches.

Certain depauperate or otherwise anomalous specimens from Eastern North America have been confused with other taxa or are puzzling. Three specimens collected by A. J. Sharp from Laurel Falls and Roaring Fork in the Great Smokey Mountains National Park of Tennessee have been cited in the past as evidence for the presence of H. cochlearifolium in eastern North America. One of these specimens was issued as Hygrohypnum cochlearifolium by A. J. Grout in # 59 of North American Musci Pleurcarpi Supplement. Comparison of these specimens with H. duriusculum have shown them to be depauperate forms of H. duriusculum. Ovate elliptic to orbicular leaves are borne appressed-
imbricate on erect branches arising from fragmented, denuded stems.
This compares favorably with similar, though more robust specimens
from farther north. The alar cells, though very poorly differentiated,
are those of *H. duriusculum*.

Another A. J. Sharp specimen from Mica Bay in the Algoma district,
Northern Ontario is also remarkable. Its crowded, orbicular, almost
plane leaves borne on short stems and branches bear a striking resem­
blance to *Hygrohypnum alpinum*. However, the presence of well differen­
tiated quadrate, short rectangular, thick-walled alar cells reveals it to
be *H. duriusculum*.

Critical study of approximately 300 specimens reveals that an oblong­
-elliptic to orbicular leaf is the usual case. Still, some variation occurs
between leaves on the same plant. In broadly ovate leaves the greatest
width is reached at a point somewhere between the lower quarter and the
lower third of the leaf. As the leaf shape approaches orbicular the widest
point rises to the middle of the leaf. The notable variation occurs when
the widest part rises above the middle of the leaf to produce a slightly
ovate-elliptic leaf shapes do occur rarely in plants that are otherwise
depauperate.

The shape of the apex readily varies from broadly acute, obtuse,
rounded or obtuse or rounded with a small apiculus.

Virtually all published descriptions of *Hygrohypnum duriusculum* make
reference to the weak serrulation of the apical leaf margin. Tab, III,
576 from Bryol. eur. was clearly referred to *Hypnum alpinum* by Schimper
(1876). However, this plate has been frequently and erroneously referred
to H. duriusculum. Figure 4a of Tab. III no doubt has been responsible for the notion that H. duriusculum has a serrulate apex. Study of more than 200 European specimens of valid H. duriusculum has shown that a serrulate margin is of infrequent occurrence. Quite often, however, the outer wall of the marginal cells seems partially resorbed, thus giving the illusion of teeth.

The areolation of Hygrohypnum duriusculum is highly variable. The lengths of median leaf cells vary from 25 to 100 µm. A few European specimens have large leaves with median leaf cells uniformly in the 60 to 100 µm range. There is no correlation between leaf size and median leaf cell length. Median leaf cells may vary in length from one side of the leaf to the other.

Zdenk Pilous erected the name Hygrohypnum dilatatum f. bulbosa and distributed two specimens of this form as numbers 429 and 485 of his musci cehoslovenici exsiccati. He based the form on the presence of small bulbs found at the apices of various stems and branches. The plants are little more than entangled, denuded stems. Examination of the bulbs has shown them to be clusters of closely spaced, tightly imbricated leaves that have enveloped the stem or branch apices. The bulbs, like the stems, are dark brown in color. The bulbs are probably the result of apical growth under severe environmental conditions and, as such, are of no taxonomic value.

Kindberg described Hypnum pseudo-arcticum in Macoun (1890) and distinguished it from H. arcticum by its crenulate leaf margin and the short double costa. Grout (1930), however, stated that the plant had abruptly acuminate apex and treated the plant as synonymous with Hygrohypnum luridum. An examination of the holotype (S-PA) reveals that Grout evaluated an admixed fragment of Hygrohypnum luridum while Kindberg, himself, described a small fragment of what is rather typical Hygrohypnum duriusculum from Western North
An examination of the holotype (NICH) of *Hygrohypnum cordifolium* Okam. reveals that it is identical with *Hygrohypnum duriusculum* (De Not.) Jamieson. The Okamura specimen agrees with *H. duriusculum* in terms of leaf shape, alar differentiation and overall appearance.

In 1869 De Notaris distributed *Limnobium duriusculum* as the exsiccatum Erbar. Crittogam. Ital. ser. II, no. 204. The label of this exsiccatum bears a complete Latin description and a reference to Lago Maggiore, Italy as the type locality. Two specimens (at G and UC) of this important exsiccati have been available for study. Index Muscorum, volume 5 (1969) indicated that the De Notaris name is a nomen nudum. Article 31 of the Seattle edition of the Rules of Nomenclature implies that names with accompanying descriptions borne on exsiccatum labels before 1 January 1953 are validly published. Consequently, *Limnobium duriusculum* De Not. is a valid name. The significance of this name is crucial for *Limnobium duriusculum* De Not. is unquestionably the same organism as *Hypnum dilatatum* Schimp. *Hypnum dilatatum* was described by Schimper (1876) based on a manuscript submitted to him by William Wilson. Therefore, *Limnobium duriusculum* has priority over *Hypnum dilatatum* and becomes the legal basionym of *Hygrohypnum duriusculum* (De Not.) Jamieson. The specimen of the De Notaris exsiccatum at G is designated as the lectotype.
Fig. 29 a – h. Variation in the habit of leafy shoots of *Hygrohypnum duriusculum* and comparisons between the wet and dry conditions in the shoots.

Each pair of figures, a – b, c – d, e – f, and g – h represents the comparison between the wet and dry condition in four different shoots. Figures a, c, e, and g illustrate the moist condition in each shoot.

Scale:

Each shoot is approximately 1 cm long.
Fig. 30 a - h. Variation in foliage leaf shape, length of marginal leaf cells and the habit of leafy shoots of *Hygrohypnum duriusculum.*

a - e. Foliage leaves

f - g. Marginal leaf cells

h. Leafy shoot

Scale:

a - e. $\frac{1}{mm}$

f - g. $\frac{100\,um}{mm}$

h. this shoot is approximately 1 cm long
Fig. 31 a - h. Variation in the apices and cellular detail of the leaves of *Hygrohypnum duriusculum*.

a - b. Leaf apices

c, e - h. Alar cells

d. Median leaf cells

Scale:

a - c, e - h.  [100μm]

d.  [100μm]
Fig. 32. *Hygrohypnum duriusculum*
Exsiccati Examined

Austin, Musci Appalachiani # 436 as H. molle. (MICH, NY, USA)
Grout,
Hand-lens Mosses # 72. (MIN, NY)
North American Musci Perfecti
# 62. (MICH, NY, TENN, UC, USA)
# 62a (UBC)
# 290 as H. molle. (MICH, MIN, NY, TENN, UC, USA)
North American Musci Pleurocarpi
# 260 as H. molle. (MIN, MO, NY, TENN, UC)
# 442 as H. molle. (COLO, MIN, MO, NY, TENN, USA)
# 446 as H. molle. (MIN, MO, NY, TENN, USA)
North American Musci Pleurocarpi Supplement
# 59 as H. cochlearifolium. (MIN, TENN, UC)

Macoun,
Canadian Cryptogams # 794 as H. pseudo-arcticum. (TRTC)
Canadian Mosses
# 394 as H. arcticum. (USA)
# 490, in part. (CANM, MICH, USA)
Canadian Musci
# 357. (CANM, NY, UC.)
# 358 as H. arcticum. (CANM, MIN, NY in part)

Sullivant & Lesquereux,
Musci Boreali-Americani
# 304. (MICH, NY, USA.)
# 451 as H. pseudo-arcticum. (MICH, NY, UC., USA)

Bauer
Musci europaei et amer. exsiccati # 1789. (BRNM, G, MO, NY)
Musci europaea exsiccati
# 1278 a. (G, NY)
# 1278b. (BRNM, G, NY)
# 1279 as H. molle. (BRNM, G, NY)
# 1663 as H. molle var. schimperianum. (BRNM, NY)
# 1664 (BRNM, CANM,G, NY)

Brotherus
Musci turkestanici
# 120. (G, H, NY)
# 121. (G, S-PA)

De Notaris, Erbar. Critt. Ital. Ser. II
# 204 as L. duriusculum. (G, UC) Lectotype at G
# 404. (G, UC)

Dismier, Bryotheca Galliae # 19. (NY)
Familer, Flora exsiccata Bavaria; Bryophyta # 381B. (S-PA)
Husnot, Musci Galliae
# 293 as H. molle. (G, NY)
# 495 as H. alpestre. (G, NY)
# 692. (G)

Kerner, Flora Exsiccata Austro-Hungarica # 1922. (BP, BRNM, G, LE, MIN, MO, NY)

Levier, Bryotheca Levier # 711. (S-PA)
Limpricht, Bryotheca Sálesiana # 90. (B, BP, LE, NY)
Lisowski, Bryotheca Polonica
Fasc. IX. # 265 as H. alpinum. (LE, S-PA)
Fasc. X, # 297. (BP, CAN, LE)
Fasc. XI. # 319. (BP, CAN)
Fasc. XXII. # 593 as H. palustre. (CAN)
Fasc. XXV. # 668. (BP, CAN)
Fasc. XLIX. # 1266. (BP, LE)

Mougeot, Nestler & Schimper, Stirpes Criptogamae Vogeso-Rhenanae
# 730 as H. molle. (G, UBC)

Museo Hist. Natur. Vindobonensi, Cryptogamae exsiccate ae # 4260 as H. molle. (NY, this particular specimen is an admixture of H. molle and H. dilatatum)

Noguchi & Hattori, Musci japonica Ser. 8. # 372 as H. tsurugizanicum, (MICH, TENN, UC)
Pilous, Musci cechoslovenici exsiccati
# 412. (G)
# 466. (G)
# 487. (G)
# 798. (G)
# 1177 as H. molle. (C, G)

Rabenhorst, Bryotheca europaea # 899. (G, NY)

Wilson, Musci Britannici # 384. (G, NY)

Verdoorn, Musci Selecti et Critici Ser. XI, # 272. (MICH, MO, NY, TENN, UC)

Zetterstedt, Zett. Musc. pyr. # 251 as H. molle. (CAN, NY)

Selected Specimens Examined

Canada

British Columbia
New Denver, Slocan Lake; McFadden. (UBC)
Osoyoos Lake; Macoun 29 May 1895 as C. arcticum. (CAN)
Macleod's Lake, 55°N; Macoun 2396 as H. smithii. (NY)
Beaton, Selkirk Mtns., Sable Creek; Tusco Oct. 1962. (UBC)
Coffee Creek, 4 miles S. of Ainsworth; Jamieson 20 Sept 1975 (UBC)

Alberta
Little Slave Lake; Mrs. Roy as H. smithii. (USA)
Kanannaska Co.; Macoun 3 Aug 1880. (TENN)

Ontario
Algoma district, near Mica Bay; Sharp CM-636. (TENN, UBC)
Thunder Bay district, Kakabeka Falls; Macoun 14 July 1869. (CANM, NY)
Algonquin Park, Petawana River; Macoun 24 July 1900. (CAN)
Ottawa district; Macoun 8 Aug 1905. (CAN)
Lake Nipogon; Moser 1 July 1884.

Quebec
Gaspe Co., Mt. Albert; Allen 30 July 1881. (NY)
St. Paul, Montmagmy; Gagnon & Masson 11206. (NY)
Mont St. Hilaire; Dupret 7 Sept 1907. (CAN)
Parc du Mont Tremblant, Riviere La Diable; Herman 16664. (CAN)
Mont Shefford, cte de Sheffond; Le Blanc 2530 (NY)
Table Top Mtn.; Allen 10 Aug 1881. (NY)

New Brunswick
Grand Falls, Fish hatchery, Femm Falls; Habeeb 355. (NY)
Queens Co., Cannaan Forks; Macoun 1899. (CAN)
Albert Co., Fundy National Park, trail to Third Vault Falls; Ireland 11470. (UBC)

Nova Scotia
Cape Breton Is., Cape Dauphin; Nichols July-Aug 1914. (NY)
Cape Breton Is., Indian Brook; Nichols 9 Aug 1909. (NY)

Labrador
Caribou River; Wickes 25 July 1938. (USA)
Churchill Falls, Bridge Camp area; Brassard 5330. (NFLD)

Newfoundland
Squires National Park, N. of Deer Lake, Humber R.; Norris 4085. (HSC)

United States

Alaska
Kodiak Group, Raspberry I. Raspberry Straight, Port Vita; Eyerdam 880. (TENN, S-PA)

Washington
Clallam Co., Olympic National Park, Olympic Hot Springs; Svilha 793. (WTU)

California
Inyo Co., Inyo National Forest, along trail on S. side of Lake Sabrina; Jamieson 5389. (UBC)

Idaho
Idaho Co., Nez Perce National Forest, Red River District; Lems M60 as H. molle. (MICH)

Nevada
White Pine Co., Snake Mts., Nevada National Forest; Lawton 2810 as H. molle. (USA)

Arizona
Santa Cruz Co., Santa Rita Mts.; Bartram 156. (NY, USA)

Montana
Glacier Co., Glacier National Park, Reynolds Creek; Hermann 20433. (Personal herbarium of F. J. Hermann)
Missoula Co., Rattlesnake Campground; Sharp M-41. (TENN)
Belt Mountains; Williams 19 Sept 1891 as H. arcticum. (MIN)

Wyoming
Carbon Co., Mill Creek; Porter 27 June 1934 as H. molle. in North American Musci Perfecti # 290. (TENN, USA, MIN, MO, NY, UC)
Johnson Co., Buffalo Tensleep Rd., Porter 1638. (TENN)
Park Co., E. of Beartooth Lake; Conard 21 Aug 1953. (UBC)
Medicine Bow Mtns., E. of Saratoga; Sharp 550. (TENN)

Colorado
Larimer Co., Rocky Mountain National Park, Larkspur Creek; Hermann 25989a. (Personal herbarium of F. J. Hermann)
Mineral Co., Falls Creek, NE of Pagosa Springs; Hermann 23343. (COLO)
La Plata Co., Above Vallecito; Knowlton 85 as H. alpinum. (USA)
Boulder Co., NW of Eldora, Middle Branch Creek; Hermann 24311. (WTU)
Outlet of Corona Lake; Grout 20 July 1914 as H. dilatatum
in North American Musci Pleurocarpi # 446. (TENN, MIN, MO, NY, USA)

New Mexico
Rio Arriba Co., Brazos Canyon; Stanley & Bollman 10794.
(NY, USA)
Santa Fe Canyon; Arsene 20335. (USA)

Utah
Duchesne Co., Uinta Mtns., Ottoson Basin; Flowers 9141. (WTU)

Minnesota
Cook Co., Grand Marais; Holzinger 19 July 1902 in North American
Musci Pleurocarpi # 260. (NY, TENN, MIN, MO, UC)

New York
Greene Co., Catskill Mtns., Haines Falls; Hermann 14338 1/2.
(MICH)
Essex Co., St. Huberts; Ketchledge 723. (UBC)

Vermont
Windam Co., Stratton; Grout 28 June 1926 in North American
Musci Perfecti 62. (TENN)
Bennington Co., Manchester; Grout 28 June 1931 in North
American Musci Perfecti 62. (UBC)

New Hampshire
Belknap Co., Mt. Belknap, Gilford; Carter 5 Sept 1904. (USA)
Warren, Baker's River; Faxon 10 July 1886. (NY)
Mt. Washington, Great Gulf; Faxon 29 July 1886. (NY)

Maine
Mt. Desert Island, Witches Hole; Patterson 208. (NY)

Massachusetts
Berkshire Co., Pittsfield, Lulu Brook; Rice 4 June 1942.
(NY, as H. dilatatum; TENN, as H. molle)

Connecticut
Ansonia; Allen 29 Oct 1880. (NY)

Virginia
Madison Co., Shenandoah National Park; Patterson 1195. (NY)

Tennessee
Sevier Co., Great Smoky Mountain National Park, Laurel Falls;
Sharp 15 Sept 1935 as H. cochlearifolium in North American
Musci Pleurocarpi Supplement 59. (TENN, MIN, UC)
Sevier Co., Roaring Fork; Sharp 36211. (TENN)

North Carolina
Yancey Co., Blue Ridge Parkway, Crabtree Falls; Jamieson
4875. (UBC)
Jackson Co., Soco Falls near Junaluska Lake; Welch 2860. (TENN)

Greenland
Nugssuag Pen., Nugssuag; Holmen 15582. (LE, S-PA, UBC)
Disco Fjord, Kuanit; Porsild 969. (S-PA)

Faroes
Fugelefjord Bygd; Jensen 19 May 1896. (CAN, NY)
Great Britain
Scotland
Clova; Fergusson July 1876. (S-PA)
Schottland; Schimper 1868. (S-PA)
Glen Coe, Rievers Glen, Binstead & Dixon 16 July 1898. (NY)
Wales
North Wales, Aber; Hunt 16 May 1868. (S-PA)
Norway
Gausta; Jaederholm July 1895. (S-PA)
Opdal; Kaurin Aug. 1881. (S-PA)
Lomsegere; Bryhn July 1879. (S-PA)
Nordland, Salten, Nyman 28 July 1893. (S-PA)
Finmarken, Kaafjord; Zetterstedt 13 July 1868. (NY)
Sweden
Smaland, Hults Hesslas dam; Larsson 11 Sept. 1941. (S-PA)
Babhusia, Kristendal; Arven 3 July 1913. (S-PA)
Upland, Atlyln Sundstra; Lindberg June 1855. (S-PA)
Vestmanland, Kingsor Runnakvarn; Ahrling 23 Aug 1880. (S-PA)
Varmland, Ostmarks sn pa Ranneberget; Larsson 24 Aug. 1936. (S-PA)
Dalarna, Norrbarki; Hakel 4 July 1965. (S-PA)
Halsingland, Bergsjö, Elfasen; Collinder 3 July 1877. (S-PA)
Harjedalen, Lyingdalen Storsjo; Thedenius Aug 1842. (S-PA)
Jamtland, Borgafjallt, Rankanlet, Frostvikens; Nyman 1 Aug. 1947. (S-PA)
Angermanland, Sabra Klochersbacen; Arnell 26 Aug. 1874. (S-PA)
Asele Lappmark, Wilhelmina; Moller 22 July 1914. (S-PA)
Lycksele Lappmark, Tarna; Stenholm 12 July 1924. (S-PA)
Lapponia Lulensis, Sarjekens, Kotikjok; Jensén & Arnell 24 July 1902. (S-PA)
Tornea Lappmark, Jukkasjarvi, Abisko National Park; Persson & Gjaerevoll 15 Aug. 1944. (S-PA)
Finland
Lapponia pomojensis, Bakalda; Brotherus 18 July 1872. (NY)
Soviet Union
Siberia, Altai Mtns., Belokurikka; Bardunov 5 June 1966. (NICH)
Siberia, Akmolinsk. Distr. Atbalaryk Ulu-tau; Ganeschin 1717. (H-BR)
Bryotheca Caucasia, Ossetia; Brotherus 26 May 1887. (H-BR)
Siberia, Jenesei, Antis ferova; Arnell 27 June 1876. (S-PA)
Turkestan, Thian Schan, inwilde fl. Narinkol.; Brotherus 27 July 1896. (S-PA)
Lapponia lmandra; A. Kohlman 24 July 1887 (C, as Amblystegium molle var. alpinum)
France
Chamonix; Bernet Julliet 1868. (G)
Switzerland
Valais, Grand St. Bernard; Jaquet 18 Aug. 1926. (S-PA)
Valais, Mattmark; Micholson & Dixon 13. (BM)
Tessin, Lago Campoluiigo; Conti Aout 1894. (G)
Austria
Steiermark, Schladming; Breidler Aug 1871. (G)
Tirol, Innervillgarten; Ganders 15 Sept 1881. (BP)
Salzburg, Lungau, Lessachtal; Breidler 16 June 1885. (BP)
Vorarlberg, St. Gallenkirsch; Hooch 26 Oct. 1928. (S-PA)
Karnten, Tandelapha bei Malta; Breidler 4 Aug. 1880. (S-PA)
Italy

Prov. Comensis, Valle de Darengo; Artaria 15 Aug. 1898. (S-PA, LE)
Campello-Monte, Forv. Noraro Pedemonti, Bei Dannai; Levier
5 Aug. 1904 in Bryotheca Italica 102. (S-PA)
Macuguaga, Val Anyasca; Nicholson & Dixon 10 July 1913. (BM)

Czechoslovakia

Slovenia, Vysoke Tatry; Smarda 13 July 1937. (Moravian)
Moravia, Hruly Jesenik; Smarda July 1947. (Moravian)
Riesengebirges (= Krkonose), Kleiner Teich; Schiffner 13 June 1886.
(S-PA)

Poland

Montes Tatri Oocc.; Lisowski 17 Aug 1956. in Bryotheca Polonica
Fasc. X. # 297. (BP)

Roumania

Carpat, merid., Montes Fogarasi; Vajada 13 Aug. 1966. (BP)
Carpat. merid., Montes Retylzlat; Vajada 3 Aug. 1969. (BP)

Bulgaria

Rila Planina, circa Gam Koruje; Podpera 7 Aug. 1908. (S-PA)
Borovec; Kovacs 29 Oct. 1956. (BP)
Baikansk, Trojanskap, Katoferskap; Kuc 30 Aug 1960. (BP)
Vitosa planima, Stara Rella; Podpera 17 July 1908. (G)

Asia

Kungei Alttau, Brotherus Aug. 1896 in Musci Turkestani # 120.
(H-BR, NY)
Kashmir, Gulmarg; Duthie 3 June 1892. (H-BR)

China

Chensi (=Shensi) Prov., Sinn tsai; Licent 209. (BM)

Japan

Mutsu Prov., Towada; Uemotsu 14 Aug. 1910. (H-BR)
Shinano Prov., Mt., Shirouma; Tishiba 17 Aug. 1909. (H-BR)
Kukuoka Prov., Kyushu, Seburi Mtns.; Amakawa 610. (NICH)
Nigano Co., Okura, Minami-saku; Shimiju Aug. 1952 as H. tsuruza
zanicum in Musci Japonica # 372. (TENN)
Mt. Hokkoda; Uemtsu July 1910. (NY)

Lectotype: Sweden, Harjedalen, Funnasdale; Thedenius. (S-PA)

Lesikea smithii Sw. in Lilj., Svensk. Fl. ed. 3:549. 1816.

Hypnum arcticum Somm. in Wahlenb., Pl. Lapp. Suppl. 65.2. 1826.

Hypnum molle var. arcticum (Somm.) Aongstr. in Fries., Summ. Veg. Skand. 1:83. 1846.

Limnobium arcticum (Somm.) Schimp., Bryol. Eur. 6:70. 578. 1853.

Stereodon arcticus (Somm.) Mitt., Journ. Limn. Soc. 8:42. 1864.


Amblystegium smithii (Sw.) Lindb., Musci Scand. 33. 1879.

Hypnum torrentis C. Muell. et Kindb. in Macoun, Canad. Pl. 6:243. 1892.


Names of taxa for which the appropriate literature was not available during this study.


Plants forming very stiff, coarse, loosely to tightly woven tufts or mats. Color variable, dull dark green, olivaceous-green, blackish-green or black, often modified by golden-green or golden-brown mottling, especially in the stem or branch tips. Stems 1 to 8 cm long, prostrate or ascending at the tips. Branching variable, nearly unbranched or frequently and irreg-
ularly branched, branches remaining prostrate and attaining dimensions similar to the stems, or branches short and ascending to erect; older extremities of both stems and branches becoming denuded or remaining clothed in persistent, but shredded leaf bases. Stems normally eradicu- lose but those plants which bear many short, erect or ascending branches may be densely radiculose. Stem cross-section revealing 3 to 4 rows of small, thick-walled, brownish cortical cells; medullary cells becoming larger and thinner walled toward the middle, becoming brown with age; cen­ tral strand well developed.

Leaves variable; (0.6) 0.8 - 1.2 (1.5) mm long X (0.4) 0.6 - 1.2 (1.4) mm wide; shape ovate, broadly ovate to orbicular, sometimes transverse ovate; apex obtuse or rounded, sometimes almost acute or abruptly tapering to an obtuse point; margins entire or weakly denticulate, plane throughout or slightly recurved near the base; leaves plane or broadly and shallowly concave; costa variable; usually coarse, single to 3/4, often variously forked, occasionally short and double; leaves sometimes rather stiffly decurrent at the base. When wet the leaves are stiffly, but loosely imbricated to erect spreading, upon drying the leaves shrink laterally slightly and twist.

Areolation variable: Median leaf cells rhomboid, fusiform, baciliform or fusiform to linear flexuose; 22 - 48 (64) mm long X (4) 5 - 7 (10) mm wide; apical cells oval rhombic or rounded; Margins often, but not always, bordered by an ill-defined row of short cells; cells generally becoming longer, wider and more incrassate toward the base, in older leaves the basal cells are often shiny yellow in color, pits few to none; alar cells similarly incrassate and yellow, variously quadrate or rectangular, but not forming a clearly recognizable group.

Plants monoicous. Perigonia ovate, perigonal leaves ovate, to 0.6 mm
long, concave imbricate, ecostate, entire. Outer and middle perichaetal leaves ovate, ovate-lanceolate or sometimes slightly elongate-triangular; costa single to midleaf, short and double or almost absent; margins entire, plane or recurved at the base; apex obtuse, variously entire or denticulate, leaf lamina plane or plicate. Inner perichaetal leaves up to 5 mm long, usually 2.5 to 4 mm long, costa single and strong, 2 - 4 plicae, margins entire and recurved, apex obtuse.

Seta 8 - 17 mm long, straight or slightly curved, red or reddish-brown, smooth; Capsule typical for the genus.

Peristome as in the genus; annulus of two rows of cells; endostome with 1 to 3 poorly to well developed cilia. Spores yellow to brown, 13 to 21 μm in diameter, usually 16 to 19 μm.

*Hygrohypnum smithii* may be recognized by its coarse, rigid habit and the usually broadly ovate to orbicular, loosely imbricated to spreading leaves and the stout, generally single costa (Fig. 33 a - e). Of these features, the rigid habit is constant, while the others may vary. In spite of this variation, these characters in combination are diagnostic for the species.

A number of features held by earlier authors as useful in recognizing the species have been shown to be unreliable by the present study.

Husnot (1894) and Lawton (1971) respectively described the stem as ranging from 3 - 5 cm and 1 - 4 cm long. The present studies have revealed continuous variation in stem length from 1 - 8 cm. North American plants are often shorter than European ones, but the differences do not appear significant.

Schimper (1853, 1860, 1876), Braithwaite (1898), Dixon (1896, 1924), Grout (1931) and Lawton (1971) commented upon the slender nature of the
species. If the thickness of a stem is correctly interpreted here to mean the distance between the tip of one leaf to that of another leaf on the opposite side of a moist stem, then the feature is too variable and too subjective a feature to be useful.

The leaves of *Hygrohypnum smithii* are generally described as broadly ovate to orbicular. It is not unusual to observe leaves that may be ovate, oblong ovate or almost triangular (Fig. 33 c, d, & e). Further, the leaves are often described as being 1 mm or less in length. In natural populations, leaves attaining lengths of 1.5 mm are not unusual. Plants grown in culture have born leaves up to 2.0 mm long.

The margin in the upper half of the leaf is frequently described as having an ill-defined border of short cells (Fig. 34 c). Such is not always the case as can be seen in Fig. 34 e.

The median leaf cells are generally quite uniform. Occasionally the median areolation exhibits very wide cells interspersed among cells of more typical dimensions (Fig. 34 f). The alar cells are undifferentiated (Fig. 34 g) or they form a small, ill-defined group of small, quadrate, incrassate cells (Fig. 34 h).

Occasionally *Hygrohypnum smithii* has been confused with *H. bestii* and *H. dilatatum*. It is significant that all three are typically very coarse to the touch. *Hygrohypnum smithii* is most readily distinguished from *H. bestii* by the marginal leaf cells. Compare Fig. 34 c & e with Fig. 37 e & f.

In Western North America very small specimens of *H. smithii* and *H. duriusculum* may be confused. Both species may assume a habit in which prostrate stems bear numerous short, ascending to erect branches. They may be differentiated best on the basis of their costae. Further, *H. duriusculum* loses considerable of its rigidity upon moistening, whereas *H. smithii* does not. The median leaf cells of *H. smithii* are usually 22 to 48 μm long, whereas those of *H. duriu-
sculum are usually 45 to 70 μm long. The alar cells of H. duriusculum typically exhibit more conspicuous differentiation than those of H. smithii.

Personal field experience with Hygrohypnum smithii has been confined to Southern British Columbia. In this area the species has been observed under a variety of conditions. In Kokanee Creek and at Whistler Mtn., H. smithii was observed growing on irrigated rocks. Both localities were at elevations in excess of 4000 feet. At Stagleap Pass H. smithii was collected from a very sluggish and seepy stream. The plants were heavily encased by dark, humic soil. This feature is most unusual, for species of Hygrohypnum normally occur in clean water. At Kokanee Lake, H. smithii was observed in another equally unusual situation. Only very rarely have I seen any species of Hygrohypnum growing completely submerged. At the outlet of Kokanee Lake H. smithii was seen growing in extensive mats on large boulders whose tops were just a few inches below the lake surface. The mats of H. smithii covered a surface area of approximately 30 square feet.

Hygrohypnum smithii was originally described as Leskea smithii by Swartz in Liljeblad's (1816) Svensk Flora. Schimper (1853) described Limnobium arcticum and based the taxon on Hypnum arcticum Sommerfeldt, which was itself described in Wahlenberg (1826). In literature not seen Lindberg (Lindberg in Hartman, 1871) evidently recognized the conspecificity of the Swartz and Sommerfeldt taxa and the priority of the Swartz name for he recognized Amblystegium smithii (Sw.) Lindb. Although Lindberg's (1872, 1879) opinion of the generic position of the plant varied from that of 1871 it is clear that he still held the Swartz and Sommerfeldt taxa as conspecific. Neither Swartz nor Sommerfeldt designated any specimens, although they specified geographical areas. Swartz indicated Norrige and Sommerfeldt designated Saltdalcn,
Nordlandiae. Schimper (1853) cited several specimens, of which the following are pertinent: Saltdalen, Nordlandiae, Sommerfeldt; Christiana, Norvige, Blytt, Schimper; Harjedalen prope Funnasdalen, Thedenius; Kleiner Teich, Sendtner. Apparent duplicates of the Blytt, Thedenius and Sendtner specimens are at S-PA. In the Schimper herbarium at BM is a specimen from Christiana, Norvige for which a collector is not designated. It may well be Schimper's own collection; this cannot be conclusively proven. These specimens are pertinent for they seem to establish the conspecificity of the Sommerfeldt and Schimper concepts of *Hypnum arcticum* and *Limnobium arcticum*. Then, if one can assume that Lindberg (1871, in Hartmann) accurately recognized the conspecificity of *Leskea smithii* Sw. and *Limnobium arcticum* Schimp., then a neotype can be selected from the specimens cited by Schimper. With this rationale a Thedenius specimen at S-PA is designated as the lectotype for *Hygrohypnum smithii* (Sw. in Lilj.) Broth.
Fig. 33 a - h. Variation in leaf shape and the habit of leafy shoots of *Hygrohypnum smithii*.

a - e. Foliage leaves.

f - h. Leafy shoots in the moist condition.

Scale:

- a - e. [1mm]

- f - h. Shoots are approximately 0.75 cm long
Fig. 34 a – h. Cellular details of the perichaetial and foliage leaves of *Hygrohypnum smithii*.

a. Foliage leaf apex.
b. Perichaetial leaf apex.
c and e. Marginal cells of foliage leaves
d and f. Median leaf cells of foliage leaves
g – h. Alar cells of foliage leaves

Scale:

a, c – f. \[ \text{100um} \]
b, g – h. \[ \text{100um} \]
Fig. 35. *Hygrohypnum smithii*
Exsiccati Examined

Bauer, Musci europaei et americani exsiccati # 2289. (BRMN)
De Notaris, Erbar, Critt. Ital, # 306 as H. arcticum. (NY, UBC)
Levier, Bryotheca Italica # 512 as L. molle. (S-PA)
Limpricht, Bryotheca Silesiaca # 292 as Hypnum arcticum. (BP, LE)
Lisowski, Bryotheca Pòlonica
   Fasc. X # 295. (BP, LE)
   Fasc. XXIV # 639. (BP, LE)
Macoun, Canadian Musci
   # 358 as H. arcticum. (NY, TENN, UC)
   # 503 as H. goulardii. (MICH, MN, TRTC, USA)
Rabenhorst, Bfeyotheca europaea # 1142 as L. arcticum. (LE)
Sullivaht and Lesquereux, Musci Boreali Americani # 194 as H. molle.
   (MICH, NY, TENN)

Selected Specimens Examined

Canada

British Columbia
   Vancouver Island, Strathcona Provincial Park, Golden Hind; Boas 356. (UBC)
   Bulkley Range; Boas 714. (UBC)
   Lake of the Hanging Glaciers; MacFadden 1096. (UBC)
   Skeena R., south of Harrison L., Schofield and Boas 21269. (UBC)
   Haines Highway, 54 mi. NW of Haines; Hermann 21794. (CAN, MICH, NY, USA)
   Kokanee Glacier Provincial Park, Kokanee L.; Jamieson 5614. (UBC)
   Garibaldi Provincial Park, Whistler Mtn.; Schofield and Jamieson. (UBC)

Alberta
   Jasper National Park, Tonquin Valley; MacFadden 27 July 1926. (UBC)

Quebec
   Gaspe, St. Anne R.; Macoun 29 Aug. 1890. (CAN)
   Anticosti I., Bececii R., Macoun Aug. 1890. (CAN)

Nova Scotia
   Cape Breton I., Valley of Barrasois; Nichols 1948. (NY)

Newfoundland
   Humber R. District, E. of Blow-Me-Down- Mtn., Williams 1601. (CAMN, HSC, MICH)
   Sops Arm, Approx. 5 mi. S., Norris 4198. (HSC)
   Trout River, approx. 4 mi. E. Norris 4655. (HSC)

United States

Alaska
   Prince William Sound, Knight I., Thrum Bay: Eyerdam 589 (MICH)

Washington
   Olympic National Park, Solduc Hotsprings, Dear Lake Trail; Schofield, Ireland & Boas 19473. (UBC)
   Snohomish Co., Monte Cristo, Trail to Glacier Basin; Schofield 20123. (UBC)
California
Mono Co. Harvey Monroe Hall Natural Area, Cabin Creek; Catchenda 4788. (CAN, MITCH, TENN)
Trinity Co., in rivulet below E. Weaver L.; Norris 9415 (HSC)

Montana
Flathead Co., Glacier National Park, Hidden Lake Trail S. of Logan Pass; Hermann 18315. (CAN, USA)
Lincoln Co., Cabinet Mtns., Leigh Lake Trail; Schofield 11978. (CAN, HSC, NY)

Colorado
Boulder Co., NW of Eldora, Diamond Lake Trail; Hermann 26660. (Herbarium of F. J. Hermann, Dupl. - UBC)

Greenland
Nigerdleg; Holmen 63-146. (NY, UBC)
Ilimaussaq Peninsula, Dynaes; Holmen & Steere 62-584. (NY, UBC)
Tunagdliarfik Fjord, Narassarssuag; Holmen & Steere 62-607. (NY, UBC)

Iceland
N. W. Iceland, Strandasyala, Reyhyavik; Johannson 3 Sept 1967. (UBC)

Faroes
Bordo, Graverdal, Jansen 17 May 1896. (NY, UAC, UBC)

Sweden
Harjedalen, Tannas, Funnasdalen; Thedenius 1842. (S-PA, Lectotype)
Jamtland, Frostviken; Hulphers 1 Sept 1934. (S-PA)
Asele Lappmark, Vilhelmina; Moller 20 July 1914. (S-PA)
Lycke Lappmark, Tarna; Angstrom. (S-PA)
Lapponia Tornensis, Mellan, Jikkasjarvi; Jäderholm 29 July 1914, (S-PA)

Norway
Christiania, Bogstadaas; Zetterstedt & Wickbom 16 June 1870. (S-PA)
Kongsvold, Dovre; Kindberg 1885. (NY, S-PA)
Nordland, Helgeland, Lerskaradalen Stopefjeld; Blytt & Arnell 20 Aug. 1870. (S-PA)
Finmarken, Hammersfest; Jorgensen 15 Oct. 1888. (S-PA)

Finland
Lapponia imandrae, Urupjok, Haarakoski; Kihlman 3 July 1892. (S-PA)
Lps. Salmijarvi, Kuotsjarvi; Roivainen July 1927. (NY)

Soviet Union
Peninsula Kolaensis, Montes Chichyny; Schljakov 20 Aug. 1947 as Hepaticae et Musci URSS Exsiccati # 49. (CAN)

Austria
Tirol Ferwell; Lorentz Sept 1866. (BP)
Steiermark, Sturzbach am Ostablang des Knallstein in der Solk; Breidler 4 Aug. 1877. (BP)
Vorarlberg, Gempadelthali in der Rhatikonkette bei Schruns; Breidler 19 July 1882. (BP)
Karnten, "Klein Eland" im Maltathal; Breidler 25 Aug. 1880. (BP)

Switzerland
Bern Canton, Oberlager am Faulhorn; Culmann 10 Aug. 1908. as Musci europaei exsiccati # 650. (S-PA)

Scotland
Aberdeen, Head of Glen Callater; Croall 11 Aug. 1853. (CAN)
Ben Lawers; Gardner 1838. (CAN)
Ben Mhur; Schimper 1869. (BP, S-PA)
Canlochan Glen, Forfar; Hunt 13 July 1868. (BP)
Clova; ex dons E. G. Britton 1868 ?? (NY)

France
Pyrenees centrales, Crabioules et Tousse de Maupas; Zetterstedt 18 Sept 1856 as Zett. Musci pyr, # 252. (CAN, S-PA)

Italy
Monte Adamello, Schneebach an der Mondronhutte; Kern 27 Aug 1901. (BP)

Poland
Montes Tatri Alti; Lisowski 29 Aug. 1956 as Bryoth. Pol. Fasc. XXIV # 639. (CAMN)

Czechoslovakia
Kleiner Teich; Herausgeber 6 Aug 1868 as Bryo. Siles. # 292. (BP, NY)
Hygrohypnum bestii (Ren. et Bryhn) Holz., Bryologist 4:12, 22. 1901.

Lectotype: Montana, vicinity of Lake McDonald, Avalanche Basin.

Leg: J. M. Holzinger and J. B. Blake 29 July 1898. (NY)


Limnobium bestii (Ren. et Bryhn) Holz., Bryol. 4:22. 1901.


Hygrohypnum molle var. bestii (Ren. et Bryhn) Hab., Rhodora 54:156. 1952.

Plants very stiff and coarse, rarely soft, in loosely woven mats or tufts. Color usually dirty olive-green, often dirty-yellow, often dull yellowish-green with golden mottling, especially near stem and branch apices, rarely bright-green. Stems (1) 3 - 7 (12) cm long, denuded in older extremities in stiff forms, foliose throughout in some soft forms; rigid leaf bases and decurrent wings characteristically persistent on the otherwise denuded posterior extremities of stems in stiff, coarse forms. Stem cross-sections revealing 2 to 4 rows of small, thick-walled cortical cells, yellow-brown to reddish-brown in color; medullary cells larger, usually thinner-walled, occasionally becoming incrassate with age in stiff, rigid stems; central strand absent or very weak. Branching irregular; in very stiff forms branches ascending or erect from prostrate, interwoven, denuded stems; in softer forms leafy stems and branches intertwine in loosely woven tufts. Eradiculose.
Leaves variable. Somewhat distantly spaced. Attitude on the stem variable from the wet to dry condition; when wet leaves weakly appressed, spreading or erect, sometimes slightly secund; variously contorted when dry, often twisting to the left in the upper half. Leaves (1) 1.5 - 2.5 (3) mm long X 1 - 1.5 (2.0) mm wide; shape ovate to broadly ovate, sometimes slightly asymmetrical; margins entire, becoming somewhat uneven in the apex, rarely weakly denticulate; apex obtuse or somewhat acute; leaves plane to broadly and shallowly concave; strongly decurrent to scarcely so, leaves often removed with difficulty from the stem because of the strong bond between the incrassate basal leaf cells and the incrassate cortical stem cells; costa variable, usually strong and double from a massive base, one or both branches reaching midleaf or beyond, or very strong and single reaching well beyond midleaf, often bearing 1, 2 or rarely 3 lateral forks, less commonly weak and double, especially in very young leaves and small branches, costa yellow-green or yellow, becoming brownish with age.

Areolation variable; median leaf cells linear flexuose to broadly rhombic flexuose, (40) 60 - 120 (170) μm long X (2) 6 - 10 (12) μm wide, median leaf cells may exhibit a fairly uniform width or very wide cells (10 - 12 μm) may be irregularly interspersed among much narrower cells, such variation occurring between leaves on the same stem and from one side to the other in individual leaves; apical cells usually rounded quadrate or rhombic, although linear flexuose cells up to 100 μm long are not uncommon; marginal leaf cells between the lower 1/3 and the upper 1/4 of the leaf vary from 60 to 250 μm long; transition from median to basal cells variable, little changed or not at all, becoming thicker or thinner-walled, mostly becoming slightly wider, basal cells usually strongly incrassate and yellowish, turning yellow-brown with age, the pigmentation often creating a radiating sun-
burst effect, or sometimes little or not at all incrassate; Pits few to none; Alar cells variable, hardly differentiated to an imprecisely differentiated group of quadrate to short rectangular, moderately incrassate cells.

Plants apparently dioicous, male and female plants similar. Perigonia borne in the axils of stem leaves and large branch leaves, inner perigonial leaves ovate, 0.75 to 0.9 mm long, deeply concave, margins at the apex slightly irregular to weakly denticulate, ecostate; Outer and middle perichaetial leaves ovate to ovate-lanceolate, ecostate, reflexed squarrose in the upper half. Inner perichaetial leaves long linear lanceolate, up to 2 mm long, costa variable, short and double, single to midleaf or absent, leaves multistratose through the middle with bistratose blades, apical margin uneven or with 1 to 4 coarse teeth.

Seta 15 to 25 mm long usually 18 to 22 mm; red to dark maroon-red in color; smooth, straight when wet, variously twisted when dry. Capsule as in the genus, Annulus of 2 to 3 or 4 rows of deciduous cells.

Peristome as in the genus, Endostome with 1 to 3 finely papillose, weakly appendiculate cilia between each tooth; spores pale yellow, finely papillose, 13 to 21 um in diameter, usually 17 to 19 um.

Of the broad-leafed species Hygrohypnum bestii is best recognized by 1. the very long marginal leaf cells, which range from 60 to 250 um, 2. the large leaves which reach 3 mm long X 2 mm wide, and 3. the dioicous sexuality. In many cases discoloration in the basal leaf cells imparts the appearance of a radiating "sunburst" in the leaf base which is typical of the species.

Hygrohypnum bestii is a very distinctive species. However, certain of
its characteristics are sufficiently variable to overlap with other
species or are simply shared with other species.

The broadly ovate leaf shape which is typical of *H. bestii* (Fig. 38 a, b),
is also shared by *H. molle* (Fig. 44 a - e). The leaves of *H. bestii* are
usually 1.5 to 2.5 mm long and as such are much larger than the typical
lengths of 0.9 to 1.3 mm attained by the leaves of *H. molle* in Western North
America. However, small plants of *H. bestii* with tiny leaves are not infre­
quent and may easily be confused with *H. molle*. The identity of such plants
can be established only by noting of the very long marginal leaf cells in *H.
bestii*.

Both *Hygrohypnum bestii* and *H. duriusculum* are described as coarse to
the touch or rigid and stiff when dry. Further, the leaves of *H. bestii* may
approach an orbicular shape that is more typical of *H. duriusculum* (Fig. 37 c).
Again, these two species may be readily distinguished by their marginal leaf
cells, where those of *H. bestii* are by far the longer (Compare Fig. 38 e & f
with Fig. 30 f & g).

As just discussed, *H. bestii* is generally very coarse or stiff to the
touch when dry. Certain specimens may be rigid even when wet. However, it
is not unusual to find specimens that are soft and flexible in both the wet
and dry state. Therefore, this feature should be employed in the field with
some discretion.

One unique feature of *H. bestii*, which seems to be of uncertain taxonomic
value has to do with the difficulty with which leaves may be removed from the
stem during dissection. The bond at the point of insertion between the leaf
and the stem is exceedingly tenacious and is reflected in the shredded and
persistent leaf bases on the older extremities of both stems and branches.
The leaves will invariably shred during dissection. A good deal of cortical
stem tissue remains attached to the leaves when they are removed from the stem.

The attitude of the leaves upon the stems may vary slightly between and within the wet and dry conditions. When moist the leaves are generally rather distant and loosely imbricated to slightly spreading. In some plants, however, the leaves may be gently folded around the stem so as to be slightly secund (Fig. 36 c). Upon drying the leaves normally exhibit some lateral shrinkage and concomitant twisting. Sometimes the leaves may be very slightly falcate, but normally the leaves are quite straight.

The alar cells in *H. bestii* vary from virtually undifferentiated (Fig. 38 h) to an ill-defined group of short rectangular cells (Fig. 38 g). Such variation can lead to confusion with either *H. molle* or *H. duriusculum*. The very long marginal leaf cells in *H. bestii* will clearly distinguish it from these two species.

The median leaf cells also exhibit some rather peculiar variation. In most cases the median areolation is uniform. However, in some plants very wide cells may be irregularly interspersed among cells of more typical widths; Curiously a similar situation occurs in *H. smithii*, which is itself a rather coarse plant. In leaves of *H. smithii* there is lateral shrinkage and longitudinal twisting that is reminescent of *H. bestii*. This is more a function of the rigidity of the plants than a fundamental relationship.

*Hygrohypnum bestii* was described originally from sterile material. Due to the confusion of *H. bestii* with *H. duriusculum* and *H. molle* the dioicous nature and the existence of sporophytes in *H. bestii* remained unclear until Lawton's (1966) report. Of 128 specimens examined in detail 11 were female, 4 were male and 8 were female and bore sporophytes. Lawton (1966) pointed out that the multistratose inner perichaetial leaves contrasted the unistrat-
ose condition in *H. molle*. The papillose apical cells in the perichaetial leaves of *H. molle* differ from the smooth cells in those of *H. bestii*.

*Hygrohypnum bestii* has one unusual form that occurs at five widely spaced localities along the Pacific Coast of North America. The plant superficially resembles *H. ochraceum*, but differs in the absence of the inflated, hyaline cortical cells. Like typical *H. bestii* the leaves usually exceed 2 mm long, but differ through a more oblong-lanceolate leaf shape (Fig. 37 f – i). The costa is stout and variously double and/or single and forked. The marginal leaf cells are very long as is typical for *H. bestii*. The form also differs in its complete lack of alar differentiation (Fig. 38 i) and a tendency for more regular pinnate branching. This form seems to be a lowland plant occurring from sea level to about 2000 ft, whereas *H. bestii* is from much higher elevations. The sterility of this form may indicate one of two situations. One, that the plant is dioicous, or two that the five known populations represent sterile outliers of an otherwise fertile mountain species that cannot reproduce at low elevations. That *H. bestii* is dioicous is no doubt significant.

*Hygrohypnum bestii* has long been viewed as a Western North American endemic (Lawton, 1971; Schofield, 1969). That Habeeb (1952) reported the species from Albert and Victoria counties New Brunswick seems to have gone entirely unnoticed. The present study has discovered other localities for *H. bestii* in Eastern North America, extending from the upper peninsula of Michigan to the Gaspe Peninsula, Quebec and Cape Breton Highlands, Nova Scotia.

In *Index Muscorum* Vol. 5 Wijk et al. (1969) reported *H. bestii* from Europe. It is possible that the species might be discovered in Scandanavia, but as yet I have seen no material to support this assertion.
Although *H. bestii* is common throughout Western North America, my own field experience has been limited to five localities in southern British Columbia and three in northern California. In these areas *H. bestii* has been observed in a variety of habitats. The elevational range, as I know it, extends from sea level to 6500 feet. In some cases the species grown on submerged rocks in clear, cold mountain streams. In other cases, it grows on rocks in small, silt- and sand-laden, apparently seasonal rivulets. In such rivulets the water tumbles over the rocks in small cascades or slowly seeps over them. Frequently considerable humic silt is present. Organic or inorganic silt and sand accumulate in the plants under such conditions. At sea level the form resembling *H. ochraceum* has been observed growing on sandstone in a seepy roadside ditch. It has also been seen in a clear, silt-free stream at an elevation of about 300 feet. I have been unable to draw any correlation between the coarseness or softness of *H. bestii* and variation in habitat.

Renauld (1901) described *Hypnum (Limnobium) molle* Dicks, ssp.*bestii* Ren et Bryhn based on a J. M. Holzinger collection of 29 July 1898 from Avalanche Basin, Montana at an elevation of 1500 m. Renauld (1901a) published a very similar and somewhat redundant paper redescribing the plant as *Hypnum (Limnobium) bestii* Ren et Bryhn. It would seem that he wished to elevate the plant to the rank of species. However, within the text he remarks, "je crois que le *H. bestii* R. et B. sera mieux a sa place comme sous-espece subordonnee au *H. molle* Dicks. (sensu stricto)." Here again, he places the plant as subordinate to *H. molle*.

Wijk et al. (1964) credited Brotherus (1909) with the authorship of *Hygrohypnum bestii*. An examination of Brotherus' treatment reveals two important points. One the presentation of *H. bestii* was preceded by that of
Hygrohypnum molle (Dicks.) Secondly, the name H. bestii, itself, was immediately preceded by an asterisk, which denoted subspecific status. For some reason Wijk et al. overlooked the asterisk. It seems clear that Brotherus wished to treat H. bestii as a subspecies and not as a species. Brotherus (1925) presented a similar treatment.

John Holzinger (1901) published a note commenting on Hypnum (Limnobium bestii Ren et Bryhn. In that paper he noted that Limnobium Schimp. was an illegal homonym of Limnobium Rich. In that paper he attempted to transfer Hypnum bestii Ren. et Bryhn to Hygrohypnum, but an editorial error prevented the transfer. In a footnote, Holzinger (1901a) stated "By typographical error in the January issue, page 12 last line, Hygrohypnum bestii (Ren. et Bryhn) Holz. was printed Hygrohypnum bestii Ren. et Bryhn. The editor alone is responsible for this." Therefore, as noted by Lawton (1966) Holzinger should be given rightful credit for the transfer.

Hygrohypnum bestii (Ren. et Bryhn) Holz. was described by Renaud (1901) based on a Holzinger specimen from Avalanche Basin, Montana. The Renaud herbarium is at PC. A search of the PC material has failed to produce any Holzinger specimens. At NY there is a specimen bearing all the data indicated by Holzinger and cited by Renaud. This specimen has been appropriately identified and is designated as the lectotype.
Fig. 36 a – e. Variation in the habit of the shoots of *Hygrohypnum bestii* and a comparison of individual shoots in the moist and dry conditions.

a. Moist; b. Dry

c. A moist shoot with secund leaves

d. Moist; e. Dry

Scale:

Each shoot is approximately 2 cm long.
Fig. 37 a - i. Variation in the leaf shape of *Hygrohypnum bestii*.

a - e. The typical leaf shape.

f - i. The leaf shape of the lowland form from the Pacific Coast of North America.

Scale: [2mm]
Fig. 38 a - i. Cellular detail of the foliage leaves of *Hygrohypnum bestii*.

a - c. Leaf apices
d. Median leaf cells
e - f. Marginal leaf cells
g - h. Alar cells
i. Alar cells from the lowland form from Pacific Coastal North America.

Scale:

a - c, g - i: \[100 \text{um}\]
d - f. \[100 \text{um}\]
Fig. 39. *Hygrohypnum bestii*
Exsiccati Examined

Allen, Mosses of the Cascade Mountains

# 141 as H. dilatatum. (MICH, MIN, NY, USA)
# 139a as H. ochraceum. (TENN, MIN)

Grout, North American Musci Pleurocarpi

# 251. (MIN, MO, NY, TENN, UC, USA)
# 382 as H. molle. (MIN, MO, NY, TENN, UC, USA)

Macoun, Canadian Mosses

# 398 as H. arcticum. (MICH, MO, USA)

Canadian Musci

# 357 as H. dilatatum. (NY, USA)
# 358 as H. arcticum. (MICH, MO, USA)
# 360 as H. ochraceum. (MO)
# 483 as Hypnum turgescens. (MICH, NY)

Holzinger, Mosses of North Western Montana

# 56. (USA)
# 62. (NY)

Selected Specimens Examined

Canada

British Columbia

Queen Charlotte Islands, Graham I., Mamin R.; Schofield 30054. (C, CAN, UBC)
Queen Charlotte Islands, Moresby I., Takakia L.; Schofield 24991. (UBC)
Manning Provincial Park, Windy Joe Mountain; Williams 329. (UBC)
Atlin, McKee Creek; Szczawinski 70/62. (USA)
Garibaldi Provincial Park, Whistler Mountain ski bowl: Jamieson 5480. (UBC)
Bulkley Range: Boas 629. (UBC)
New Denver, Denver Glacier; MacFadden 13 Sept 1925. (UBC)
Roger's Pass, Selkirk Mountains; Macoun 2 Aug 1890. (UBC)
Vancouver Island, Burman L.; Boas 254. (UBC)
Pasulko Lake, N. of Lytton; Schofield 17936. (UBC)
Prince Rupert, Slopes of Hays Mountain; Schofield & Sharp 11 Sept 1964. (TENN)
Vancouver, Point Grey; Schofield 13198. (CANM, UBC as Hygrohypnum ochraceum. Lowland form.)
West Vancouver, Lynn Canyon; Schofield 13347. (CAN, UBC)
Vancouver L., Bear Creek, San Juan R.; Boas 25. (CAN, UBC)
Saltspring L. Weston L.; Boas 424. (CAN, UBC)

Alberta

Kicking Horse Pass, Kicking Horse L.; Macoun Aug. 1890 as Canadian Musci # 483. (NY)
Waterton Lakes National Park, divide on E. side of Cameron L.; Bird 6353. (NY)
Oldman River Watershed, Race Horse Creek; Bird and Lakusta 18227. (CAN, UACIA)

Quebec

Gaspe Sud, Gaspe Bay near Penoville; Crum and Williams 10798. (UBC)
Gaspe Nord, Ruisseau-a- Rebours; Crum & Williams 10747 as H. dilatatum. (UBC)
Gaspe Co., St. Joachim de la Tourelle; Victorin et al. (MICH)

New Brunswick
Albert Co., Alma: Habeeb 1640 as H. molle var.bestii. (NY)
Victoria Co., Grand Falls; Habeeb 918. (In the literature Habeeb 1952)

Nova Scotia
Cape Breton Highlands National Park, Beulach Ban Falls; Ireland 11845 as H. dilatatum. (UBC)
Cape Breton Highlands National Park, Aspy R.; Schofield 4890 as H. dilatatum. (CANM)

United States

Alaska
Denali Highway, NW of Paxson, Hermann 21225. (CANM, MICH)
Kodiak Is. Group, Raspberry I., Port Vita; Eyerdam 880 as H. molle. (TENN)
Aleutian Is., Attu Is., Massacre Bay; Howard 51 as H. dilatatum. (TENN)
Skagway; Williams 27 Aug 1899 as H. bestii (NY)
Anchorage, Fire Lake; Lepage 22312. (5-PA)
Aleutian Is., Amchitka Is., W. of Banjo Pt.; Shacklette 7621. (MICH)
Unalaska; Setchell 28, (UC)

Washington
Olympic Mountains; Piper Oct. 1890 as L. dilatatum. (NY)
Mt. Ranier, Goat Mountain; Allen 24 Sept 1898 as H. dilatatum (UBC)
Scenic; Frye 3222. (NY)
King Co., 2 mi. N. of Cedar Falls; Ireland 5817 (WTU as Hygrohypnum dilatatum. Lowland form.)

Oregon
Hood R. Co., Mt, Hood, Timberline Lodge; Hale 21576 as H. molle. (UBC)
Klamath Co., Crater Lake National Park, Kerr Notch; Hermann 22873 as H. bestii. (CANM)
Multnomah Co., Cloud Cap Inn; Schofield 19668 as H. dilatatum. (CANM)
Region of the Alsea (a river); Van Wert May 1923 as H. dilatatum. (MIN)
Benton Co., Oak Creek Lab Oregon St. Univ., Hughes. (UBC, lowland form)

California
Tehama Co., Bridge 8 - 69 on Deer Creek, Highway 32; Kowalski 4 May 1970 as H. molle. (CANN)
Plumas Co., Indian Falls on Indian Creek, Route 89; Lawton 3136 as H. molle. (UBC)
Fresno Co., Sequoia National Park, Stoney Creek; MacFadden 8 July 1959 as H. molle. (CANN)
Del Norte Co. Griffing Creek at Smith River, Highway 199; Norris 8849. (HSC)
Siskiyou Co., Salmon R. near Big Bar; Norris 9280. (HSC)
Modoc Co., Soup Creek Campground E. of Likely; Norris 9451. (HSC)
Calaveras Co., Bolander (USA)
Shasta Co., Lassen National Park, Dersch Meadows; Mueller 6739. (UC)
San Bernadino Co., Parrish 3804. as H. *pseudo-arcticum*.
(NY, UBC)
Marin Co., Muir Woods National Mon., Hermann 17477 (USA, lowland form)
Humboldt Co., Prairie Creek, Redwoods State Park; Jamieson 0099. (HSC, lowland form)

**Idaho**
Elmore Co. Boise National Forest, Hwy between Atlanta and Queen's R.; MacPadden 18706 as H. *molle*. (UBC)
Idaho Co., 80 mi. ENE of Kooskis along route 12; Hermann 20210. (UBC)
Lake Pend d'Orielle, Creek near Blueslide; Leiberg 1891. (NY)

**Montana**
Flathead Co., Vicinity of Lake McDonald, Avalanche Basin; Holzinger & Blake 28 - 29 July 1898 as *Hypnum turgescens* in Mosses of North Western Montana # 62. (NY)
Carbon Co., Red Lodge, Bench Creek Picnic Area; Conard 27 Aug. 1953 as H. *bestii*. (NY)
Lake Co. Flathead Lake, Station Creek; Schofield 12189 as H. *dilatatum*. (UBC)

**Wyoming**
Yellowstone National Park, Black Sand Basin; Lawton 1871 as H. *molle*. (CANN)
Teton Co., Cascade Canyon; Conard 14 Aug. 1953 as H. *bestii*. (CANN)
Fremont Co., To-Gwo-Tee Pass; Porter 1619 as H. *molle*. (TENN)
Albany Co., Centennial Hills; Nelson 2804, as H. *smithii* (TENN)

**Colorado**
Pitkin Co., S. of Redstone, route 133, Crystal R.-Hays C; Hermann 25635 as H. *molle*. (UBC)
Boulder Co., Left Hand Creek; Prettyman 25 Feb 1960. (COLO)
Mineral Co. San Juan Mtns., NE of Pagosa Springs; Hermann 23340. (COLO)
Jackson Co., Mt. Zirkel Wilderness, Lone Pine Creek Trail; Hermann 26740. as H. *bestii*. (UBC)
Grand Co., 1/2 mi S. of Rolling Pass; Hermann 25660. (WTU)
Larimer Co., Rocky Mountain National Park, Mill Creek; Hermann 25996. (WTU)
Garfield Co., 31 mi. S. of Glenwood Springs, SW of Trappers Lake; Hermann 24258. (WTU)
Clear Creek Co., 6 mi. SW of Silver Plume, Quale Creek; Hermann 24918. (WTU)

**New Mexico**
Rio Arriba Co., Vicinity of Brazos Canyon; Stanley & Bollman 10712 as H. *dilatatum*. (USA)

**South Dakota**
Lawrence Co. Eleven miles SW of Lead; Hermann 25360. (WTU)

**Michigan**
Keweenaw Co., Hebard Park; Steere Sept 1936 as H. *molle* (MICH)
Utah

Brookbank, City Creek; Flowers 7165 as *H. ochraceum*. (DUKE)
Hygrohypnum cochlearifolium (Vent. in De Not.) Broth., Nat. Pfl. 1(3): 1039. 1909.


Limnobium cochlearifolium Vent. in De Not., Erbar. Critt. Ital., ser. 2, fasc. 10, n 453. 1871. (Lectotype NY)


Hedwigia (5):70 - 73. 1872.


Hypnum arcticum ssp. goulardii (Schimp.) Ren., Rev. Bryol. 10:51. 1883.

Hypnum arcticum var. goulardii (Schimp.) Husn., Musc. Gall. 414. 1894.


Hygrohypnum smithii var. goulardii (Schimp.) Wijk et Marg. Ind. Musc. 5:577. 1969.

Names of dubious or otherwise unclear status

Hypnum cochlearifolium Vent., Known only from Index Musc. 3:39. 1964.

"Limnobium cochlearifolium Vent.", Known only from the above source.
Names treated as synonyms in other publications, but whose original literature was unavailable during this study.


Amblystegium goulardii (Schimp.) C. Jenns., Medd. Groenland. 15:433. 1898.

Plants very soft, forming loosely woven, easily fragmenting, often mud-clogged patches or small, tightly woven patches. Color variable, dull, dirty green to yellow, usually yellow to yellow-green with conspicuous rusty mottling. Stems (1) 2 - 3 (5) cm long. Mostly unbranched or infrequently and irregularly branched, branches either large and of similar size to the stems and arising from near the stem bases, or branches slender and short, seldom exceeding 1 cm, arising irregularly along the stems, all branches either prostrate or ascending. Stem cross sections with 1 to 2 rows (sometimes a third more or less incomplete row) of small, thick-walled, brownish cortical cells; medullary cells larger and mostly thinner walled, hyaline or becoming brownish with age; central strand small, poorly differentiated. Plants eradiculose.

Leaves variable, Crowded to very distant. Leaf attitude upon the stem varying from the wet to dry condition; when moist the leaves may be loosely imbricated to spreading and tumid; attitude more variable upon drying, either changing little from the wet condition or visibly shrinking, leaves near the stem tips of very large plants frequently exhibit considerable lateral shrinkage, though little other crisping, in smaller plants the leaves retain their concavity upon drying. Leaves (0.5) 0.8 - 1.2 (1.5) mm long x (0.3) 0.6 - 1.0 (1.3) mm wide; shape usually oblong or oblong-elliptic, sometimes orbicular; apex usually obtuse or rounded, occasionally acute, regularly cucullate; margins
entire, variously recurved, particularly in the smaller leaves, or plane, especially in larger leaves; concavity clearly evident throughout the species, very deep to cochleariform, plicae present throughout, irregular in number and arrangement; costa variable, usually short and double with one arm sometimes reaching midleaf, less often short and single, single to midleaf or absent, in all cases the costa is slender; leaves sometimes narrowly decurrent at the point of insertion.

Areolation variable; median leaf cells short fusiform, short linear flexose or rhombic, 26 - 48 (55) um long X (4) 5 - 6 (8) um wide; cells becoming slightly shorter and more rhombic toward the apex; changing little toward the margin; marginal leaf cells short, less than 50 um; basal cells variable, gradually becoming slightly longer and wider or changing little; pits few to none; alar cells thin walled, undifferentiated or of a few quadrate or short rectangular cells, never forming a clearly defined group.

Sexuality poorly understood, plants usually sterile. Perigonial details unknown. Outer and middle perichaetial leaves triangular lanceolate, costa short and single, margins recurved, slightly squarrose reflexed in the upper half. Inner perichaetial leaves oblong lanceolate, up to 2.5 mm long, erect, apex mostly acute, either entire or faintly denticulate, a few papillae on the abaxial leaf surface, margins recurved; Costa single, fading above midleaf.

Seta yellowish to reddish-brown; 12 to 16 mm long, smooth; Capsule as in the genus; Spores immature, unmeasurable.

Peristome as in the genus, annulus present, of two cell rows, endostome with 2 to 3 cilia.

This plant exhibits several features which, in combination, may serve to distinguish the taxon. The leaves are broadly ovate, oblong-ovate or orbicular. No other taxon in the genus has such deeply concave leaves. In
some specimens the concavity may be as deep as 3/4 of the length of the leaf. The species is exceedingly soft. There is no rigidity whatever to the moist stems. It is rare that patches of these plants do not exhibit conspicuous rusty mottling or variegation over a primarily yellow or yellow-green coloration.

Certain characters within this taxon exhibit variation that warrants discussion. The variety varies in overall size, leaf shape, shape of the apex, recurvature of the leaf margin, attitude of the leaves upon the stem or branches, and the spacing of the leaves along the stem. In smaller plants i.e. those with short stems, the small leaves are crowded and closely appressed-imbricated. The concavity of the leaves imparts a julaceous aspect to the stems. The leaves are regularly recurved along the margin. In larger plants, i.e., those whose stems vary from 3 to 4 cm long, the leaves are more distantly spaced, often exceedingly concave and more or less erect-spreading to sometimes almost erect when moist. In these large plants the leaves in the older portions of the stems will be crowded and rather julaceous, whereas younger leaves, though of equal size, will be distant and more spreading.

Both Venturi in De Notaris (1871, 1872) and Schimper (1876) noted the narrowly recurved leaf margins. Nyholm (1965) also remarked upon this character in distinguishing the variety from Hygrohypnum norvegicum. This feature is variable. Among small plants the margin is regularly and conspicuously recurved (Fig. 40 h - k). In larger plants the margin is recurved (Fig. 40 a - e) or plane (Fig. 40 f). In those leaves with plane margins the leaf looks virtually like a spoon.

These plants vary considerably in the placement of the leaves along the stems and branches. In some specimens they may be crowded, while in others they are so widely spaced as to barely overlap.
The leaves of *Hygrohypnum cochlearifolium* are often irregularly plicate. However these plicae are not a clearly integral part of the leaves as are the plicae of the perichaetal leaves. Instead, they appear to be a function of the extremely flaccid nature of the leaves and their corresponding inability to resist the various physical pressures of water or the soil and sand particles that accumulate in the leaf concavity. The plicae are generally more frequent among the larger leaves, perhaps as a result of more exposed surface area. Generally leaves that have been thoroughly cleaned during examination have few if any plicae.

The sexual condition of *Hygrohypnum cochlearifolium* is unclear. Most authors have described it as monoicous. Only Kindberg (1897) has said it is dioicous. The species is most frequently sterile. Only one plant bearing perigonia has been examined. The plants may be monoicous and very infrequently sexual or it may be clearly dioicous. This matter has yet to be resolved.

The nomenclature of *Hygrohypnum cochlearifolium* (Vent. in De Not.) Broth. is highly confused. This species was originally described very clearly by Venturi as *Limnobium cochlearifolium* in De Notaris' *Erbar. Crittog. Ital. Ser. II n. 453* in 1871. The label of this exsiccatum bears a complete description and a reference to a collecting site. The only specimen of this important exsiccati available to me is at NY, where it is filed with *Hygrohypnum smithii*. The rules of nomenclature indicate that on or after 1 January 1953 only descriptive material distributed independent of an exsiccati may effect valid publication. The 1871 date of issue is well within the limit. Further, De Notaris and Baglietto (1872) published the label of the exsiccati.

*Index Muscorum,* vol 3 cites the name *Hygrohypnum cochlearifolium* De Not.,
Erbar. Critt. Ital. ser. 2, 10:n. 453. 1871 as nom. nud. in synon. Index
Muscorum further indicates this name to be synonomous with "Limnobium
cochlearifolium Vent.", an obvious misspelling, which is in turn held as
synonymous with Hygrohypnum smithii (Sw.) Broth. var. goulardii (Schimp.)
Wijk et Marg. It is obvious that Limnobium cochlearifolium Vent. in De Not.
and Hypnum cochlearifolium De Not. are based on the same exsiccati. A
careful examination of the label borne on this exsiccati clearly shows only
the name Limnobium cochlearifolium. Nowhere on the label is there an indi­
cation of the use or the preference for the use of Hypnum instead of Limno­
bium.

Further confusion is added by the fact that the basionym for Weymouthia
cochlearifolia (Schweagr.) Dix. is Hypnum cochlearfolium Schweagr., Spec.
Musc. Suppl. 1(2):221. 88. 1816. Were the name Hypnum cochlearfolium De
Not. a reality, it would still be a latter homonym of the earlier Schweag­
richen name.

Schimper (1876) described Hypnum goulardii from material collected by
Goulard in the Pyrenees. An examination of the Schimper type at BM reveals
that it unquestionably the same organism as Limnobium cochlearifolium Vent

Venturi (1879) clouded the issue, himself, by citing Hypnum cochleari-
forme as a synonym of "Hypnum gounodii Schimp." an obvious misspelling of
Hypnum goulardii Schimp. This would seem to imply that Venturi looked upon
his own plant as identical to Schimper's latter named plant. If in this act
Venturi transferred his Limnobium cochlearifolium to Hypnum cochlearifolium
as a new combination and a synonym of Hypnum goulardii Schimp., then the new
combination becomes an illegal homonym of Hypnum cochlearifolium Schwaegr.

In 1884 Venturi and Bottini reported Limnobium cochlearifolium for Italy.
An unfortunate misinterpretation of the Venturi report by Van der Wijk and
Margadant (1969) treated Venturi and Bottini as the parenthetical authors of *Hygrohypnum cochlearifolium* as cited by Brotherus (1909) and *H. smithii* var. *cochlearifolium* of Monkemeyer (1927). Brotherus (1909) clearly referred his name to *Limnobium cochlearifolium* in Venturi's exsiccati. Monkemeyer (1927) also referred his name to Venturi. However, Monkemeyer curiously cited Venturi's use of *Hypnum*. I have not been able to trace Venturi's apparent use of the name *Hypnum* of his species.

Confusing though this situation is, *Limnobium cochlearifolium* Vent. in De Not. is the basionym for *Hygrohypnum cochlearifolium* (Vent. in De Not.) Broth.

Various authors have treated *Hygrohypnum cochlearifolium* as a variety. (Husnot, 1894; Monkemeyer, 1927) or a subspecies (Renauld, 1883) of *H. smithii*. However, neither these authors nor Boulay (1884) adequately clarified the similarities between the two taxa. Several features indicate that *Hygrohypnum cochlearifolium* is a species clearly distinct from *H. smithii*. *Hygrohypnum cochlearifolium* is exceedingly soft. No other taxon in the genus is as soft. *Hygrohypnum smithii* is exceedingly stiff and rigid. Neither taxon exhibits any reciprocal tendency towards softness or rigidity. Both *Hygrohypnum smithii* and *Hygrohypnum cochlearifolium* have concave leaves. However, the leaf concavity of *Hygrohypnum smithii* is simply not comparable to the cochleariform concavity of *H. cochlearifolium*. The overall areolation of the two taxa is different. Associated with the rigid nature of *Hygrohypnum smithii* is the incrassate nature of the leaf cells. On the contrary, the leaves of *Hygrohypnum cochlearifolium* are very flaccid and correspondingly thin-walled. The basal cells of *H. smithii* are also incrassate and yellowish in color. The basal leaf cells of *H. cochlearifolium* are thinner-walled, sometimes lax and either hyaline or slightly brown in color. The costa of *H. smithii* is usually thick, yellowish, single
and/or forked, although short and double costae are not infrequent. The stout nature of the costa imparts considerable rigidity to the leaves. On the other hand, the costa of *Hygrohypnum cochlearifolium* is usually slender, faint, short and double. The slender and faint quality of the costa no doubt influences the flaccid nature of the leaves. The leaf margins of *Hygrohypnum smithii* are always plane whereas those of *H. cochlearifolium* may be plane or recurved. Although the inner perichaetial leaves of both species have recurved margins, the apex of the inner perichaetial leaves is rounded, whereas that of *H. cochlearifolium* is acute.

For a comparison between *Hygrohypnum cochlearifolium* and *H. norvegicum* see the discussion under the latter species.
Fig. 40 a – m. Variation in the leaf shape and the habit of the moist shoots of *Hygrohypnum cochlearifolium*.

a – c, e – f, h – k. Variation in leaf shape.

d. Leaf "c" as seen in cross-section. Note the reflexed margins.

g. Leaf "f" as seen in cross-section. Note the plane margin.

l – m. Variation in the habit of the shoots.

Scale:

a – k; ___1mm_____

l – m; Both shoots are approximately 0.6 cm long.
Fig. 41 a - e. Cellular detail of the foliage leaves of *Hygrohypnum cochlearifolium*.

a. Leaf apex.

b - c. Median leaf cells.

d - e. Alar cells.

Scale:

a - c;  

\[ \text{100um} \]

d - e;  

\[ \text{100um} \]
Fig. 42. Hygrohypnum cochlearifolium
Exsiccati Examined

De Notaris, Erbar. Critt. Ital. ser. 2, fasc. 10, n. 453 as Limnobium cochlearifolium. (NY, Lectotype)
Institutium Botanicum nomine V. L. Komarovii Academiae Scientiarum URSS, Hepaticae et Musci URSS Exsiccati # 48 as Hygrohypnum cochlearifolium. (CAN, LE, UBC)
Lisowski, Bryotheca Polonica.
Fasc. X, # 296. (BP, LE)
Fasc. XXV, # 667. (BP, CAN)
Fasc. XXIV, # 637 as H. viridulum (BP, CAN, LE)
Fasc. XXIV # 638 (BP, CAN)
Fasc. XV, # 418. (LE)
Museo Hist. Natur. Vindoboneasi, Cryptogame exsiccati # 2895. (BP, UC, F)

Selected Specimens Examined

Canada
Yukon, Haines Highway, Mile 100; Crum and Schofield 9637 as H. norvegicum. (CAN, MICH)
Northwest Territories, Baffin Is., Cape Searle; Hale 17 - 18 Aug 1950 as H. smithii var. goulardii. (UBC)

United States
Alaska
Brooks Range, Endicott Mtns; Steere 18115a as H. cochlearifolium. (NY)
Mt. McKinley National Park, Mt. Eielson; Weber & Vierck 10301 as H. cochlearifolium. (CAN, NY), DUKE)

Montana
Electric Peak; Rydberg & Bessey 18 Aug. 1897 as L. goulardii. (NY).

Colorado
Clear Creek Co., Mt. Evans; Vaarama & Evans 11 Oct. 1963. (COLO)

Greenland
Godthavn; Berggren 1870 as H. norvegicum. (NY, S-PA, F)
Disco Is. Diskofjord, Kuanit; Porsild 954 as H. cochlearifolium. (CANM)
Svartenhuk Penn. Simiap kua; Holmen 12350 as H. cochlearifolium. (CAN)
Scoresbyland, Megtevig; Holmen 18043 as H. cochlearifolium. (CANM)
Nugssuaq Penn., Nugssuaq; Holmen 15577. (S-PA, LE)
Martleak; Beggren 1870. (S-PA)
Hurry Inlet; Dusen 7 Aug. 1899. (H)

Spitzbergen
Advent Bay; Berggren 1868 as H. molle. (S-PA)
Robbe Bay; Berggren 1868 as H. molle. (S-PA)

Norway
Tromso amt, Nordreisen Galslovare; Arnell 23 Aug. 1893. as H. goulardii. (S-PA)
Filejeld; Bryhn Aug. 1887 as H. goulardii. (S-PA)
Dovre rensis Foksjriko; Bryhn Aug. 1906 as H. cochlearifolium. (S-PA)
Finmarken, Talirk, Jorgensen 27 July 1890 as _H. goulardii_.
(S-PA, H, NY)

Sweden
Harjedalen, Storsjo, Smith 10 Aug. 1914 as _H. cochlearifolium_.
(S-PA)
Lule Lappmark, Tarrekaisse, Nilsson 12 Aug. 1897 as _H. norvegicum_.
(S-PA)
Lule Lappmark, Sarjekensis, Rapsdalen, Jensen & Arnell 31 July 1902 as _A. cochlearifolium_ (S-PA, H)
Torne Lappmark, Fausirujaka Jukajarvi, Hulphers 18 July 1944 as _H. cochlearifolium_ (S-PA)

Finland
Karesuando, Smith & Arnell 14 Aug. 1939. (S-PA)
Finska Lapm. Euontelis, Kotilainen 10 July 1920 as _A. viridulum_.
(S-PA)
Prov. Le., Par O-Kahpeusvarri, Roivainen 352 as _H. viridulum_.
(S-PA, UAC)

Soviet Union
Kola Pen., montes Chibiny, Schljakov 24 Aug. 1947. (UBC, CANM)
Jenisei, Nischznje Tauguska, Arnell 13 July 1876 as _A. viridulum_.
(S-PA)

Switzerland
Valais, St. Bernard, Amann 19 July 1932 as _H. cochlearifolium_.
(S-PA)
Valais, Mt. Mora, Culmann Aug. 1886 as _H. goulardii_. (S-PA)
Bern, Faulhorn, Culmann 16 Aug. 1885 as _H. goulardii_. (H)

Austria
Tirol, Glungezer Nordseite, Schiffner 4 Sept. 1903. (S-PA)
Karnten, Follach, Breidler 6 Aug. 1861 as _H. goulardii_ (S-PA, H)
Steiermark, Schladming, Breidler 20 Aug. 1882 as _H. cochlearifolium_.
(H)
Salzburg, Sulzbachthal, Breidler 13 Aug. 1890 as _H. goulardii_. (H)

Italy
Tirol Italiano, Saent, Venturi, Erbar, Critt, Ital. ser. 2 n. 453 as _L. cochlearifolium_. (NY)

Spain
Gallia merid. Maladetta, Goulard 1873 as _H. goulardii_. (BM)

Poland
Montes Tatri, Lisowski 1 Sept 1957 as _H. cochlearifolium_ and
Bryotheca Polonica # 638. (CAN)

Czechoslovakia
Vysoke Tatry, Mlynica, Pllous 263 as _H. cochlearifolium_. (CAN)
Hygrohypnum norvegicum (Schimp.) Amann, Fl. Mouss. Suisse 1:188 et 2: 358. 1912.

(Holotype, S-PA)

Hypnum norvegicum (Schimp.) Schimp., Syn. 637. 1860.

Amblystegium viridulum Lindb., Musci Scand. 33. 1879.


Plants forming small, soft, loosely to tightly woven tufts or patches. Color usually shiny, pale yellow-green, occasionally becoming a light brown with age. Stems 1 to 3 cm long, usually less than 1.5 cm, prostrate or with the tips slightly ascending. Branching irregular, branches 1.0 - 1.2 (1.5) cm long, ascending. Stem cross-sections revealing 2 to 3 rows of small, thick-walled, brownish cortical cells; medullary cells larger and thinner-walled; central strand present, often discolored. Rhizoids variable, red-brown, sparse, arising from the base of ventral stem leaves.

Leaves ovate, rarely broadly ovate; (0.4) 0.5 - 0.8 (0.9) mm long X (0.2) 0.4 - 0.5 (0.6) mm wide; apex usually acute, occasionally obtuse in the more broadly ovate leaves; sometimes the apex may be slightly squarrose; margins entire, variably plane or rarely very narrowly recurved, recurvature variable, but never excluding the leaf apex, recurvature may be confined to the lower 1/4 of the leaf or may occur throughout the margin exclusive of the apex; leaves plane to shallowly, but clearly, concave; costa short and double, one arm often reaching midleaf, very rarely slender and single to just above mid-
leaf. Leaf attitude upon the stem varying from the wet to dry conditions; when wet the leaves are straight and loosely imbricated to loosely spreading, very rarely they may be slightly falcate; when dry the leaves tend to become crisped, usually shrinking laterally and concomitantly inrolling or twisting.

Areolation variable; median leaf cells short rhombic, bacilliform, fusiform or linear flexuose, (16) 20 - 30 (48) mm long X 5 - 6 mm wide; cells decreasing slightly in length toward the apex; marginal leaf cells always less than 50 μm; basal cells variable, gradually elongating and widening from the median cells, or widening slightly, but changing little in length, or changing little in length or width, hyaline or becoming slightly golden-brown with age; pits few to none; alar cells undifferentiated or forming a small irregular group of a few, quadrate to short rectangular, slightly incrassate cells, hyaline or becoming brown with age.

Plants monoicous. Perigonia ovate; perigonial leaves ovate, 0.2 to 0.6 mm long, deeply concave imbricated, ecostate, margins entire. Outer and middle perichaetial leaves ovate to ovate lanceolate, squarrose-reflexed in the apex, ecostate to short single or short and double, margin entire. Inner perichaetial leaves lanceolate, erect, up to 1.8 mm long, apex gradually tapering to a point or acute, costa variable single and slender or double, reaching midleaf, 2 to 4 plicae, cells from the base to midleaf pitted, margins entire to very finely and irregularly toothed.

Seta 6 to 10 mm long, yellow to reddish-brown, smooth-walled, straight or slightly curved when wet, variously twisting and contorting upon drying. Capsule as in the genus.

Peristome as in the genus. Annulus of two cell rows. Spores dark, dusky-yellow, 9 to 17 um in diameter. Endostome with 2 to 3 well developed cilia, often falling away.
In spite of a monographic study, *Hygrohypnum norvegicum* remains a poorly understood species. There are just too few specimens of this taxon from which to generate a sound concept of its variability.

In combination, four characters may serve to distinguish *Hygrohypnum norvegicum*. These characters are the very tiny leaf size, the ovate leaf shape, the acute leaf apex and the loosely spreading nature of the moist leaves.

In his original description Schimper (1853) remarked upon the similarities and differences between *L. norvegicum* and what is now known as *Hygrohypnum luridum*. Later, he (Schimper, 1876) noted the similarity of *H. norvegicum* and *H. molle*, as did Limpricht (1904). From the present studies it seems entirely unlikely that *H. norvegicum* could be confused with either *H. luridum* or *H. molle*. The following chart may serve to clarify the situation.

<table>
<thead>
<tr>
<th></th>
<th><em>H. norvegicum</em></th>
<th><em>H. molle</em></th>
<th><em>H. luridum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Length</td>
<td>0.4 to 0.9 mm</td>
<td>0.9 to 2.0 mm</td>
<td>0.9 to 2.5 mm</td>
</tr>
<tr>
<td>Leaf Apex</td>
<td>Acute</td>
<td>Acute and blunt</td>
<td>Gradually tapering to a point.</td>
</tr>
<tr>
<td>Leaf Apex Margin</td>
<td>Entire</td>
<td>Denticulate or entire</td>
<td>Entire</td>
</tr>
<tr>
<td>Leaf Margins</td>
<td>Plane to variously recurved</td>
<td>Plane</td>
<td>Plane to inrolling in the upper 1/2:</td>
</tr>
<tr>
<td>Alar cells</td>
<td>Undifferentiated or small group of quadrate to short rectangular cells.</td>
<td>Undifferentiated</td>
<td>Well-developed group of quadrate to short rectangular cells.</td>
</tr>
</tbody>
</table>

The very smallest leaves of *H. luridum* may overlap in size with the very largest leaves of *H. norvegicum*. However, the differences mentioned above will clearly separate them.
In Europe and North America leaf length may be used as a general criterion for distinguishing *Hygrohypnum molle* from *H. norvegicum*. In Europe the average leaf length for *H. molle* is 1.2 to 1.7 mm and very few leaves have ever been observed exhibiting shorter lengths. In Western North America the average leaf length for *H. molle* is 0.9 to 1.3 mm and it is, therefore, understandable that various reports of *H. norvegicum* from south of 60°N. have been based upon misdeterminations of *H. molle*. The specimen of *H. norvegicum*, which effects the remarkable disjunction of the species from Alaska into southern British Columbia, clearly differs from *H. molle* by its entire, recurved leaf margins and its very short leaves (0.7 mm).

The specific limits between *Hygrohypnum norvegicum* and *H. cochlearifolium* are weak. Both taxa tend to merge as a consequence of similar patterns of variation in leaf dimensions, leaf concavity, leaf marginal recurvature and the nature of the leaf apex. The following chart will point out the general differences.

<table>
<thead>
<tr>
<th></th>
<th><em>H. norvegicum</em></th>
<th><em>H. cochlearifolium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Length</td>
<td>0.4 to 0.9 mm</td>
<td>0.8 to 1.5 mm</td>
</tr>
<tr>
<td>Leaf Shape</td>
<td>Ovate</td>
<td>Broadly ovate to almost orbicular</td>
</tr>
<tr>
<td>Leaf Apex</td>
<td>Acute</td>
<td>Obtuse</td>
</tr>
<tr>
<td>Leaf concavity</td>
<td>Plane to Shallow</td>
<td>Deeply concave to cochleariform</td>
</tr>
<tr>
<td>Leaf margins</td>
<td>Plane to recurved</td>
<td>Recurred to plane</td>
</tr>
</tbody>
</table>

The leaves of *H. norvegicum* are generally loosely imbricated to slightly spreading. The leaves of *H. cochlearifolium* may also be loosely imbricated, but in very small specimens, which are most readily confused with *H. norvegicum*,
the deep leaf concavity imparts a distinctly tumid appearance to the plants. The leaf apices of *H. norvegicum* are almost always acute. The leaf apices of *H. cochlearifolium* are generally obtuse, but in small specimens certain leaf apices may be acute.

Schimper (1853) described *Limnobium norvegicum* based on a Blytt specimen from Gulbrandsdalen, Norway. Nyholm (1965) offered two sets of illustrations of *H. norvegicum*, one of which was ascribed to the Blytt type. In personal communications Nyholm remembered that the Blytt specimen was in the Schimper collection at BM. A thorough search of the BM material has not yielded the Blytt specimen. Hartmann (1849) described *Hypnum viridulum*. Hartmann's species is the same taxon as *Limnobium norvegicum*, however, it is a later homonym of *Hypnum viridulum* Brid. The Hartmann type, at S-PA is a Holmgren specimen from Sarkevare, Lule Lappmark, Sweden. The second set of illustrations cited by Nyholm (1965) for *Hygrohypnum norvegicum* was based on the Hartmann type. A careful study of all the available descriptions and specimens has shown that I completely agree with Nyholm's treatment of the Scandanavian material. Based on my agreement with her work, I can only assume that she accurately assessed the conspecificity of the Schimper and Hartmann types. I have accordingly based my concept of *Hygrohypnum norvegicum* on the Hartmann type.
Fig. 43 a – j. Variation in the leaf shape, the cellular detail of the foliage leaves and the habit of the shoots of *Hygrohypnum norvegicum*.  

a – d. Leaf shape  
e – f. The habit of the moist shoots.  
g – h. Leaf apicies  
i. Alar cells  
j. Median leaf cells  

Scale:  
a – e; [0.5mm]  
e – f; Both shoots are approximately 0.5 cm long.  
g – j; [100um]
Fig. 44. *Hygrohypnum norvegicum*
Selected Specimens Examined

Canada

British Columbia
Salmo area, Porcupine Creek; Jamieson # 5598. (UBC)

United States
Alaska
Mt. McKinley National Park, trail above Riley Creek; Croasdale B-23. (USA)

Greenland
Scoresby Sund, Rypefjord; Holmen 18767 as Hygrohypnum viridulum. (NY)

Norway
Lille Elvedal, Teadfaler lac a Gronne Grotto; Kaurin Aug. 1892 as Hypnum viridulum. (S-PA).
Lille Elvedal, prope Fladfater, "Gronne Grotto"; Kaurin Aug. 1888 as Hypnum viridulum. (S-PA)
Dovre, Knudhoe; Bryhn Aug. 1887. (S-PA)
Dovre, Zetterstedt 11 July 1854. (C, S-PA)
Lille Elevedal, Gronne Grotto; Kaurin Aug. 1887. (S-PA)

Sweden
Norbotten, Overtornea; Lonnqvist 22 Aug. 1963 as Hygrohypnum norvegicum. (S-PA)
Jamtland, Undersakers s; n Sylarna; Krusenstjerna 12 July 1938 as Hypnum viridulum. (S-PA)
Pite Lappmark, Arjeplog sn, Lul. Istjakk; Wistrand 2 July 1936 as Hypnum viridulum. (S-PA)
Lulea Lappmark, Sarkavaare; Holmgren June 1848; cited as Amblystegium viridulum. (Holotype for Hypnum viridulum, S-PA)
Lulea Lappmark, St. Sjofallet; Holmgren 9 July 1867. (S-PA)
Lapponia Lulensis, Sareks; Jensen & Arnell 3 Aug. 1902 as Amblystegium viridulum. (C, S-PA)

Finland
Lapp. ov., In alpe Schelesnaja prope pagu Kantalaks; Brotherus 29 July 1872. (H-SOL)

Austria
Steiermark, Schladming; Breidler 27 Aug. 1869 as Limnobium sp. (BP)
Hygrohypnum molle (Hedw.) Loesk., Moosfl. Harz. 320. 1903.

Neotype: Scotland, Ben Mac Dhui, by streamlets from perpetual snow:

G. E. Hunt, July 1871. (S-PA)

Hypnum molle Hedw., Spec. Musc. 273. 70f. 7 - 10. 1801.


1807.

Hypnum molle var. rigidulum Hartm., Handb. Skand. Fl. ed. 5:324.

1849. nom. illeg. incl. type spec.


1331. 1863. nom. nud.

Hypnum Schimperianum Lor., Moostud. 123. 5c. 1864. (Holotype, G)

Hypnum taurense Mol. in Lor., Moostud. 123. 1864. nom. nud. in synon.

Hypnum alpestre var. turgescens Lor., Moostud. 123. 1864. nom. nud.

in synon.

Hypnum molle var. schimperianum (Lor.) Schimp., Syn. ed. 2:775. 1876.


Amblystegium molle (Hedw.) Lindb., Musci Skand. 33. 1879.

Amblystegium molle var. schimperianum (Lor.) Lindb., Musci Skand. 33. 1879.

Hypnum dilatatum ssp. molle (Hedw.) Ren., Rev. Bryol. 10:51. 1883.

Hypnum molle var. maximum Boul., Muscin. France 24. 1884.


10:8. 1901.
Hypnum bestii var. pyreniacum (Ren.) Ren., Rev. Bryol. 28:8. 1901.

Hygrohypnum molle var. schimperianum (Lor.) Loesk., Hedwigia 49:52. 1909.

Hygrohypnum molle var. pyreniacum (Ren.) Podp., Consp. 576. 1954.

Plants soft, in loosely to tightly woven mats or patches. Color variable, bright yellow-green, olive-green, yellow-green or golden variegated yellow-green above, yellow-brown, golden-brown or brown below, usually yellowish-green, olive-green, occasionally bright-green throughout; stems (1) 3 - 7 (10) cm long, procumbent. Branches irregular, very widely spaced, often attaining the length of the main stem, especially within radially symmetrical patches, or branches short and ascending from prostrate stems. Stems usually leafy throughout, infrequently the lower 1 or 2 cm of old stems may be denuded. Stem cross-sections with 2 to 3 rows, occasionally and incomplete fourth rows, of yellow to reddish-brown, small, thick-walled cortical cells; medullary cells larger, thinner-walled though sometimes becoming incrassate and discolored with age; central strand weakly to strongly differentiated, often discolored. Rhizoids red to reddish-brown, arising from the base of ventral stem leaves, but of irregular occurrence.

Leaves variable; closely spaced to distant, especially on young branch tips. Attitude on the stem little different from the wet to the dry condition; loosely imbricate or slightly spreading. Leaves straight, rarely slightly secund, young branch leaves sometimes slighted twisted at the apex when dry. Leaves broadly ovate, rarely ovate or almost orbicular, generally tapering gradually to an acute, but blunt apex, (0.8) 1.0 - 1.75 (2.0) mm long X (0.6) - .75 - 1.2 (1.25) mm wide; margin variable, entire, undulate or finely
denticulate in the upper half, especially in the apex, margins sometimes slightly recurved at the insertion point; shallowly to deeply concave; narrowly or hardly at all decurrent; costa variable, usually short and double with slender arms, the longest arm reaching midleaf or slightly beyond, or double with both arms reaching midleaf, rarely single to midleaf and/or forked.

Areolation rather uniform; Median leaf cells rhomboid to linear fusiform flexuose, thin-walled, (24) 32 - 52 (74) mm long X (3) 5 - 6 (8) mm wide, it is not uncommon for unusually long or short cells to occur in leaves with an otherwise long or short areolation; usually little change from the median to the apical cells, but in some leaves the apical cells become short rhombic to short fusiform; marginal cells in the upper half of the leaf 15 to 60 um long, usually 30 to 50 um. cells reaching 60 um are rare; basal cells becoming longer or shorter, slightly wider, slightly more incrassate, pits few to none, discolored or not at all; alar cells undifferentiated or a few slightly incrassate, unpitted quadrate to short rectangular cells, hardly different from surrounding cells, rarely discolored.

Plants autoicous; perigonial leaves ovate with an apiculate apex, deeply concave and ecostate; outer perichaetial leaves ovate, tapering to an acute apex, up to 1.1 mm long, weakly short double costate; inner perichaetial leaves linear lanceolate, 2.0 to 3.5 mm long, 2 to 4 long plicae, costa absent, faint and double, or single to midleaf; apex acute or obtuse, certain cells on the abaxial surface of the leaf apex bearing a few papillae formed by overriding distal endwalls.

Seta 6 to 15 mm long, usually 7 to 11 mm, orangish-red, reddish-brown to deep maroon, smooth, straight when wet variously, twisted when dry; Capsule as in the genus; Annulus of 2 to 3 rows of deciduous cells.
Peristome as in the genus; Endostomal cilia rudimentary or wanting; Spores smoky brown, finely papillose, 12.5 to 18.7 um in diameter, usually 14.6 to 16.6 um.

*Hygrohypnum molle* can be distinguished from other species in the genus by 1. the broadly ovate, concave leaves (Fig. 45 a & b), which generally taper into an acute, but blunt, and often denticulate apex (Fig. 46 a & b), 2. the undifferentiated alar cells (Fig. 46 f & h) and 3. the inner perichaetial leaves in which the cells on the abaxial surface of the leaf apex are papillose by means of overriding distal endwalls (Fig. 46 d).

*Hygrohypnum molle* does exhibit some variation with respect to growth habit, leaf shape and size, toothing of the leaf apex and leaf concavity.

Throughout Europe and in some specimens from North America *Hygrohypnum molle* forms loosely woven tufts or patches in which the stems branch at irregular intervals and the branches quickly grow to lengths close to the lengths of the stems. On the other hand, most North American specimens, especially those from Southern British Columbia and adjacent Washington, form tightly woven, but soft patches or mats in which branching is irregular and both branches and stems are short and more or less ascending.

Leaf shape is generally broadly ovate (Fig. 45 a & b). Certain specimens may exhibit ovate (Fig. 45 c) or almost orbicular leaves (Fig. 45 d & e). Leaf concavity is usually more evident in the more orbicular leaves.

Throughout the entire range of *Hygrohypnum molle* the leaf length varies more or less continuously from 0.8 to 2.0 mm. Lawton (1971) noted that leaves of North American plants were slightly smaller than those of European specimens. The present study has borne out those observations. In Europe the average leaf length varies from 1.2 to 1.7 mm, whereas in North America, and especially in British Columbia and Washington, the average length is 0.9 to 1.3 mm. The
very largest leaves from North American plants have not been observed to exceed 1.5 mm.

The leaf apex is generally described as acute, but blunt and finely denticulate (Fig. 46 a). However, it may vary from acute to obtuse and coarsely denticulate to entire.

Concavity seems to vary somewhat, relative to leaf shape. There is a tendency for large ovate leaves to be shallowly or not at all concave, whereas broadly ovate leaves are deeply concave. However, the correlation is not absolute.

The costa is generally short and double, however, it may vary from double with one arm reaching midleaf or beyond, double with both arms reaching midleaf or beyond or single and/or forked to midleaf or beyond.

The early works of Bridel (1812, 1827), Sprengel (1827) and Hampe (1837) noted a similarity between *Hygrohypnum molle* and *H. alpestre*. Further, Schimper (1853) illustrated *H. alpestre* with a drawing of *H. molle*. Both of these species have straight, concave leaves that are loosely imbricated or with the shoots sometimes julaceous. At the apex of some stems and branches the young leaves are so crowded that the stem or branch apex appears obtuse. Though these characters reflect a common bond within the genus, they mask very fundamental differences at the species level.

The following chart will illustrate the important differences.
<table>
<thead>
<tr>
<th></th>
<th><strong>H. molle</strong></th>
<th><strong>H. alpestre</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leaf shape</strong></td>
<td>Broadly ovate</td>
<td>Oblong or oblong lanceolate.</td>
</tr>
<tr>
<td><strong>Leaf apex</strong></td>
<td>Acute but blunt, plane</td>
<td>Apiculate and reflexed</td>
</tr>
<tr>
<td><strong>Concavity</strong></td>
<td>Shallowly to deeply so</td>
<td>Deeply so, often quite boat shaped in the apex.</td>
</tr>
<tr>
<td><strong>Alar cells</strong></td>
<td>Essentially undifferentiated.</td>
<td>Large group of quadrate cells.</td>
</tr>
<tr>
<td><strong>Median leaf cells</strong></td>
<td>Usually 32 to 52 um long</td>
<td>Usually 65 to 90 um long</td>
</tr>
<tr>
<td><strong>Inner perichae­tial leaves</strong></td>
<td>Apex coarsely denticu­late and papillose</td>
<td>Apex long tapering, entire, smooth.</td>
</tr>
</tbody>
</table>

Ill founded concepts of *Hygrohypnum molle* and *H. duriusculum* have long caused confusion between these two clear-cut taxa. The following chart will perhaps clarify the differences.

<table>
<thead>
<tr>
<th></th>
<th><strong>H. molle</strong></th>
<th><strong>H. duriusculum</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Leaf Shape</strong></td>
<td>Broadly ovate, gradually tapering to an acute but blunt tip.</td>
<td>Oblong-elliptic to broadly ovate, more abruptly tapered to an obtuse, broadly acute or apiculate apex.</td>
</tr>
<tr>
<td><strong>Alar cells</strong></td>
<td>Undifferentiated</td>
<td>Well developed groups of quadrate, incrassate, discolored cells.</td>
</tr>
<tr>
<td><strong>Stem cross section</strong></td>
<td>2 to 3 rows of small incrassate cortical cells</td>
<td>3 to 4 rows of small, incrassate cortical cells.</td>
</tr>
<tr>
<td><strong>Inner perichae­tial leaves</strong></td>
<td>Apical cells papillose by distally overriding endwalls.</td>
<td>Apical cells smooth</td>
</tr>
<tr>
<td><strong>Inner peristome</strong></td>
<td>Endostome smooth, cilia rudimentary.</td>
<td>Endostome finely papillose with well developed cilia.</td>
</tr>
</tbody>
</table>
Hygrohypnum molle and *H. cochlearifolium* have a number of common features. Both plants are quite soft, although *H. cochlearifolium* is the softer of the two. The leaves of both are generally loosely imbricate to slightly spreading (Fig. 45 f & g with Fig. 40 l). The leaves of *H. molle* are generally broadly ovate and shallowly concave, but certain specimens may exhibit broader leaves with a deeper concavity (Fig. 45 d & e) that are more comparable with *H. cochlearifolium* (Fig. 13 d). Both taxa frequently exhibit a similar pattern of golden-brown mottled coloration. The costa morphology is similar and has already been pointed out in the discussion of *H. cochlearifolium*.

The two taxa may be distinguished from one another by the following features:

<table>
<thead>
<tr>
<th>Feature</th>
<th><em>H. molle</em></th>
<th><em>H. cochlearifolium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf Shape</td>
<td>Broadly ovate</td>
<td>Mostly oblong-elliptic to almost orbicular</td>
</tr>
<tr>
<td>Leaf Length</td>
<td>0.8 to 2.0 mm</td>
<td>0.5 to 1.5 mm</td>
</tr>
<tr>
<td>Leaf Margins</td>
<td>Plane; denticulate to entire</td>
<td>Usually recurved, sometimes plane; entire or weakly crenulate</td>
</tr>
<tr>
<td>Leaf Apex</td>
<td>Gradually tapering to an acute but blunt point</td>
<td>Apex broadly rounded obtuse</td>
</tr>
<tr>
<td>Leaf Concavity</td>
<td>Shallow</td>
<td>Very deep to cochleariform</td>
</tr>
<tr>
<td>Alar Cells</td>
<td>Undifferentiated</td>
<td>Undifferentiated or a few quadrate cells</td>
</tr>
<tr>
<td>Endostome</td>
<td>Cilia rudimentary or wanting</td>
<td>Cilia 2 to 3</td>
</tr>
<tr>
<td>Perichaetal</td>
<td>Apex coarsely denticulate; margins plane; apical cells papillose</td>
<td>Apex entire; margins recurved; apical cells smooth, rarely 1 or 2 papillae</td>
</tr>
</tbody>
</table>
As an autoicous species the presence of antheridia and archegonia on the same individual would theoretically enable H. molle to freely reproduce sexually. If the number of herbarium specimens bearing sporophytes is a reasonable measure of a species fecundity, then it appears that Hygrohypnum molle reproduces sexually very infrequently. Barely ten percent of the several hundred specimens studied bear sporophytes and the majority of fertile specimens are from Western North America.

At the inception of this study four subspecific taxa were recognized for Hygrohypnum molle (Wijk et al., 1962). Hygrohypnum molle ssp. bestii (Ren. et Bryhn) Broth. is treated here as a species. Sakurai (1932) described H. molle var. japonicum. Examination of the holotype from the Makino Herbarium has revealed that the plant is only a form of Hygrohypnum ochraceum.

Hygrohypnum molle var. pyreniacum (Ren.) Podp. was described by Renauld in two slightly varying descriptions in the Academe de Geographie Botanique Bulletin Vol. 10 and Revue Bryologique Vol. 28 in 1901. Renauld remarked upon the similarity of the plant to Hypnum bestii. A specimen whose label bears the data given by Renauld for the type specimen is at NY. It seems likely that this specimen is a duplicate of the type that Renauld may have sent to J. M. Holzinger. Examination of the plant reveals that it is a moderately large specimen of H. molle. It does not have the very long marginal leaf cells that would otherwise align it with H. bestii.

Lorentz (1864) described Hypnum molle var. schimperianum. At G (Sheet 3079/247) there is a specimen agreeing with the collecting information indicated by Lorentz. A careful examination of this specimen reveals that it is not sufficiently different from other specimens of Hygrohypnum molle to warrant taxonomic recognition.

Although the principle of priority credits Hedwig with the authorship of
Hygrohypnum molle (Hedw.) Loesk., it is clear that he based his concept on Hypnum molle Dicks. Similarly, Schimper (1853) based his concept of Limnobium molle, in part, on Dickson's concept. The type locality as given by Hedwig (1801) is "ad rivulorum ripas in alpibus Scotius." Schimper (1876) narrowed the earlier heterogeneous concept of L. molle Schimp. by extracting Hypnum dilatatum and H. alpinum. The more restrictive concept was again equated with that of Hypnum molle Dicks. and several specimens were cited as the basis for the concept. Among the specimens was one collected by G. E. Hunt from Ben Mac Dhui in Scotland. At S-PA there are two specimens bearing these data and both specimens are equally representative of the concept of Hygrohypnum molle as perceived in the present study.

One problem in the typification of Hygrohypnum molle lies in the fact that the only specimen bearing the name Hypnum molle Dicks. in the Hedwig-Schwaegrichen herbarium at G. is a mixture of Hygrohypnum luridum (Hedw.) Jenn. and H. duriusculum (De Not.) Jamieson. That a specimen is in the Hedwig herbarium does not necessarily mean that Hedwig ever saw it. A comparison of the broadly ovate leaves of the troublesome specimen with Hedwig's type description of the leaves of Hypnum molle as "folia ovato-lanceolata" and an examination of Tab. LXX clearly reveals a lack of agreement. Therefore, this anomalous specimen from the Hedwig herbarium is rejected as representative of Hygrohypnum molle.

In the absence of any Dickson material or appropriate Hedwig material and based on a careful study of several hundred specimens bearing the names Hypnum molle and H. duriusculum I select the following specimen to serve as the neotype of Hygrohypnum molle (Hedw.) Loesk.:

Scotland, Ben Mac Dhui, by streamlets from perpetual snow.

Leg. G. E. Hunt, July 1871
ex herb. G. Stabler & ex herbario S. O. Lindberg.

At S-PA.
Fig. 45 a - g. Variation in the leaf shape and the habit of the shoots of *Hygrohypnum molle*.

a - e. Foliage leaves.

f - g. The habit of moist shoots.

Scale:

\[
\begin{array}{c}
  a - e; \quad [1\text{mm}]
  \\
  f; \quad \text{The shoot is approximately 0.6 cm long}
  \\
  g; \quad \text{The shoot is approximately 2 cm long}
\end{array}
\]
Fig. 46 a - h. Cellular detail of the foliage and perichaetial leaves of *Hygrohypnum molle*.

a - b. Foliage leaf apices

c & e. Marginal leaf cells

d. Perichaetial leaf apex

f & h. Alar cells

g. Median leaf cells

Scale:

a - b; \[ \text{100um} \]

c, e and g; \[ \text{100um} \]

d, f and h; \[ \text{100um} \]
Fig. 47. *Hygrohypnum molle*
Exsiccati Examined

Allen, Mosses of the Cascade Mtns., Washington.
   # 142 as H. arcticum. (MIN, NY, TENN, USA, DUKE)
Macoun, Canadian Mosses
   # 393 as H. pseudo-arcticum. (CANM)
   # 394 as H. arcticum. (USA)
   # 398 as Hypnum arcticum. (LE)
Bauer, Musci europaei exsiccati
   # 649 as Hygrohypnum schimperianum. (S-PA, BRNM)
   # 1663 as H. molle var. schimperianum. (CANM, S-PA)
Kerner, Flora Exsiccata Austro Hungarica
   # 1923 as Hypnum schimperianum. (BRNM, MIN, S-PA)
   # 1924. (BRNM, G, LE, MIN, MO, NY, UC, BP', C)
Lisowski, Bryotheca Polonica
   Fasc. XV # 418 as H. viridulum. (CANM)
   Fasc. XV # 419. (CANM, LE)
   Fasc. XXV # 669. (CANM)
   Fasc. XXV # 668. (LE)
   Fasc. XXXI # 824. (CANM, NICH)
Museo Hist Natur Vindobonensi, Cryptogamae exsiccati
   # 4260 as H. molle. (G, LE, NY)
   # 4362 as H. molle. (G, LE)
Museum Botanicum Universitatis Cluj, Flora Romaniae Exsiccati
   # 1411 as H. molle var. schimperianum. (MO, S-PA)
Zmuda, Bryotheca Polonica
   # 150. (S-PA)

Selected Specimens Examined

Canada
   British Columbia
      Mt. Seymour Provincial Park, 1st Pumph Peak; Schofield 15968 as H. alpestre. (CANM)
      Garibaldi Provincial Park, Whistler Ski Bowl; Jamieson 5486. (UBC)
      Vancouver Island, Strathcona Provincial Park, Burman Lake; Boas 254. (UBC)
      Gold Ranges; Macoun 10 Aug. 1889 as H. pseudo-arcticum in. Canadian Mosses # 393. (CANM)
      Rocky Mountains, Hector; Macoun 8 Aug. 1904 as H. arcticum in Canadian Mosses # 398. (CANM)
      Eagle Pass Mtns., near Revelstoke; Taylor 21 Aug. 1921 as H. dilatatum. (MICH, USA)

United States
   Washington
      Mt. Ranier National Park, Mt. Ranier; Allen 119 as H. arcticum in Mosses of the Cascade Mtns., Washington # 142. (NY, TENN, USA, MIN)

   Oregon
      Hood River Co., Cloud Capp Inn; Frye 29 Aug. 1907. (WTU)
      Mt. Hood; Roell 1140 & 1411. (NY)
California
Mono Co., H. M. Hall Natural Area, Spuller Lake; Catchende
47138. (MICH)
Eldorado Co., Echo Lake; Conard 5 Sept. 1947. (MICH)
Montana
Flathead Co., Sperry Glacier Trail, Akaiyan Falls; Hermann
20757. (NY, WTU)
Colorado
Larimer Co., Rocky Mountain National Park, Longs Peak;
Kiener 4113. (CANM, MICH)
Alaska
Juneau Icefield, Taku Anunatak; Ward 8-27-49-28 as H.
subeugyrium. (MIN)

Great Britain
Scotland
Ben Mac Dhui; Fergusson July 1873. (S-PA)
Ben Nevis; Boner 1870. (NY)
Ben Nevis; in the Red Burn; Dixon 11 July 1898. (NY)

Norway
Jotuukjeldene supra hospitium Gjendeboden; Kaurin Aug. 1891.
(S-PA)
Finnmarken, aunt Tanen Burkelium; Kaurin July 1895. (S-PA)
Norefjeld; Bryhn July 1900. (S-PA)
Knudshoe; Bryhn Aug. 1885. (S-PA)
Effes vagen Vidasoeter Groslli; Jensen 1 July 1937. (S-PA)
Opdal, in Monte Snehetta; Olsson 31 July 1885. (LE, NY)

Sweden
Harkedalen, par Tanass; Einander 3 - 4 Aug. 1891. (S-PA)
Jamtland, Kalls sn Lillanjeskutan; Hakelier 13 July 1966.
(S-PA)
Brannkyika; Clive 1857. (S-PA)

Finland
Lapp. rossit., Kipina; Angstrom. (S-PA)
Lapponia imandrau, Umptek; Kihlman 30 July 1892. (S-PA)
Kemi Lapp. Kolari; Kotilainen 11 Aug. 1927. (S-PA)
Lapponia murr., Litsa; Brotherus 3 June 1887. (NY)

Soviet Union
Lapponia murmanica, Sitsa, Kola; Brotherus Aug. 1887. (C, S-PA)

Germany
Matrei, Algau, Siegerlandhusse; Leg. 7 8 Aug. 1929. (BRNM,
accession number 08719)

France
Chamoix; Payot 1854. (G, 3079/210)
Mt. Blanc; Leg. ?. (G, 3079/208)
Valle de Barbarine, sur les Roches Seliceuses a Fontanabran;
Bernet 13 Aout 1903. (G, 3079/259)

Switzerland
La Fibbia, St. Gotthard; Weber 7 Aug. 1881. (G, 3079/228)
Valais, Grand St. Bernard, Combe des Morts; Rhodes 1705 as
H. molle. (NY)

Austria
Tirol, Innervillgarten; Ganders 15 Sept. 1881. (B, 1720/89)


Salisburgia, Montes Lanschitzbar prope Lessach; Breidler as Flora Exsiccata Austro-Hungarica # 1924. (G, 3079/205) Steiermark, Singsdorfer; Breidler 25 July 1887.

Italy
Genoa, rupes Fonalis; Lorentz 12 Aug. 1864. (S-PA)

Czechoslovakia
Vysoke Tatry, Furkota; Smarda 3 July 1957. (BRNM)

Poland
Montes Alti, valle Dolina; Lisowski 27 Aug. 1956 as Bryotheca Polonica # 419. (CANM)

Romania
Transylvania, distr. Hunedosra, In montes Retezal; Peterfi 24 July 1914 in Flora Romaniae Exsiccati # 1411. (S-PA)

Hypnum (Limnobium) styriacum Limp., Flora (Jena) 65:201. 1882.


Limnobium styriacum (Limpr.) Roth, Eur. Laubm. 2:638. 56 f. 2. 1905.

Names from the literature but not available for assessment:


Plants variously soft to slightly rigid, in loosely to tightly woven patches or mats. Color usually dull yellow-green with a rusty mottling, less often a dirty brownish yellow-green or a uniform dull green. Stems 1 - 4 (6) cm long; variously foliose, either foliose throughout or denuded in the lower portions, especially in the very long stems; stems mostly prostrate, sometimes somewhat ascending. Branching irregular. Sparsely radiculose. Stem cross-sections revealing 2 to 3 rows of small, thick-walled cortical cells; medullary cells gradually becoming larger toward the middle, often becoming thicker-walled and discolored with age; central strand well developed.

Leaves variously disposed along the stem, decidedly distant to slightly crowded, crowding often more evident near the stem and branches apicies. Attitude variable from the wet to dry condition; when wet the leaves are spreading all around the stem, less often slightly falcate; upon drying the leaves shrink laterally to a marked degree, often concomitantly twisting in various attitudes, either spreading, especially so in smaller branches, spreading, weakly imbricated, particularly near stem and branch apicies or
falcate; Leaf shape quite uniform, ovate with an abruptly or gradually acuminate apex, usually straight, or slightly falcate, in which case the apex usually tapers gradually; apex is sometimes sharply reflexed; Leaves (0.7) 1.0 - 1.75 (2.0) mm long X (0.3) 0.5 - 1.0 (1.1) mm wide; margins entire; conspicuously broadly concave when wet; very weakly decurrent or not at all; cortical stem cells often adhere to the leaf base; costa strong and thick, short and double, single and/or forked, or infrequently single to above the middle.

Areolation quite uniform, median cells generally short, variously rhombic, short fusiform or bacilliform; thick-walled (18) 28 - 40 (50) μm long X (4) 5 - 7 (9) μm wide; little changed toward the apex; cells varying toward the base, those cells nearer the costa becoming longer and narrower toward the base, those cells near the margin becoming shorter and broader, these tendencies are general, however all cells become thicker-walled toward and within the leaf base; alar cells variable, but never sharply delimited, undifferentiated or recognizable as a small group of quadrate or short rectangular cells grading imperceptible into other basal or lower median cells.

Plants pseudo-paroicous; perigonia and perichaetia clustered into aggregations and subtended by common bracts; a single perigonium is situated immediately beside a single perichaetium or between 2 to 4 perichaetia, in all cases the perigonal-perichaetial complex is enclosed within 2 to 3 small bracts; the entire complex is borne in the axil of a vegetative leaf; common bracts are broadly-ovate with a rounded or 1 to 3 lobed apex; perigonal leaves are ovate to ovate-lanceolate, the apex is often abruptly acuminate like the foliage leaves, ecostate, areolation becoming rather incrassate and distorted, margins entire or very finely serrulate, 0.4 to 0.6 mm long; outer and inner perichaetal leaves differing in little but size, linear-lanceolate, variously ecostate
or faintly single costae, deeply plicate-sulcate, margins entire or very irregularly toothed, leaves up to 2 mm long.

Seta 9 to 21 mm long, variously red to reddish-yellow, smooth, straight or slightly inclined when wet, twisting to the left and becoming variously contorted upon drying. Annulus deciduous, of 1 or 2 rows of cells. Capsule as in the genus.

Peristome double; as per the genus; Endostome with 2 to 3 cilia, which are sometimes poorly developed. Spores smoky yellow, finely papillose, 12 to 23 um in diameter.

As noted by Limpricht (1882) the most unique feature exhibited by H. styriacum is the pseudo-paroicus sexuality. In the absence of sexual reproductive structures the species may be recognized by a combination of characters which include leaf shape, the nature of the leaf apex, the alar differentiation and the structure of the costa.

The leaves are basically ovate, but the apex is normally abruptly tapered to an acuminate point (Fig. 48 a - h). The alar cells are undifferentiated or exist as a few short rectangular cells (Fig. 49 f & g). The costa is short and double or single to slightly beyond midleaf. In leaves of comparable size the costa of H. styriacum is stouter than those of H. luridum.

Although Hygrohypnum styriacum (Limpr.) Broth. is a distinctive species, it is regularly confused with H. luridum and in Pacific Coastal North America it often is mistaken for H. norvegicum. Grout (1931) remarked that "H. styriacum (Limpr.) Broth. is regarded by Limpricht himself as a subspecies of H. palustre and I have been unable to differentiate American plants referred to it from forms of palustre." It is obvious that Grout could not distinguish the two taxa. However, I have seen no literature corroborating the assertion ascribed to Limpricht.
When sex organs are available for examination the unique perigonial-perichaetial complex of *Hygrohypnum styriacum* is clearly different from the autoicous condition present in *H. luridum*. Further, careful dissection of operculate capsules of *H. styriacum* will reveal an annulus at the base of the peristome. *Hygrohypnum luridum* does not possess an annulus.

In the absence of sex organs and sporophytes *Hygrohypnum styriacum* and *H. luridum* may be distinguished through the contrasting gametophytic characters presented in the following chart.

<table>
<thead>
<tr>
<th>Leaf Shape</th>
<th><em>H. styriacum</em></th>
<th><em>H. luridum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Ovate with an abruptly tapered acumen.</td>
<td>Usually lanceolate or oblong lanceolate with a slight apiculus.</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Alar Cells</th>
<th>Little different from other basal cells or a few quadrate or short rectangular cells.</th>
<th>Well defined group of quadrate to short rectangular cells.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Median Leaf Cells</td>
<td>Usually 28 - 40 μm</td>
<td>Usually 30 - 55 μm.</td>
</tr>
<tr>
<td>Costa</td>
<td>Stout</td>
<td>Slender</td>
</tr>
</tbody>
</table>

The abruptly narrowed acumen in *H. styriacum* varies in a number of ways. In some cases it is squarrose (Fig. 48 j), in others it may be straight (Fig. 48 i), or it may be decidedly turned to one side imparting a slightly falcate appearance to the leaves (Fig. 48 j & k). In some cases the apex is more gradually tapered and such leaves are usually decidedly falcate. In general, however, the leaves are usually straight. Upon drying, the apex tends to roll up and twist, thus acquiring a filiform appearance (Fig. 48 i).

Specimens of *Hygrohypnum styriacum* exhibiting slightly or decidedly falcate leaves may be confused with the falcate forms of *H. luridum*. In falcate forms of *H. luridum* the alar cells are frequently excavated, a condition never observed in *H. styriacum*. 
Hygrohypnum norvegicum is best distinguished from H. styriacum on the basis of its ovate leaves, which have acute apicies.

The attitude of the leaves upon the stem and the length of the internodes may vary. In general, moist leaves are more or less straight and loosely imbricate (Fig. 48 i). In the imbricated condition the leaves are close together. Often the internodes are long in specimens with spreading leaves. Those specimens with falcate leaves are also generally imbricate (Fig. 48 j & k).

A number of earlier authors reported observations on certain features of Hygrohypnum styriacum for which this study has revealed greater variability than previously known or that or are different from present observations. Limpricht (1904) noted that the common bracts subtending the perigonial-perichaetial complex were 2 to 3 lobed. I have found them to vary from entire to 3 lobed. Limpricht (1904) also noted that the inner perichaetial leaves were broadly costate. Roth (1905), on the other hand, said they were ecostate. Nyholm (1965) showed in an illustration (fig. 302) that they were strongly and broadly costate. This study has revealed that perigonial leaves and outer perichaetial leaves are ecostate, whereas middle and inner perichaetial leaves may be ecostate or weakly to strongly single costate. Limpricht (1904) described the stems of H. styriacum as filiform. I have found the species to be no more slender than other Hygrohypna. Limpricht (1904) and Roth (1905) described the inner peristome teeth as not being cracked along the midline. I have found them to be irregularly cracked. Monkemeyer (1927) described the spores as smooth walled, when, in fact, they are very densely papillose.

In the original description Limpricht (1882) cited four specimens collected by Bréidler as the basis for the species. However, he did not designate a holotype from among these specimens. I have seen all of the cited specimens and a number of their duplicates. Of these specimens I have selected the following
specimen from the Limpricht herbarium at BP as being most representative of the species and designate it as the lectotype: Leg. J. Breidler 1 Sept 1880, Abhang am Schiedek die Patzenalm bei Schladming ca 2800 m. There is a slight discrepancy between the citation of this specimen in the original description and the data borne on the label. The citation in the description says "Nordabhand des........" and makes no mention of the proximity to Schladming.
Fig. 48 a - k. Variation in leaf shape and shoot habit of *Hygrohypnum styriacum*.

a - h. Variation in leaf shape.

i - k. Variation in the habit of the shoot in the moist condition.

Scale:

a - h; [1mm]

i - k; Each shoot is approximately 1 cm long.
Fig. 49 a–g. Cellular detail of the foliage leaves of *Hygrohypnum styriacum*.

a. Leaf apex.
b and d. Median leaf cells.
c and e. Marginal leaf cells.
f and g. Alar cells.

Scale:

a, f and g; [100um]

b – e; [100um]
Fig. 50. *Hygrohypnum styriacum*
Exsiccati Examined

Bauer, Musci europ. et amer. exsiccati # 1790. (BRNM, S-PA)
Lisowski, Bryotheca Polonica
  Fasc. XXIV; # 636. (BP, CANM, S-PA, LE, NICH)
  Fasc. XXV, # 666. (BP, CANM, S-PA, LE)
  Fasc. XXXI, # 823. (BP, CANM, S-PA, LE, NICH)

Selected Specimens Examined

Canada

British Columbia
  Garibaldi Provincial Park, Sentinal Glacier at the E. end of Garibaldi L; W. B. Schofield 32918. as Hygrohypnum luridum. (UBC)
  Garibaldi Provincial Park, Whistler Mtn. Ski Area; D. W. Jamiesson # 5472. (UBC)
  Vancouver Is., Strathcona Provincial Park, Golden Hinde; Boas 297 as Hygrohypnum luridum. (UBC)
  Selkirk Mtns., Zincton, Rambler Mine; F. A. MacFadden 3880 as Hygrohypnum palustre (UBC)
  Kitchener Krag; Boas 1960 as Hygrohypnum palustre. (UBC)
  Zincton, Lucky Jim Mine; F. A. MacFadden 3864 as Hygrohypnum palustre. (UBC)
  Wilmer, near Windemere, Paradise Mine; F. A. MacFadden 3878 as Hygrohypnum palustre. (UBC)
  Sandon District, Rambler Mine; F. A. MacFadden 11 Sept.: 1927 as Hygrohypnum palustre. (MO, TENN)
  Eastern Pacific Coast District, Skagway (Alaska Quadrangle) Along the Haines Hwy, 83 miles NNW of Haines; F. J. Hermann 21843 As H. norvegicum. (USA)
  Paradise Mine; F. A MacFadden 1 Aug. 1928 as Hygrohypnum palustre (MO, UC)

Alberta
  Jasper National Park, Tonquin Valley; F. A. MacFadden 3875 as Hygrohypnum palustre (UBC)
  Bow River Watershed, S. tributary of Three Isle Creek. W. of Upper Kananaskis L.; Bird & Glenn 13826 as Hygrohypnum luridum. (UAC & UBC)
  Jasper National Park, Wilcox Falls; E. Whitehouse 25745 as Hygrohypnum palustre. (USA)
  Jasper National Park, N. of Sunwapta Pass Campsite; O. D. Bird 5232. as Hygrohypnum luridum (UAC)

United States

California
  ?; Kellog. (USA)
  Water courses near Summit; H. Bolander: 1864 - 1880. as Hypnum styriacum (NY)
  Trinity Co., Bullard's Basin; D. H. Norris 9287. as Hygrohypnum luridum (HSC)

Idaho
  Custer Co., Adair Creek; F. A. MacFadden 7 Aug. 1941. as Hyphnum palustre (CANM, MICH, NY, TENN, TRTC)
  Lemhi Co., 8 miles N. of ghost town of Gibbonsville; T. C. Frye 1 Sept. 1929 as Hygrohypnum ochraceum (WTU)
Montana
Glacier National Park, Hidden L. overlook-Logan Pass; F. J. Hermann 18094 as *Hygrohypnum luridum* (TENN)
Glacier National Park, Hanging Valley-Logan Pass; F. J. Hermann 18088 as *Hygrohypnum luridum* (NY)
Between forks of Cut Bank Creek; R. S. Williams 26 July 1897 as *Hypnum styriacum* (C, MO, NY)

Utah
On stream above Salt Lake; P. A. Evans 15 Aug. 1924 as *Hygrohypnum palustre* (NY)

Wyoming
Battle Lake Mtn.; A. Nelson 4202. (NY)

Norway
Sorfolden; M. Kotilainen 25 July 1922 as *Hygrohypnum styriacum* (C, S-PA)

Sweden
Lule Lappmark, Roveguaare, Kvikkjokk; Hulphers 12 July 1937 as *Hygrohypnum viridulum* (S-PA)

Austria
Tirol, Zunig bei Windisch-Matrei oberhalb.....?; J. Baumgartner 16 Sept 1905 as Musci europ. et-amer. exsiccati # 1790. (BRNM, S-PA)
Steiermark, Abhang am Schiedek die Patzenalm bei Schladming, ca. 2000 m; J. Breidler 1 Sept 1880. LECTOTYPE. (BP)

Pólańđ
Montes Tatri Alti, vallis Dolina; Lisowski 27 Aug. 1956 as Bryotheca Polonica Fasc. XXIV, # 636. (BP, CANM, S-PA)

Neotype: "In Suecia ad trabes molendinica"; Swartz (G, sheet 3079/156)

Hypnum luridum Hedw., Spec. Musc. 291. 1801. (Lectotype at G, sheet 3079/156)

Hypnum palustre Huds. ex Brid., Musci Rec. 2(2):117. 1801.

Hypnum molendinarium Lam et Cand., Fl. Franc. Ed 2, 2:358. 1805. (Lectotype at G)


Hypnum palustre var. aquatilis (Mart.) Brid., Bryol. Univ. 2:640. 1827.

Hypnum palustre var. ferrugineus (Brid.) Brid., Bryol. Univ. 2:641. 1827.

Hypnum palustre var. luridum (Hedw.) Hamp., Flora (Jena) 20:274. 1837.

Hypnum palustre var. subsphaericarpon Schwaegr. in Hamp., Flora (Jena) 20:274. 1837.


(Type at S-PA)


Hypnum roesei Schimp., Coroll. 131. 1856.

Hypnum palustre var. tenellum Schimp., Syn. 634. 1860.

Hypnum subeverve (Schimp.) Schimp., Syn. 634. 1860.

Hypnum palustre var. hamulosum (Schimp.) Schimp., Syn. 634. 1860.

Hypnum palustre var. julaceum (Schimp.) Schimp., Syn. 635. 1860.

Hypnum palustre var. laxum (Schimp.) Schimp., Syn. 634. 1860.


Amblystegium palustre (Brid.) Lindb., Musci Scand. 33. 1879.

Hypnum krauseii C. Mull., Flora (Jena) 70:219. 1887. (Holotype at S-PA)

Hypnum columbico-palustre C. Muell. et Kindb. in Macoun, Cat. Canad. Pl. 6:241. 1892.

Scleropodium krausei (C. Muell.) Macoun et Kindb. in Macoun, Cat. Canad. Pl. 6:203. 1892.

Hypnum pseudo-montanum Kindb. in Macoun, Cat. Canad. Pl. 6:243. 1892.


Brachythecium krausei (C. Muell.) Par., Ind. Bryol. 136. 1894.
Amblystegium palustre var. hamulosum (B.S.G.) Braithw., Brit. Moss. 3:60. 1898.
Hypnum palustre var. reesei (Schimp.) Roth, Hedwigia 38:265. 1899.
Hygrohypnum palustre (Hedw.) Loesk., Mossfl. Harz. 319. 1903.
Hygrohypnum palustre var. subsphaericarpon (Schleich. ex Brid.) Loesk., Moosfl. Harz. 320. 1903.
Hygrohypnum palustre var. julaceum (B.S.G.) Loesk., Moosfl. Harz. 320. 1903.
Hygrohypnum palustre var. laxum (B.S.G.) Loesk., Moosfl. Harz. 320. 1903.
Limnobium palustre var. tenellum (Schimp.) Roth, Eur. Laubm. 2:637. 1905.

Hygrohypnum palustre var. tenellum (Schimp.) Warnst., Krypt. Fl. Brandenburg 2:1060. 1906.


Hygrohypnum krausei (C. Muell.) Par., Coll. 16. 1909.

Hygrohypnum subenerve var. hamulosum Glow., Carnolia n. ser. 4: 143. 1913.


Hygrohypnum palustre var. subsphaericarpa (Schleich.) B.S.G. in Moenk., Susswassfl. 151. f52c. 1914.

Hygrohypnum palustre var. subsphaericarpa fo. julacea (B.S.G.) Moenk., Susswassfl. 151. f52d. 1914.


Hygrohypnum palustre var. tenella fo. subenervis (Schimp.) Moenk., Susswassfl. 151. f52e. only. 1914.

Hygrohypnum palustre var. subenervis (Schimp.) Moenk., Susswassfl. 151. 1914.

Limnobium pseudochraceum Amann ex Roth, Hedwigia 57:139. 4f. 6.
1915.


Hygrohypnum luridum var. eu-luridum fo. vulgare (Moenk.) Podp. Consp. 571. 1954.


Hygrohypnum luridum var. eu-luridum fo. laxum (B.S.G.) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. tenellum (Schimp.) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. tenellum fo. subenerve (Schimp.) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. tenellum fo. plumulosum (Amann) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. tenellum fo. hamulosum (Glow.) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. tenellum fo. tenuissimum (Warnst.) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. malacocaulon (Herz.) Podp., Consp. 572. 1954.
Hygrohypnum luridum var. julaceum (B.S.G.) Podp., Consp. 572. 1954.

Hygrohypnum luridum var. subsphaericarpum fo. cataractum (Loesk.) Podp., Consp. 572. 1954.

Hygrohypnum luridum var. pseudochraceum (Amann) Podp., Consp. 572. 1954.

Hygrohypnum luridum var. pseudochraceum fo. alpinum (Amann) Podp., Consp. 572. 1954.

Nomina Nuda

Hygrohypnum luridum var. eu-luridum fo. complanata (Roell) Podp., Consp. 571. 1954.

Hygrohypnum luridum var. obtusatum (Loesk. et Stolle in Roell) Podp., Consp. 572. 1954.

Hygrohypnum palustre var. complanatum Roell, Hedwigia 38:265. 1899.

Hygrohypnum palustre var. obtusatum Loesk. et Stolle in Roell, Hedwigia 56:267. 1915.


Hypnum palustre var. pfefferi Lor. in Limpr., Krypt. Fl. Schles. 1:63. 1876.

Nomena Nuda not seen


**Hypnum palustre** var. **gracilis** Ren. in Holzinger, Bryologist.
13:53. 1913.

Names treated as synonyms elsewhere, but for which the literature was unavailable for assessment during this study.

**Hygrohypnum luridum** fo. **intextum** C. Muell., Syn. 2:142. 1851.


**Limnobium subsphaericarpon** (Brid.) Lindb., Medd. Soc. F. Fl. Penn.

Names of certain taxa and their alleged synonyms for which the literature was examined, but found inadequate for effective assessment of the taxon in the absence of the type specimens.

**Hypnum ruderale** var. **intricastum** Brid., Bryol. Univ. 2:584. 1827.

**Hygrohypnum luridum** fo. **intricastum** (Brid.) C. Jens. Skand. Bladmfl.
465. 1939.

**Hypnum palustre** var. **prolixum** Mat., Hedwigia 44:44. 1905.

**Hygrohypnum palustre** var. **prolixum** (Mat.) Warnst., Krypt. Fl.
Brandenburg 2:1060. 1906.

**Hygrohypnum luridum** fo. **prolixum** Podp., Conspr. 571. 1954.

Names of taxa not present at the designated sites in the literature.

1939. fide Index Muscorum.


Plants slender to robust, forming loosely to tightly woven patches or tufts, often forming extensive mats; when loosely woven the patches or tufts easily fragment; plants frequently clogged with silt to varying degrees. Color variable, yellow-green to yellow-green with rusty mottling, less often yellow-brown, bright green, blackish-green or brownish-black, at times all color variations may grade from one to another within the same plant. Stems (1) 3 - 5 (6) cm long; mainly prostrate and creeping, but ascending at the apex; stems sometimes hooked at the apex; usually foliose throughout, in some old specimens the leaves near the stem base may be badly abraded, but seldom are the stems clearly denuded. Branching irregular, branches 1 - 2 (3) cm long, generally ascending, sometimes erect, stem cross-sections revealing 3 to 4 rows of small, yellowish or brownish, thick-walled cortical cells; medullary cells thinner-walled, increasing in size toward the middle; central strand well developed, of numerous small cells; medullary cells and the central strand generally becoming more darkly pigmented with age; rhizoids of variable frequency, reddish-brown, arising at the base of ventral stem leaves.

Leaves variable, but changing little from the wet to dry condition; (0.5) 1.0 - 1.5 (2.5) mm long X (0.25) 0.4 - 0.75 (1.1) mm wide; shape variable, lanceolate, oblong-lanceolate, ovate and occasionally broadly ovate; leaves straight for falcate, rarely almost circinate; apex in lanceolate or severely falcate leaves usually tapering gradually to an acute point; in oblong-lanceolate, ovate or less severely falcate leaves the apex usually tapering into a small abruptly differentiated apiculus; margins entire, inrolling variously, frequently inrolling on one side of the leaf creating infolded wings; in oblong-lanceolate or ovate leaves margins frequently inroll on both sides of the leaf in upper quarter accentuating the abruptly tapered apiculus. Leaves
variously distant to crowded; attitude upon stem variable, spreading, loosely to tightly imbricated, almost juliaceous or any variation of falcate from slightly curved to almost circinate; two or more of these variations may occur as a gradient along a given length of stem or branch, the most frequent variation combination being imbricate-falcate or vice versa; frequently a degree of correlation exists between leaf shape or degree of falcation and leaf position upon the stem--lanceolate leaves seem to exhibit a greater frequency in the spreading attitude; among falcate leaves there is an occasional tendency for leaves positioned dorsally on prostrate stems to be strongly falcate with decidedly inrolled margins while leaves positioned on the flanks of such prostrate stems are often rather ovate, gently falcate with the dorsally proximal margin infolded as a wing, and the ventrally placed leaves may either be squarrose-canaliculate or variously falcate in the upper half. Leaves almost plane, shallowly concave or canaliculate, especially when falcate. Costa varies continuously throughout the species and within individual leaves of the same plant; single and short to percurrent, short and double or absent.

Areolation extremely variable; median leaf cells variously short rhombic to long, linear flexuose, (28) 30 - 55 (95) um long X (4) 5 - 7 (12) um wide; the average dimensions of median leaf cells may vary from one leaf to another on the same stem; apical leaf cells generally shortening gradually or changing little from the median cells; basal leaf cells become shorter and wider than median leaf cells or only slightly wider: in either case the basal cells may be weakly to strongly pitted if at all; alar cells variable, present as a well-defined group of quadrate, short rectangular or irregularly shaped cells; varying from thin and hyaline to incrassate and discolored yellow-brown or reddish-brown; plane or excavated, excavated cells sometimes be inflated to
varying degrees.

Plants autoicous; perigonia ovate; perigonal leaves ovate to ovate-lanceolate 0.3 - 0.7 mm long, deeply concave imbricate, entire, ecostate, enclosing several antheridia and numerous paraphyses. Outer and middle perichaetial leaves ovate lanceolate or lanceolate, squarrose recurved in the upper half, costa single or absent; inner perichaetial leaves long tapering lanceolate, to 3.5 mm long, erect, entire, costa strong and single or long and double or almost absent, stout or slender.

Seta 8 - 24 mm long, smooth walled, erect or arching when moist, variously twisting upon drying. Capsule 1 - 3 mm long; when wet usually inclined arcuate, less often erect cylindrical; upon drying the capsule may or may not constrict below the mouth, when constricted below the mouth the lower half of the capsule is rather bulbous. Capsule wall cells incrassate, yellow or reddish-brown, oval, quadrate, rectangular or irregular. Capsules with tapering neck bearing 8 - 30 superficial stomata.

Peristome typical for the genus; annulus absent, endostome with 1 - 3 poorly to well defined cilia. Spores dusky yellow, papillose, 10 - 26 um in diameter.

Hygrohypnum luridum (Hedw.) Jenn. is an extremely variable species. A measure of this variability is seen in the 115 names ascribed at the specific and subspecific levels. However, this study shows that H. luridum must be viewed as a single, exceedingly polymorphic species that cannot be effectively subdivided into morphologically consistent taxa. The species varies virtually continuously in nine or ten features, which have been used singly or in various combinations as criteria for the recognition of numerous subspecific taxa. These are overall plant size, leaf shape, attitude of the leaves on the stem, degree of falcation, degree of inrolling of the leaf margin, internode length,
costal structure, degree of leaf concavity, alar differentiation and the
degree to which the alar cells are excavated.

The size or overall robustness of this species varies widely. This
variation is difficult to measure and is dealt with in qualitative terms,
which unfortunately are vague and imprecise. *Hygrohypnum luridum* can form
small patches or tufts a few centimeters square all the way to extensive
mats several decimeters across. These may be very loosely woven and easily
fragmented or tightly woven with little fragmentation. These patches or
mats may be thin due to the prostration of their component branches or they
may be thick and almost turf like as a consequence of the ascending branches
and stem tips. Stems can be slender, that is less than 1 mm in diameter, or
thicker, ca. 2.5 mm. (Thickness is the distance in moist plants from leaf
tip to leaf tip from one side of the stem to the other.) Variation in stature
is a frequent environmental response among plants, thus it seems reasonable
to assume that variation of this sort is such a response.

The leaves are exceedingly variable. Certain features vary and these
variations in turn influence the variation of other leaf features. Conse­
quently, the variable leaf characters are difficult to treat individually.

Basic leaf shape varies from narrowly lanceolate (Fig. 51 m) to ovate
(Fig. 51 b). The most common shape is ovate lanceolate or oblong-lanceolate
(Fig. 51 f, g, i, o, p, q etc). Leaves exhibiting such shapes often occur
on the same plants and in rare instances they may occur immediately adjacent
one another with out leaves transitional shapes between them.

The leaf apex may gradually taper to a sharp point (Fig. 51 j & m), but
in most instances appears to taper abruptly to an apiculate point (Fig. 51
f, p, etc). This is most evident in oblong ovate or oblong lanceolate leaves.
In reality the apices gradually taper to an acute point (Fig. 53 a & b) but appear apiculate resulting from the inrolling of the leaf margin just below the apex. This accentuates the taper and artificially differentiates the apiculus.

As continuous as the variability of leaf shape is with its attendant modifying features, certain features show a correlation with leaf shapes.

Narrowly lanceolate to ovate lanceolate leaves are frequently variously falcate. Such leaves vary from slightly falcate (Fig. 51 n) to almost circinate (Fig. 52 v). An entire leaf may be falcate (Fig. 52 u) or only the upper half (Fig. 52 p). The asymmetry of a leaf as a consequence of the falcation may also be more evident on one side of the leaf (Fig. 51 e).

Very commonly the degree of falcation may depend on the dorsal, lateral or ventral insertion of the leaves upon the prostrate stem. Dorsally placed leaves may be severely falcate to almost circinate and deeply tubulose. Such leaves arch high above their point of insertion, curving abruptly toward the substrate and occasionally the tips curve completely beneath the stem (Fig. 50 d). In other instances the dorsal leaves simply curve gradually toward the substrate. Sometimes in the more ovate lanceolate leaves the expression of falcation is confined to the upper half of the leaf, or is at least more conspicuous there. In these the falcate upper half is severely curved and deeply tubulose (Fig. 51 l). Leaves inserted laterally on the prostrate stem may either be severely falcate as those dorsally inserted or may be falcate by means of an inrolled leaf margin. In this latter situation the leaf nearer the dorsal side of the stem is inrolled toward the leaf midline. Such a leaf may be gradually or abruptly falcate. The more ovate lanceolate leaves inserted laterally generally are more gradually falcate than narrower leaves. Less falcate ovate lanceolate leaves are placed adaxial side down on a micro-
scope slide and covered with a cover slip, they are seen to lose their falcate appearance. Thus the inrolled wing opens when the leaf is placed adaxial side down. The pressure of the cover slip flattens the leaf, making it appear more truly ovate lanceolate. This, however, is a variable phenomenon. Leaves situated ventrally on a prostrate stem are also variably falcate. Sometimes these are not so much falcate as they are squarrose tubulose in the upper half (Fig. 51 c) and occasionally, the squarrose tubulose upper half is deflected to one side by the substrate. On some plants with primarily falcate the ventral leaves are perfectly ovate lanceolate with no hint of falcation. In these, the ventral leaves are imbricated among themselves.

Narrowly lanceolate or ovate leaves may vary still further. Generally the leaves are quite crowded along the stem or they may be quite distant. There distant leaves may occur in two regions; on slender branches, or in posterior portions of older stems. If often appears that concavity varies directly with falcation. The more pronounced the falcation, the more pronounced the leaf concavity or caniculation.

Frequently, the narrowly lanceolate or ovate lanceolate leaves are straight, exhibiting no falcation. In these instances, there is variation in the attitude of the leaves upon the stem, spacing of the leaves along the stem, the leaf concavity and the inrolling of the margin. These leaves vary from tightly imbricated to very widely spreading and they vary from crowded to distant. In some cases, those leaves that are widely spreading and distant are also crisped when dry and exhibit considerable lateral shrinkage coupled with some twisting. Not infrequently, those axes bearing crisped, widely spaced, spreading leaves are rather spindly secondary branches. In straight, narrowly lanceolate to ovate lanceolate leaves concavity when present is more
evident than in falcate leaves which often particularly evident when the leaves are imbricated. Sometimes in very long, old stems the narrowly lanceolate to ovate leaves are widely spaced and grade from very small size to normal from the stem base to the apex. This phenomenon appears to be the result of maturation from juvenile to adult leaves.

In a significantly large number of specimens leaves occur in such shapes as; ovate, but narrowing to an acuminate tip; oblong to oblong ovate with acute tip; and broadly ovate or broadly lanceolate. These basic shapes grade imperceptibly from one to another, varying in a number of minor features. Most importantly, leaves of these shapes are most typically straight. Beyond this, these leaves may vary in their attitude upon the stems, their spacing along the stem, their concavity and the degree of inrolling of the leaf margins. A frequent modification among these leaves has to do with the inrolling of the leaf margin and the delimitation of a small apiculus. In all of these leaf shapes it is common for the margin to inroll slightly from near midleaf to shortly below the apex. As a result of the inrolling, the taper of the leaf near the apex is abruptly changed such that an apical apiculus is evident.

The spacing of these variously shaped leaves on the stem varies from very widely spaced to very crowded. They may further vary from spreading to imbricated. Sometimes they are concave or weakly tumid. At other times they are virtually plane. Frequently, much of this variation may be evident along a gradient from posterior of the stem to the stem apex. In such cases the leaves at the posterior stem extremities are widely spaced and spreading to almost erect spreading. Toward the stem apex the leaves become gradually more crowded and conspicuously imbricated. The concavity of these leaves varies quite widely and in some cases the leaves are almost cuculate, whereas, in others, the concavity is very shallow. A consequence of the pronounced concavity in
some leaves the stems are julaceous.

Typically *Hygrohypnum luridum* has a well defined group of quadrate to short rectangular or occasionally irregularly shaped alar cells (Fig. 54 a & b). Typically the cells are incrassate, but they may be somewhat thin walled. They may be hyaline or strongly discolored yellow to red-brown and may vary from plane to decidedly excavated (Fig. 54 d - f). Each of these variables may occur on the same plant and in the same leaf. There does seem to be a greater frequency for excavated alar cells in falcate leaves than in straight leaves. Alar cells of *Hygrohypnum luridum* have never been described as inflated. However, a few alar cells in falcate leaves with excavated alar zones may be quite inflated (Fig. 54 f). Among straight, almost broadly ovate leaves there is also a greater frequency of thin-walled, hyaline or only slightly discolored alar cells.

The costa of *Hygrohypnum luridum* is exceedingly variable and is so independent of any other leaf character. The costa varies from strong, single and percurrent to short and double to virtually absent. Among the very smallest leaves the costa is more frequently absent; but this does not mean that larger leaves have more well developed costae. In fact, they too may completely lack a costa. As with other leaf features it is not uncommon for the entire range of variation to occur within one plant.

In the original description of *Hypnum luridum* Hedwig (1801) did not designate a type specimen. Hedwig did give habitat and geographical date indicating that the plant was collected from decaying matter in Sweden and Germany. Thorough study of the species has revealed that only two specimens that are attributable to Hedwig and/or his herbarium are in existance. Both specimens are at G. One specimen bearing no collecting date is named *Hypnum subsphaericarpon*. It bears the G accession number 3079/184. The second
specimen is entirely representative of the falcate forms of the species, it comes from an acceptable geographical area and at least offers the possibility of having been seen by Hedwig. Therefore, I designate G sheet number 3079/156 as the neotype for *Hygrohypnum luridum* (Hedw.) Jenn.

From out of the mass of character variation that is *Hygrohypnum luridum* numerous past workers have perceived and described as assortment of subspecific taxa. The non-existence of the type specimens for many of these taxa or at least their unavailability for the purposes of this study and the ambiguity of many of their type descriptions has made difficult an assessment of their reality. Careful study of the available type descriptions, other critical literature and a detailed analysis of over 500 specimens of the species from throughout its range has permitted an assessment of the species and its alleged subspecific taxa as recognized by Index Muscorum (1959 - 1969). It is the author's opinion that there are no morphologically consistent entities within the species. All of the subspecific taxa have been based on variable features or have been erroneously placed within the species.

*Hygrohypnum luridum* var. *subphaericarpon* (Brid.) C. Jens., *Hygrohypnum luridum* fo. *alpinum* (Amann) Podp. and *Hygrohypnum luridum* fo. *nervosissimum* (Parr.) Podp. have been based primarily on the strength of their costae. Of *Hypnum subphaericarpon*, Bridel (1812) noted "nervo fubexcurrenente" and went on to say "supreme tantum falcato-fecundo nervo craffo ferrugineo-fusco ad apicem producto fpecifico distintum." Amann (1912) characterized the leaves of *H. luridum* var. *alpinum* as having conspicuously inrolled margins near the apex and a strong costa prolonged to just beneath the apex. Parriat (1952) noted that *Hygrohypnum nervosissimum* had apiculate leaves with the margin inrolled and a single costa disappearing just below the apex, sometimes with a costal
branch reaching midleaf. That these plants are clearly recognizable is indisputable. However, as discussed earlier the costa varies continuously throughout the species. It is easy to find plants resembling each of these taxa in all respects, but possessing a short double costa or a variable mixture of strong single and short and double costae. Each of these taxa simply represent that end of the spectrum of costal variation in which the costae are all, or almost all, strong and single. Consequently, these taxa do not warrant taxonomic recognition.

*Hygrohypnum luridum* fo. *laxum* (B.S.G.) Podp., *Hygrohypnum luridum* fo. *tenuissimum* (Warnst.) Podp., *Hygrohypnum luridum* var. *tenellum* (Schimp.) Podp. and *Hygrohypnum luridum* fo. *subenerve* (Schimp.) C. Jens. are all based on similar features. In general they are characterized as slender or small plants. Schimper (1853) described var. *laxum* as "gracilores, partim denudatue. Folia remotiuscula, undique patentia, ovato-lanceolata." Schimper (1876) further characterized *Limnobium palustre* var. *tenellum* as "minus, formis majoribus *H.* incurvati simili, folis illis var. (Laxum) sat similibus, subito acuminatis." Schimper (1853) described *Amblystegium subenerve* as "laxue caespitosum, rigidulum; caule divisio partim denudato vage pinnatim ramuloso; folis acuminate-ovatis, valde concavis, semi-costatis, costa lutescente simplici vel bifurca, interrimis......" Finally, Warnstorff (1906) described *H. palustre* var. *tenuissimum* as stems very short, asending,......, leaves moderately loosely spaced, mostly clearly secund, small lanceolate, 0.5 to 0.8 mm X 0.2 to 0.3 mm, ecostate or with a very short, very thin simple costa. Only the type of *Amblystegium subenerve* Schimp. (at S-PA) was available for study. However numerous specimens variously determined as one or the other of these taxa have been examined. In most cases, such plants are invariably very poor and fragmented specimens, often consisting of only a few stems. These plants appear to have grown under less than optimal environmental conditions. It is likely, there-
fore, that each of these alleged taxa are morphological aberrations and not worthy of taxonomic recognition.

Overall size, leaf falcation, and costal morphology, all variable characters, have been used to characterize Hygrohypnum luridum var. subsphaericarpon (Brid.) C. Jens., H. luridum fo. hamulosum (B.S.G.) C. Jens., H. luridum ssp. pseudomontanum (Kindb.) Wijk et Marg., H. luridum var. malcocaulon (Herz) Podp. and H. luridum fo. tenuissimum (Warnst.) Podp. Various workers (Bridel, 1812; Schimper, 1853, 1876; Limpricht, 1904; Moenkemeyer, 1927; Nyholm, 1965; Grout, 1931; Lawton, 1971; Dixon, 1924; Braithwaite, 1898; Husnot, 1894; Roth, 1905; Jensén 1939; Milde, 1869; Sprengel, 1827) have all variously described H. luridum var. subsphaericarpon as a very robust plant with large, very falcate secund, concave leaves with a strong, slender costa reaching 3/4 of the leaf length. Similarly, many of these same authors (Schimper, 1853, 1876; Limpricht, 1904; Husnot, 1894; Braithwaite, 1898; Dixon, 1924; Nyholm, 1965; and Moenkemeyer, 1927) variously described fo. hamulosum as a small, slender plant with falcate-secund leaves. However, only Schimper, Dixon, Braithwaite and Husnot remarked on the short and double nature of the costa. Kindberg (1897) observed the similarity of ssp. pseudomontanum with Hygrohypnum montanum on the basis of the variously incurved or recurved falcate leaves. He distinguished the subspecies on the basis of its longer more robust stems, the larger, thinner more loosely disposed, longer decurrent, less distinctly serrulate leaves, whose alar cells were larger and whose costa was simple and prolonged to above the middle. Warnstor (1906) characterized var. tenuissimum as having very short (1 cm), ascending stems, bearing rhizoids only near the base and whose leaves were rather loosely spaced, clearly secund, narrowly lanceolate, usually 0.5 to 0.6 mm long X 0.2 mm wide, ecostate to short costate and bearing a few quadrate to short rectangular alar cells.
Study of var. *subsphaericarpon*, fo. *hamulosum* and fo. *tenuissimum* have shown them to based on continuously variable overall plant size, leaf falcation and costal morphology. Very large, robust falcate leaved plants may have short and double or single costae or they may be ecostate. Similarly, small, slender falcate leaved plants may have strong single or short double costae. The ambiguous concepts of robust and small and slender have caused previous workers to call plants of essentially the same size both var. *subsphaericarpon* and fo. *hamulosum* regardless of the plant's real linear dimensions. A more fundamental problem among these taxa is the very frequent occurrence of straight leaves on stems bearing a majority of falcate leaves. It is not unusual to come upon stems that have segments of falcate leaves alternating at irregular intervals with segments bearing straight leaves. As a consequence, none of the characters serving as the basis for these taxa are sufficiently consistent to serve as a sound taxonomic base. Therefore, I do not recognize these taxa.

The position of *Hygrohypnum luridum* ssp. *pseudomontanum* in this group is somewhat ambiguous. As noted earlier, Kindberg (1971) treated the supposed subspecies as a species allied with *Hygrohypnum montanum*. The facts are that the supposed subspecies is not even remotely related to *H. montanum*, but is a variant of *H. luridum*. Kindberg accurately noted the frequent similarity of the variable incurvature and recurvature of the leaf margins. He mistakenly noted the less distinctly serrulate leaf margins. The alleged subspecies is in fact clearly entire. Kindberg correctly observed that the leaves of the so called subspecies were larger than those of *H. montanum*. However, the leaf size of ssp. *pseudomontanum* should be compared with the slender, falcate leaved forms of *H. luridum* that have been attributed to fo. *hamulosum*. The subspecies was originally described from Owen Sound, Ontario. Plants from this area and the adjacent Great Lakes area are often slightly larger than the
traditional fo. hamulosum. Grout (1931) accurately noted the slightly blunter leaf apices which often occur in ssp. pseudomontanum. However, the character merges imperceptibly with other small falcate leaved variants of H. luridum in the Great Lakes area. Grout (1931) accurately noted the simultaneous occurrence of straight and falcate leaves in ssp. pseudomontanum, but did not attach any significance to the fact. Hygrohypnum luridum ssp. pseudomontanum is not worthy of formal recognition.

Plants bearing straight, julaceous or loosely imbricated, oblong ovate to broadly lanceolate leaves with more or less abruptly acuminate apicies and having strong single costae have long been treated as the variety or form julaceum of Hygrohypnum luridum. These plants have been so treated by Schimper (1853, 1876), Limpricht (1904), Grout (1931), Dixon (1924), Husnot (1894) and Roth (1905). As noted previously the costa varies more or less continuously throughout the species. Much weight has been placed on straight and falcate leaves in the recognition of subspecific taxa in Hygrohypnum luridum. Leaves of both shapes are frequently observed on the same stems in the species and thus invalidate the characters as useful in this species.

Müller (1887) described Hypnum krausei from Takhim Valley, Alaska. Grout (1931) treated the plant as synonymous with Hygrohypnum alpestre. Examination of a duplicate of the type at NY reveals that the plant is the common western North American form of Hygrohypnum luridum.

Hygrohypnum luridum var. crassinervium (Baur.) Podp. is a depauperate form of Hygrohypnum smithii (Sw. in Lilj.) Broth.

Hygrohypnum luridum var. ehlei (Arn.) Wijk et Marg. is a falcate leaved form of H. polare (Lindb.) Loesk. For a complete discussion of the Arnell plant see the treatment of H. polare.
Roell (1899) used the epithet complanatum for what he viewed as new variety of \textit{H. luridum}. The name was used in the absence of a formal Latin description nor was a specimen cited. The name is a \textit{nomen nudum}.

Later Roell (1915) published the name \textit{Hygrohypnum palustre} var. \textit{obtusatum} which he credited to Loeske. The name was accompanied neither by a Latin description nor a cited specimen and is therefore a \textit{nomen nudum}.

Wijk et al. (1964) credit De Notaris for authoring the names \textit{Limnobium reptiliforme} and \textit{L. ambiguum}. Neither descriptions nor specimens of such plants have been available for study. Further, Wijk et al. (1962) noted that Jensen (1939) reduced the two De Notaris taxa to forms of \textit{Hygrohypnum luridum}. The Wijk reference to Jensen's work is mistaken for Jensen clearly makes no mention of the De Notaris taxa in that work. Consequently, the status of these two taxa is unclear.

Wijk et al. (1962) noted that Jensen (1939) recognized \textit{Hypnum intextum} Voit. in Sturm and \textit{Hypnum ruderale} var. \textit{intricastum} Brid. as forms of \textit{Hygrohypnum luridum}. Again, the reference to Jensen's work is mistaken, for if Jensen did discuss these taxa it was clearly not in his \textit{Skandinavien Bladmossflora}.

Bridel (1827) described \textit{Hypnum ruderale} var. \textit{intricastum}. In the absence of the type, the description is inadequate to clearly deal with the name. Similarly, the description of \textit{Hypnum intextum} Voit has been unavailable for study and the taxon cannot be effectively dealt with. The validity of the taxon is at best doubtful.

\textit{Hygrohypnum luridum} var. \textit{pseudoehraceum} (Roth) Podp. was described as \textit{Limnobium pseudoehraceum} by Amann in Roth (1915). Amann characterized the taxon as being very similar to \textit{Limnobium ochraceum} and noted in particular the exceedingly strong and wide costa. The plant vaguely resembles \textit{Hygro-}
hypnum ochraceum and seems only to be a coarse variant of *H. luridum*.

The type was examined from S-PA:

Amann (1928) described *Hygrohypnum subenerve* (B.S.G.) Loesk. var. *plumulosum*. None of the specimens cited by Amann have been available for study and the description does not allow for clear recognition. One feature noted by Amann which is most unusual for a species of *Hygrohypnum* is the biseriate nature of the leaves. The status of the taxon is, as yet, unclear. Podpera (1954) however, did reduce it to a form of *Hygrohypnum luridum*. 
Fig. 351 a – j. Variation in the habit of moist shoots of *Hygrohypnum luridum*.

Scale:
Fig. 52 a – q. Variation in the leaf shape of *Hygrohypnum luridum*.

Scale: [ ] mm
Fig. 53 a-v. Variation in leaf shape of *Hygrohypnum luridum*.

Scale: [1mm]
Fig. 54 - h. Variation in the cellular detail of the foliage leaves of *Hygrohypnum luridum*.

a - b. Leaf apices

c, f - h. Median leaf cells
d, e. Marginal leaf cells

Scale:

a, b;  

c - h;
Fig. 55 a–f. Variation in the alar cells of *Hygrohypnum luridum*.

Scale: \[ \text{100um} \]
Fig. 56. **Hygrohypnum luridum**
Exsiccati Examined

Allen, Mosses of the Cascade Mountains, Washington # 140 as *Hypnum palustre*. (MICH, MIN, NY, USA, TENN)

Austin, Musci Appalachiani # 435 as *Hypnum palustre*. (MICH, NY, UBC, USA)

Bauer, Musci europ. et ameri. exsiccati.

# 2090 as *Hygrohypnum palustre*. (NY)
# 2091 as *Hygrohypnum subenerve*. (BRNM, NY)

Musci eur. exsiccati

# 1285a as *Hygrohypnum palustre*. (BRNM, NY, NICH)
# 1285b as *Hygrohypnum palustre*. (NY)

Brotherus, Musci Turkestanici # 129. (H-BR, LE, MIN as *Amblystegium palustre var. subsphaericarpon*)

Musci Turkestanici # 256 as *Amblystegium palustre var. subsphaericarpon* (H-BR)

Musci Turkestanici # 257 as *Amblystegium palustre var. subsphaericarpon* (H-BR)

Bryotheca Fennica # 286 as *Hygrohypnum palustre* (B, LE)

De Notaris, Erbar. Crittogam. Ital. #906 as *Limnobium palustre*. (B, NY)

Ser. II. # 3 as *Limnobium subsphaericarpon*. (UC, BM)

Delogne, Les Mousses de l'Ardenne # 95 as *Hypnum palustre*. (C)

Desmazieres, Plantes Cryptogams de France # 443 as *Hypnum palustre*. (G)

Drummond, Musci Americani # 195 as *Hypnum palustre*. (CANM, MICH, NY)

Felfoldy, Flora Hungarica # 423 as *Hygrohypnum palustre*. (B)

Fleischer & Warnstorf Bryotheca Europ. meridion cent III # 298 as *Hygrohypnum palustre var. laxum*. (C)

Gravet, Bryotheca Belgica # 349 as *Hypnum palustre*. (G, NY)

Grout, North American Musci Perfecti # 118 as *Hygrohypnum palustre*. (MICH, LE, NY, TENN, USA, F)

North American Musci Pleurocarpi # 362 as *Hygrohypnum palustre*. (MICH, MIN, MO, NY, TENN, UC, USA)

Hesselbo, Bryophyta Danica Exsiccata # 333 (BP, LE, NICH, CANM)

Husnot, Musci Galliae

# 494 as *Hypnum palustre var. subsphaericarpon*. (NY, BM)
# 292 as *Hypnum palustre*. (NY, BM)

Jack, Leiner & Stizenberger, Kryptogamen Badens # 96 as *Limnobium palustre*. (G, NY, BM, BP)

Kerner, Flora Exsiccati Austro-Hungarica # 1515 as *Limnobium palustre*. (G, LE, MO, UC, BP, C)

Kopsch, Bryotheca Saxonica # 284 as *Hygrohypnum palustre*. (MICH)

Limpricht, Bryotheca Silesiana # 249 as *Hypnum palustre*. (B, LE, NY)

Lisowski, Bryotheca Polonica

Fasc. IX # 266 as *Hygrohypnum palustre*. (CANM)

Fasc. XV # 420 as *Hygrohypnum palustre var. hamulosum*. (B)

Fasc. XXII # 593 as *Hygrohypnum palustre* (BP, LE, NICH)

Fasc. XXXI # 819 as *Hygrohypnum palustre var. tatricum*. (B, LE)

Fasc. XXXI # 820 as *Hygrohypnum palustre var. julaceum*. (B, BP, LE, NICH)

Fasc. LXVIII # 1746 as *Hygrohypnum var. julaceum*. (LE, NICH)

Macoun, Canadian Mosses # 398 as *Hypnum palustre*. (MICH, MO, USA, C)

Canadian Musci

# 341 as *Limnobium palustre*. (CANM)
# 356 as Hypnum palustre (MIN, MO, NY, TRTC, UC USA, C)
# 357 as Hypnum eugyrium. (MIN)
# 493 as Hypnum columbico-palustre. (MICH, MIN, NY, TRTC)
# 527 as Hypnum pseudomontanum. (TRTC)
# 535 as Hypnum dilatatum. (MO)
Flora Canadensis # 760 as Hypnum palustre. (TRTC)
Matouschek, Kryptogamen exsiccati # 2195 as Hypnum palustre. (B, LE, C, NY)

# 1587 as Hypnum palustre var. sub-sphaericarpon (LE, C)
Migula, Cryptogamae Germaniae, Austriae, Helvetiae exsiccati
# 272 as Hypnum palustre. (B, MICH, NY, UBC, C)
G. Muller, Westfallen Laubmoose # 123 as Hypnum palustre (BP)
Mougeot, Nestler & Schimper, Stirpes Cryptogamae Bogeso-Rhennanae
# 521 as Hypnum palustre (G, NY)
# 48 as Hypnum palustre var. hamulosum (LE)
Pilous, Musci cechoslovenici exsiccati
# 74 as Hygrohypnum palustre. (B)
# 117 as Hygrohypnum subenerve. (G)
# 237 as Hygrohypnum palustre fo. julaceum. (B)
# 279 as Hygrohypnum palustre var. julaceum. (B)
# 733 as Hygrohypnum palustre. (B)
# 819 as Limnobium palustre var. tenellum fo. subenerve. (B, C)
Rabenhorst, Bryotheca europaea
# 294 as Limnobium palustre. (NY, BM, C)
# 393 as Hypnum palustre. (NY)
# 550 as Hypnum palustre var. subenerve. (G, NY, BM C)
# 1347 as Hypnum palustre. (NY)
# 1347b as Hypnum palustre. (NY)
Regensberg, botanischen Gesellschaft, Flora exsiccati Bavaria
Bryophyta
# 381 as Hypnum palustre. (B)
# 384 as Hypnum subenerve. (B)
Schultz, herbarium mormale Cent 12,
# 1183 as Hypnum palustre (C)
# 1183 bis as Hypnum palustre (C)
Societe dauphinose # 3137 as Hypnum palustre. (G)
Wartmen & Schenk, Schweizerische Kryptogamen # 395 as Hypnum palustre.
(G, NY)
Williams, North American Mosses - Yukon Region # 767 as Hypnum palustre.
(USA)
Wilson, Musci Britishi # 383 as Hypnum palustre var. subsphaericarpon
(G, NY)
Zmuda, Flora Galiciae # 96 as Hygrohypnum subsphaericarpon (G)

Selected Specimens Examined

Canada
British Columbia
Kootney National Park, Vermillion R. near Vermillion Crossing;
Crum and Schofield 5490. (UBC)
Vancouver Island: Halbert 6187
N. of Fort Nelson along the Alaska Hwy, 58°40 N, 124°42 W; Correll 12051 as *Hygrohypnum palustre*. (UBC)
Lytton, 8 miles S.; Schofield & Boas 17815. (UBC)
Armstrong; Wilson, March 1904. (UBC)
Bowron R., 25 N. of Bowron Lake; Boas 547. (UBC)
Kamloops District, Kamloops, Jamison Creek; MacFadden 3870. (TENN)
Roger's Pass; Macoun 21 July 1890 in Canadian Musci # 341 (CANM)
Spence's Bridge; Macoun 21 May 1889 as *Hypnum palustre*. (CANM)
Yoho Valley; Macoun 478 as *H. alpestre*. (CANM)
Mt. Quest, Cinnamosun Narrows, Shuswap L.; Macoun 27 July 1889 as *Hypnum palustre*. (CANM)
Kootenay National Park, Kimpton Creek below Sinclair Pass; Crum C-65. (CANM)
MacLeod's Lake; Macoun 26 June 1875. as *Hypnum palustre* var. subjulaceum. (NY)
Pavillion Lake; Boas 1960. (UBC)
Queen Charlotte Islands, Moresby Is., Kaisoun; Schofield 31112. (UBC)
Queen Charlotte Islands, Graham Is., Van Inlet; Schofield 32088. (UBC)
Fruitvale, Kelley Creek; Jamieson 5580. (UBC)
Michel Creek, B.C. Hwy 3 near Sparwood; Jamieson 6065. (UBC)
Ten Mile Creek, Slocan Lake; MacFadden 10 June 1926. (UBC)
Inver Creek, between Skeena R. and snow patches E. of Prince Rupert; Schofield & Sharp 9/10-118a. (TENN)
Wilmer, Lake of Hanging Glacier; MacFadden 4376 as *Hygrohypnum palustre*. (TENN)
Garibaldi Provincial Park, Whistler Mtn Ski Area; Schofield & Jamieson. (UBC)

**Alberta**
Lundbreck Falls, Coleman-Kananaskis Road; Jamieson 6118. (UBC)
Bearspaw Dam, S. side of Bow R. west of Calgary; Bird 9039. (NY, UBC)
Jasper National Park, Miette Hot springs; Crum & Schofield 4703 (MICH, UAC, UBC)
Bow River Watershed, Elpoca Creek along Coleman-Kananaskis Road; Bird & Glenn 13494. (UBC)
Waterton National Park, above Anderson Lake; Crum & Schofield 5939. (UBC)
Banff National Park, Louise Creek; Jamieson 6190. (UBC)
Jasper National Park, Sunwapta Pass Camp ground; Bird 5232. (ALTA)

**Manitoba**
The Rock, on the Hays River; Scoggan 75. (UBC)
Churchill, Eskimo Point; Crum & Schofield 7155. (MICH)
Lower Hays River, York Factory Region, Hudson Bay Lowlands; Ritchie 4130. (CANM)
Herb Lake Village, Wekusko Lake, N. E. of the Pas; Scoggan 102. (CANM)
Hansen's Creek, E. of Rennie on Hwy 44; Bird 3286. (CANM)
Saskatchewan
Swift Current; Macoun 6 Sept 1880 as *Hypnum palustre*. (CANM)

Ontario
Grey Co., Indian Falls near Balmy Beach; Crum 11352. (TRTC)
Bruce Co., Sauble Falls; Moxley 24 May 1936. (TRTC)
Peel Co., Credit Forks; Cain 1413. (TRTC)
Kenora District, Cedar Lake, N. of Vernillion Bay; Cain 4914. (TRTC)
Owen Sound; Macoun 28 July 1871 in Flora Canadensis as *Hypnum palustre*. (TRTC)
Thunder Bay District, lake shore N. End of Simpson Is; Garton 6280. (CANM)
Algoma District, N. end of Bachawana Bay; Sharp CM-631. (UBC)
Elora, Grand River; Moxley 7 June 1933. (TENN)
Manitoulin Island, shores of Manitou Lake: Hermann 16044. (USA)

Quebec
Anticosti Island, Jupiter River; Macoun 20 Aug. 1883. (UBC)
James Bay, Rupert House; Lepage 18969. (USA)
Bonaventure Co., Nouvelle River, St. Jean l'Evangeliste
Colins & Fernauld 3313-AB. (MICH)
Lake Mistassini, New Quebec; Lepage 4328. (TRTC)
St. Rimon Rimouski; Lepage 2828. (TRTC)
Parc de la Gaspesii, S. of St. Anne-des-Monts; Ireland 11170. (CANM)
Montmorency River, Fairy Creek; Macoun 30 June 1905. (CANM)

New Brunswick
Victoria Co., Grand Falls; Habeeb 1 July 1943. (UBC, E)
Albert Co., Fundy National Park; Ireland 11565. (UBC)
Queens Co., Moser 1889. (CANM)

Newfoundland
Bay of Islands, Brichy Cove; Waghorne 23. (MO).
Lomond R. at its intersection with Provincial highway 44. Norris 4584. (HSC)
Cataracts Provincial Park, 7 km NW of Colinet; Weber 534 (NFLD)

Labrador
Churchill Falls, Bridge Camp Area; Brassard 5178. (NFLD)
L'Anse au Clair; Waghorne 8 Sept 1894. (NY)

Yukon
Lake LeBarge; Williams 765. (MO)
Rancheria River, 60°10'N, 130°08'W.; Corell 12160. (MICH)
Dawson City District, Hunker Creek; Macoun 22 July 1902. (CANM)
Haines Highway, 83 miles NW of Haines, Alaska; Hermann 21848. (CANM)
Francis Lake, on Money Creek; Jamieson 1976. (UBC)

North West Territories
Ellesmere Island, Head of Tanquary Fjord; Brassard 1614. (CANM)
Victoria Island, Kaskyak River, Minto Inlet; Wynne 18860. (NY)
Great Bear Lake, E. end of McTavish Arm, vicinity of Eldorado Mine; Steere 10070a (NY)
Campbell Lake, Scotter 9742 (C, as *Hygrohypnum alpestre*).

United States
Alaska
Skagway, Williams 27 Aug. 1899 in North American Mosses-Yukon Region # 767. (USA)
Mount McKinley Region, Garner, Bragstad Creek; Sherrard C-18. (USA)
Anchorage-Seward Highway, McHugh Creek Campground; Sharp 14 June 1971. (TENN)
Brooks Range, Sik-Sik-Puk River, Gorgeous Gorge, 30 miles W. of Anaktuvik Pass; Spatzman 15 Aug. 1951. (NY)
Takhin Valley; Krause 20 July 1882. (NY, as Hypnum krausei; isotype)
Brooks Range, S. of Cape Thompson, Ogotoruk Creek; Steere 63-652. (NY)
Brooks Range, Endicott Mountains, SW of Chandler Lake; Steere 18333. (NY)
Brooks Range, Franklin Mountains, Schrader L. Peters L. area; Steere 18926a. (NY)

Washington
King Co., Green River Gorge, E. of Black Diamond; Ireland 9606. (CANM)
Upper Valley of the Neaqually; Allen 28 June 1898 in Mosses of the Cascade Mountains, Washington # 140. (USA, CANM)
Olympic Peninsula, Mouth of Sekim River; Svhila 703. (MICH)

California
Sequoia National Park, Halstead Trail; Degener & Peiler 16914. (MO)

New Mexico
Hermit's Peak; Arsene 18479. (USA)
Cumber's Pass; Vreeland 31 Aug. 1900. (NY)
San Miguel Co., Pecos Valley Holy Ghost Creek; Studhalter & Man 3089 (COLO)
Taos Co., Angosturo Creek, Tres Ritos; Studhalter & Man 3258 (COLO)

Arizona
Coconine Co., West Fork of Oak Creek Canyon; Dunn 417. (?)

Idaho
Custer Co., Sawtooth Wilderness Area, Forks of Baron Creek; Morton 8537. (USA)
Kootenai Co., Lake Pend d'Oreille; Leiberg June 1889. (NY)

Utah
Salt Lake Co., Brighton; Darker 5897. (MICH.)
Marysvale, Falls above Bullion Creek; Jones 5899. (MO, UC)

Montana
Lincoln Co., Kootenai River, Kootenai Falls Overlook, 7 miles E. of Troy; Hermann 22481. (TENN)
Flathead National Forest, Echo Lake; Kaufman July 1928. (TENN)
Park Co., Silver Gate, Wyoming Creek; Conard 25 Aug. 1953. (CANM, TRTC)
Columbia Falls; Williams 24 July 1895. (C, MO)
St. Ignatius, near Mary's Lake; Frye 2137. (CANM)
Glacier National Park, SW shore of Bowman Lake; Hermann 18017. (CANM)
Carbon Co., SW of Red Lodge, Trail to Falls of Basin Creek; Lawton 2156. (CANM)

Wyoming
Carbon Co., Elk Mtn.,; Gooding 21 Aug. 1901. (MIN, USA)
Big Horn Mountains, Granite Creek; Whitehouse 25916. (USA)
Albany Co., Libby Creek; Porter 1536. (TENN)
Park Bo., Absaroka Range; Kiener 4047. (MICH)
Yellowstone River; Knowlton 10 Aug. 1888. (USA)
Albany Co., Medicine Bow Mountains, 9 miles W. of Centinal
Hermann 17692. (CANM)
Beartooth Mountains; shores of Beartooth Lake; Welch 16600.
(CANM)

Colorado
La Plata River; Baker, Earle & Tacey 20. (USA)
Manitou, Ruxton Creek; Jewett 18 July 1910. (USA)
Collected mostly within 100 miles of Canon City; Brandegee
1874 – 1878. (USA)
Gunnison Co., vicinity of Gothic, East River Valley;
Welch 9096.
Larimer Co., Rocky Mountain National Park, 7 miles SE Chambers
Lake; Hermann 26783. (UBC)

Minnesota
1902. (MIN)
Cook Co., Schroeder, Cross River Gorge; Olson 761. (CANM)

Michigan
Ontanogon Co., Porcupine Mountains State Park, Trail to Buck­
shot Cabin; Ireland 5214. (USA)
Keweenaw Co., Gratiot R., 2 miles W. of Cliff; Hermann 16389
(USA)
Alger Co., Miner's Falls; Sharp 22 July 1955. (USA)
Isle Royale National Park, Scoville Point; Van Dyk Aug. 1955.
(USA)
Cheboygan Co., Mill Creek; Vitt 304. (ALTA)
Marquette Co., Huron Mountains, Cliff River, Nichols Aug.
1934. (NY)

Wisconsin
Bayfield Co., Near Herbster on Lake Superior; Cheney
6913. (TRTC)

Ohio
Ottawa Co., South Bass Island; Schnoobeger 3586. (USA)

New York
Watkins; Austin 17 July 1874 (NY)
Herkimer Co., Newville; Austin 1868. (NY)
Cayuga Lake Basin, Foot of Island Fall, Fall Creek; Dudley
25 Nov. 1882. (NY)

New Jersey
Sussex Co., West Vernon; Austin Sept 1867. (NY)

Vermont
Caledonia Co., Peacham; Blanchard 5 Nov. 1885. (USA)

New Hampshire
Bekknap Co., Gilford, Mt. Belknap; Carter 5 Sept 1904.
(USA)

West Virginia
Mingo; Gray M-1408. (TENN)
Uffington; Herrod 20 June 1930. (USA)

Guatamala
Dept. of Huehuetenango, Taquia; Vogel B-9009. (NY, TENN)
Greenland
Qroge Peninsula, Inukavsaits Fjord, Sagediaruseq; Holmen 17054. (NY)
Scoresby Land, Mestersvig, Blyminen; Holmen 18045. (NY)

Great Britain
Scotland
Sutherland Co., near Inchnadamph; Crundwell 12 June 1951. (G)

Wales
Black Mountain, Brechnoch, N slopes of Darenlwyd; Liflin 18 May 1959. (FLAS)

Northern Ireland
Belfast; Stewart 12 May 18-7. (NY)

Faroes
Stømjø, Gjøven at Vestmannahavn; Jensen 9 June 1896. (NY)

Iceland
S.-Icel., Rangarvallasjsta, Drangshlid; Johannson 14 July 1965. (FLAS)

Denmark
Jutland, bei Bjornsholm; Jensen in Bryotheca europaea # 393. (NY)
Zealand, Lake Fureso; Hesselbo 8 July 1903 in Bryophyta Danica Exsiccati # 333. (S-PA)
Bornholm, Bobea; Jensen 2-4-1882. (H)

Netherlands.
W. E. plas; Wasschen 29 June 1956. (GRO)
Dordrecht; van der Sande Lacoste. (GRO)

Belgium
Dinant (Namur); Gravet in Bryotheca Belgica # 349. (G)

France
Chambery Sabaudiae, Cascade de Coux; Paris 10 July 1861 as Hypnum palustre. in Bryotheca europaea # 550. (G)
Villare de Lans, Isere; Ravaud IN Societe dauphinose # 3137. as Hypnum palustre. (G)
Haute Savoie, Foret de la glaciere au Mont Brezon; Bernet 29 July 1883. (G, S-PA)
Blanche, au Mont Blanc; leg. ?. (B, accession # 7720/345)

Haute Garonne, Devesoir du Lac Vert pres Luchon; Husnot as Musci Galliae # 592. (S-PA)
Montauban; Lange 7 Sept 1857. (S-PA)

Germany
Allgau, Hindelang, Wildbachtabel bei Oberdorf; Bornmuller 26 Aug. 1922. (B)
Krahenberg; Winter April 1902. (B)
Fichtelgebebirge, bei der Ruine Waldstein; Familer & Schwab Aug 1903 as Flora Exsiccati Bavaria; Bryophyta # 384. (B)
Mark Brandenburg, Potsdam; Benkert Nov. 1960. (B)
Ruisse, Walkenreid; Loeske 1/6/1903. (B)
Ruhland; Moenkemeyer Juli 1910. (NY)
Waren bei Mwritz; Struck. (S-PA)
Bayern, Partenkirchen; Suse March 1916. (S-PA)
Wurtemburg, Alpirsbach; Walde 1897. (S-PA)
Rheinland, Merzig a. d. Saar; Winter. (S-PA)
Rheinland, Bensberg (near Koln); Schlueger. (S-PA)
Hessin, Eberstadt; leg. ?. (S-PA)
Baden, Heidelberg; Arschoug Mai 1861 (S-PA)
Thuringer, Jena; Roell 27 July 1871. (S-PA)

Austria

Neider Oestereich, Schrattenstein, Stixtenstein; Redinger 28 June 1931.
Neider Oestereich, Schneeberg, Alpelleiten zwischen Baumgartnerhaus-Lackerboden; Redinger 19 July 1931. (B)
Dachsteinengebieites; Morton 1923. (B)
Tirolia centralis, in valle Gschnitzel; Kerner in Flora Exsiccati Austro-Hungarica # 1515.
Voralberg, Walscatal Aufsberg zwei Fleu; Bornmuller 30 July 1936. (B)

Neider Oestereich, Obersee bei Lunz; Redinger 16 June 1930. (B)

Switzerland

Silveretta Gruppe; Bornmuller 26 July 1932. (B)
In den Arve bei Genf; Bernet Juli 1863 in Schweizerische Kryptogamen # 395. (G)
Via.Mala; Reuter Aug. 1854. (G)
Neuchatelon; Bruch. (S-PA)
Zurich, Huntwangen; Frymann Feb 1893. (S-PA)
Zermatt; Husnot in Musci Galliae # 292 (S-PA)
Gemhi Pass; Renisch. (S-PA)
Lugano, Monte Are; Kindberg 27 June 1892. (S-PA)

Italy

Carravella (Canzeglio); Fleischer 23 July 1895. (B)
Dintori Serraville alla Scrivia; Ferrari 1862. in Erbar, Crittogam. Ital. # 906. (B)
Ligurien, im Bogo bei Rapallo auf kalk; Fleischer Aug. 1896.
in Bryotheca Europ. meridion Cent. III # 298. (B)
Tarvisina, ad flumen, Flavino; Saccardo. (S-PA)
Lago d'Como; Leg. ?. (S-PA)

Czechoslovakia

Moravia, Mariental ad thermán Teplitz pr. Mahr-Weisskirchen; Matouschek in Kryptogamen exsiccati # 2195. (B)
Slovakia, Mont Mala Fatra, prope Krasnany; Pilous May 1935.
in Musci checoslovenici exsiccati # 74. (B)
Bohemia, Trutnov, prope Volanov; Pilous June 1949 in Musci
dechoslovenici exsiccati # 819. (B)
Slovakia, Montes Belske Tatry, prope Zdarska Vidia; Pilous Aug. 1947. in Musci
dechoslovenici exsiccati # 279. (B)
Marienbad (=Marianske Lazne); Suse 11/9/1915. (S-PA)

Poland

Tatry Zachonie, Montes Tatra Occ., vallis Dolina; Lisowski 8 May 1956 in Bryotheca Polonica Fasc. XXXI # 820. (B)
Monś Piłsko, (Beskidi Alti), torrentis Cebula; Lisowski 5 May 1957.
in Bryotheca Polonica.Fasc. XXII # 593. (S-PA)
Gleiwitz in Oberbflinfinu (? spelling); Kabbatk. (S-PA)
Elbing, Vogelsanger Wald, Kalmuss 1895. (S-PA)

Hungary

Comit. Borsod., vallis Garadna-volgy supra Omassa; Boros 16 Oct. 1959. (B)
Comit. Zala, lacus Balton ad Tihany; Boros 4 April 1957. (B)
Comit. Esztergom, vallis Ramszaka dek prope Domos; Boros
7 Aug. 1949. (BP)
Comit. Veszprm, vallis Zurokvolgy prope pag Bakouykti; Vajda
30 May 1954. (BP)
Comit. Pest., montes Nagyszensas prope pag Nagykovasci; Vajda
16 Oct. 1955. (BP)
(BP)

Rumania
Carpat, merid., Comit, Csiih, vallis Uzvolgy prope pag Csikszents-
mahtom; Vajda 28 Aug. 1970. (BP)
Carpat, merid., vallis Radesului prope Gura Api, montes Retyezat;
Vajda 12 July 1968. (BP)
Banat., rivi Csernapatak, ad Hetforras prope pag Baile Herculane;
Vajda 7 Aug. 1967. (BP)

Turkey
Prov. Rise, District Hemsin, Ortakoy-Cat; Davis 21311. (C)

Norway
Nordland, Sorfolden; Nyman 19 Aug. 1899. (S-PA)
Troms, fjlke Tronso; Arnell 11 July 1891. (S-PA)
Sor-Trondlag, Trondherim; Arnell Juni 1869. (S-PA)
Trondfjeldet; Kindberg 22 July 1897. (S-PA)
Gudbrandsdalen; Zetterstedt 25 June 1858. (S-PA)
Dovre; Hartman 1872. (S-PA)
Hordaland, Hardangervidda stras o om Dyrskar vid vagen mellan
Oslo och Haugesund; Stridvall 4 Aug. 1970. (S-PA)

Sweden
Skane, Vinslof sn i baken N vid landvagen 2 km USV on Lommarp;
Johansson 10/7/1916. (S-PA)
Bleckinge, Sisseback, fra steu; Medelius 4/9/1922. (S-PA)
Halland, G Karujs kyrka; Florin 15 June 1923. (S-PA)
Smaland, Jonkoping Torpa; Arven 15 Sept 1896. (S-PA)
Gotland, Lummalunda; Jaederholm 1 July 1923. (S-PA)
Ostergotland, Omberg; Mosen 12 Sept 1871. (S-PA)
Vastergotland, Skovde, Havstena, Tomtangen; Hulphers Juli 1930.
(S-PA)
Bohuslan, Fishebackskil ogavdun; Hulphers Aug. 1927. (S-PA)
Dalsland; Bergstrom 16 Sept 1913. (S-PA)
Narke, Karlsruund; Weldheim 26 May 1923. (S-PA)
Sodermanland, Vardinge sn Sjunda; Florin 4/9/1927. (S-PA)
Uppland, Upsala, Krasenbo; Jaederholm 1888. (S-PA)
Vastmanland, Grythytte Skatviken; Stenholm 6/8/1925. (S-PA)
Varmland, Persberg; Larsson 9/6/1914. (S-PA)
Dalarn, par Boda, Osmundsberg, Arnell 17 Aug. 1896. (S-PA)
Gatrikland, Valbo; Hartman June 1858. (S-PA)
Medepad, Torp sn Johannisberg; Huss 1882. (S-PA)
Harjedalen, paroec Tannas Ljusnedal; Ostmann 19 June 1905. (S-PA)
Jamtland, Offerdals sn Hallberget; Florin 25 June 1944. (S-PA)
Lycksele Lappmark, Tarna; Hulphers 15 July 1940. (S-PA)
Angermanland, par Tasso Tasjeberget; Arnell 14 July 1894. (S-PA)
Lule Lappmark, Jikmkok; Nyman Aug. 1893. (S-PA)
Laponia Tornensis, Roukoajokk (Jukkasjarvi); Jaederholm 27 July
1912. (S-PA)
Laponia Tornensis, Abiskojokk; Jaederholm 12 July 1917. (S-PA)
Soviet Union

Caucasus, in fl. Rion pr. Eltsevi; Brotherus 10 July 1877. (NY)
Altai Mountains, Katung pr. Techeposch; Grano. (H-BR)
Siberia, Yamarovka; Mikkvo 24 June 1904. (H-BR)
Tomsk District, Tomsk Junge; Matoejeff 12 July 1912. (H-BR)
Siberia, Jenesei, Hantai; Sahlberg 1876. (H-BR)
Siberia, Jenesei, Tostoinis; Arnell. (H-BR)
Siberia, Lena, Kamachsur; Nilsson-Ehle 6 Aug 1898. (C,S-PA)
Siberia, Lena, Balagnach; Nilsson-Ehle 15 July 1898. (C,LE)
Siberia, Jenesei, Plachino; Arnell 22 July 1876. (C, S-PA)
Karelia ladogensis, Par Sivistamo, Kaaherjoki Laynavaara;
Kotilainen 22 Sept 1926. (H, S-PA)
Prov. Uchta, Archangelsk; Liskendrath June 1885. (H)
Prov. Perm; Keller. (H)
Rossia Bor. porp Vologda; Dohle 1/7 1907. (H)
Irkutsk District, Verzholensk in valle fl. Tachikan; Kusenezou
Jenesei District, Turuchansch Chantaish; Kusnezow at Rever-
datto 7 July 1914. (H-BR)
Pamir in angustatis Chargusti; Paulson 4/9/ 1898. (H-BR)
Altai Tschemal; Verestchagin. (H-BR)
Altai, ad fl. Mena; Krylow. (H-BR)
Amur, Tukuringra an Ufer des Saja; Kuseneva 9/7/ 1915. (H-BR)
Jakutsk, Jenkovshi spitze; Kusenova. (H-BR)
Semiryelschensk, Almatinka minor props Vjernoyi; Regal 20/3/ 1876.
(S-PA)
Terskei Alatau, fl. Dschuka; Brotherus 5 Aug 1896 in Musci
Turkenstanici #130. (H-BR)
Kungei Alatau, as fontes fl. Koissu; Brotherus Aug 1896 in
Musci Turkenstanici # 256. (H-BR)
Brotherus 25 July 1896. (H-BR)
Siberia, Ust ' Kut, in valle flum Lena; Nilsson-Ehle 4 June 1898.
(S-PA)
Jenesei, Nischnaja Tunguska; Arnell 14 July 1876. (S-PA)
Kashmir
Karakorum Range, upper end of the Hushe Valley, Atosar Valley;
Webster & Nasir 6090. (TENN)
Lind Valley near Sonamarg; Duthie 17 Aug 1893. (H-NR)
Balliston, by water course W. of Dras; Duthie 24 Aug 1893.
(G-BR)
Gulmarg; Duthie 8 Jan 1892. (H-BR)
Indian
Uttar Pradesh, Kimaun, Kulti Valley; Duthie 7 Sept 1894. (H-BR)
Tibet
Kargall, Darass Valley; Khan 26 June 1901. (H-BR)
Finland
Kuusamo, rivulo Kulmakkapuro; Hallstrom 18 July 1911 in
Bryotheca Fennica # 286. (B, LE)
China
Interior provincia, Schen-si sept, in medio monte Kuan-tou;
Giraldi 1894. (G)
Yunnan Prov., head waters of the Mekong R.; Handel-Mazetti
#1565. (H-BR)
Setchwan Prov., In montium Daliang-schan (territori Lolo), ad
orientum urbis Ningyuen regione calide temperata ad rivulum
prope vicum Sikwai; Handel-Mazetti # 391. (H-BR)
Japan

Tshihau Prov. Yubari Mtn; Yasuda 518. (H-BR)

Spitsbergen,

King's By District; Arnell & Mortensson 26 July 1956 (C)
Hygrohypnum alpestre (Hedw) Loesk., Verh. Bot. Ver. Brandenburg 46:

198. 1905.

Neotype: "molle"; from Swartz herbarium: annotated by Nyholm (S-PA).

Hyphnum rivulare Sw., Disp. syst. musc. Suec. 1799 - not seen - cited from Hedw. 1801 & Broth. 1924 nom. illeg. hom.

Hyphnum alpestre Hedw., Spec. Musc. 247. 64f. 1-4. 1801

Hyphnum molle var. alpestre (Hedw.) Hamp., Flora 20:274. 1837.

Limnobium alpestre (Hedw.) Schimp., Bryol. Eur. 6:68. 1853.

Figure 577 not included.

Amblystegium rivulare (Sw.) Lindb, Musc Scand. 33. 1879.

nom. illeg.


Hygrohypnum rivulare (Sw.) Broth., Laubm. Fennosk. 500.

1923. nom. illeg.

Plants usually soft, rarely somewhat stiff, usually forming loosely woven patches or tufts, often easily fragmenting. Color variable, yellow or yellow-green with or without rusty mottling above, older extremities dirty brown, reddish-brown or reddish-black, rarely green or yellow-green throughout. Stems (1) 2-4 (9) cm long, prostrate or ascending near the apex; stems foliose throughout or denuded toward the base or clothed in persistent leaf bases, frequently clogged with silt. Branching irregular, branches usually ascending. Stem cross sections revealing 2-3 concentric rows of brownish, thick-walled cortical cells; medullary cells larger, thinner walled, hyaline, becoming discolored and sometimes incrassate with age; central strand well developed. Rhizoids infrequent,
arising on young stem or branch segments from the bases of ventral leaves, generally absent or obscured in the older extremities.

Leaves variable, closely spaced and julaceous, sometimes spreading, especially in some young stem or branch tips, spreading leaves sometimes shrinking laterally and twisting slightly upon drying, otherwise changing little from the wet to the dry condition; leaves oblong to oblong lanceolate; straight, never falcate; (0.9) 1.4-1.6 (1.9) mm long x (0.4) 0.6-0.7 (0.9) mm wide; deeply concave, almost boat shaped in the apex, generally tumid julaceous; apex acute to slightly obtuse, becoming reflexed as a squarrose apiculus, apiculus generally worn away in older leaves; margins entire or uneven in the apex, narrowly recurved, especially in the upper 1/3 and the apex; shortly and narrowly decurrent at the point of insertion; costa variable, usually long and double with one arm reaching midleaf, less frequently single to beyond midleaf or short and double, in all cases slender and faint.

Aerolation uniform, median leaf cells long linear flexuose (55) 65-90 (105) um long x 5-6 um wide, apical cells vary with the shape of the apex, usually longer in acute apices cells toward the base becoming shorter, somewhat wider and more incrassate; pits variable, few to none; alar cells slightly enlarged, rounded quadrate or short rectangular, thick-walled cells, becoming discolored with age, sometimes excavated.

Plants autoicous; perigonial leaves ovate with a small tip, concave imbricate, ecostate; outer and middle perichaetical leaves ovate to ovate lanceolate, ecostate, squarrose in the upper half; inner perichaetal leaves linear lanceolate to lanceolate, to 2. mm long, straight, plicate, margins entire or sometimes toothed in the apex; costa faint and slender, double to midleaf, single to midleaf or absent.
Seta 7 to 16 mm long, smooth, reddish brown; capsule typical for the genus.

Peristome typical for the genus; annulus composed of two rows of cells; inner peristome with 3, sometimes 2, finely papillose, slightly appendiculate cilia between adjacent segments; spores 10 to 18 um., usually 12 to 16, finely papillose, dusky yellow.

Among the species of Hygrohypnum, H. alpestre is most easily diagnosed by its narrowly recurved, squarrose leaf apex (Fig. 57h). Tough obscured in slide preparations for the compound microscope, the squarrose apex is easily seen with a dissecting microscope or a hand lens. One must examine young stem or branch leaves for the squarrose apex for the apex is frequently worn away in older leaves.

Other useful characters are the boat shaped concavity of the leaves, the oblong to oblong lanceolate leaves (Fig. 57a-g) the normally slender and long double costae, the uniformly long median leaf cells (Fig. 58 c and d) and the rounded quadrate alar cells (Fig. 58 f-h).

The leaf concavity is very deep, but does not extend all the way to the apex. Instead, the concavity ends shortly below the apex, thus delimiting a planar zone just below the squarrose apiculus (Fig. 57e). The upper 1/3 to 1/2 of the leaf thus appears boat shaped.

Normally the stems of H. alpestre are strongly tumid-julaceous (Fig. 57h). Occasionally the leaves are loosely spreading.

Of all the Hygrohypna, H. alpestre remarkable exhibits a very uniform median leaf areolation. The median leaf cells do not have unusually short or unusually long cells scattered through an otherwise uniform median areolation as do some species.

In the past, Hygrohypnum alpestre has been confused with H. molle,
H. luridum and H. eugryium. For a comparison of H. alpestre and H. molle, see the discussion under the latter species. The following chart will point out the pertinent differences between the remaining three species.

<table>
<thead>
<tr>
<th></th>
<th>H. alpestre</th>
<th>H. luridum</th>
<th>H. eugryium</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf shape</td>
<td>Oblong to oblong lanceolate.</td>
<td>Lanceolate to oblong lanceolate.</td>
<td>Lanceolate to oblong lanceolate.</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>Acute, with a squarrose, recurved apiculus.</td>
<td>Acute, straight, secondarily apiculate by inrolled margins.</td>
<td>Acute, straight, one or both margins inrolled.</td>
</tr>
<tr>
<td>Leaf symmetry</td>
<td>Straight.</td>
<td>Straight or falcate.</td>
<td>Falcate or straight.</td>
</tr>
<tr>
<td>Leaf attitude</td>
<td>Tumid-julaceous throughout.</td>
<td>Julaceous to spreading.</td>
<td>Imbricate to spreading.</td>
</tr>
<tr>
<td>Costa</td>
<td>Usually slender, long and double.</td>
<td>Strong and single or short and double, of equal frequency.</td>
<td>Usually short and double faint.</td>
</tr>
<tr>
<td>Alar cells</td>
<td>Quadrate to slightly enlarged.</td>
<td>Quadrate short, rectangular, rarely enlarged or inflated.</td>
<td>Quadrate to short rectangular, inflated.</td>
</tr>
</tbody>
</table>

The only forms of Hygrohypnum luridum with which H. alpestre can be easily confused are the straight leaved, julaceous ones. Here, the two taxa can be readily separated by the squarrose leaf apex of H. alpestre.
On rare occasions a few workers have confused *H. eugryrium* with *H. alpestre*. These two taxa may be separated most easily by the squar-rose leaf apex of *H. alpestre*. It is also worth noting that the known distributions of the two taxa are not sympatric.

In the type description Hedwig (1801) based *Hypnum alpestre* on a Swartz specimen from alpine Norway. At the present time there are no specimens of *Hypnum alpestre* in the Hewwig herbarium. At S-PA there are two specimens of *Hygrohypnum alpestre* in the Swartz herbarium, both of which are equally representative of the species as understood here. One specimen bears no other data other than the penciled name "molle" and a Nyholm annotation label calling the plant *H. alpestre*. The second specimen is mounted on a very fibrous paper and bears a few notes concerning other literature citations. This second specimen is selected as the neotype.

Warnstorf (1915) described *Hygrohypnum alpestre* var. *scorpioides*. The type of this variety has not been available for examination. The description points out three characters that are unusual for the species, if in fact the variety is *H. alpestre*. The leaves of the variety are described as being up to 2.5 mm. long. This clearly exceeds the leaf size for the species as determined by the present study. The leaves of the variety are further described as being "secundo-imbricata." The leaves of the species have never been observed to be secund. In other species, that leaves be straight, secund or falcate has been shown to be varibel. The stem and branch tips are always straight, though they may be "catkin-like" or hakenformig. The status of the variety is unclear and certain reservations are justified.
Fig. 57 a - k. Variation in the leaf shape and the habit of the shoot of *Hygrohypnum alpestre*.

a - g, i - k. Variation in leaf shape.

h. The habit of a moist shoot.

Scale:

a - g, i - k;  

h; The shoot is approximately 1 cm long
Fig. 58 a - h. Cellular detail of the foliage leaves of *Hygrohypnum alpestre*.

a. Leaf apex.
b, e. Marginal leaf cells.
c, d. Median leaf cells.
f - h. Alar cells.

Scale:

```
| 100um |
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| 100um |
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Fig. 59. Hygrohypnum alpestre
Exsiccati Examined

Bauer, Musci europ. exs.
   # 643. (BRNM, NY)
   # 1277. (BRNM)
Husnot, Musci Galliae # 750 as Hypnum alpinum. (S-PA)
Rabenhorst, Bryotheca europaea #913. (NY)

Selected Specimens Examined

Canada
British Columbia
   Lake Lindeman; Williams 27 May 1898 as Hypnum alpestre. (NY)
Manitoba
   Seal River, W. of Great Island; Ritchie 1946. (CANM)
Ontario
   Thunder Bay District, Oskondaga River NNE of Shabaqua Station, Goldie Township; Garton 10685 as Drepanocladus revolvens. (CANM)
   Thunder Bay; Macoun July 1869 as Hypnum molle. (MO, NY)
Current River; Macoun 19 July 1869. (MO)
Labrador
   Churchill Falls, Bridge Camp Area; Brassard 5523. (NFLD)
North West Territories
   Great Bear Lake, Port Radium, vicinity of the Eldorado Mine; Steere 10246. (CANM)
   Campbell Lake, 68° 08’ N, 133° 27’ W; Scotter 9742. (C)
   Hudson's Bay, Belcher Islands, Tukarak Is., near Long Lake; Donitt #355. (MICH, NY)
Queen Elisabeth Islands
   Baffin Island, Head of Clyde Inlet, Falcon River, Wynne-Edwards 9285. (CANM, NY)

United States
Alaska
   Brooks Range, Endicotte Mountains, SW end of Chandler Lake; Steere 18252a. (NY)
   Brooks Range, northern slope of the DeLong Mountains, vicinity of Noluck Lake; Steere 63-380. (NY)
Greenland
   Godhavn; Berggren 1870. (NY, S-PA)
   Martlek; Berggren 1870. (S-PA)
   Jacobshaven; Berggren 1870. (S-PA)
   Ritenbenk; Berggren 1870. (S-PA)
   Svartenhuk Peninsula, Umlarfik Fjord, Amitsoq; Holmen 12002. (CANM, LE, NY)
   Christianhamb; Holmen 12066. (NY)
   Scoresby Sund, Sydlap; Holmen 18461. (NY)
   Geographical Society Islands; Holmen 18634. (NY)
   Renland, Rypefjord; Holmen 19166. (CANM, NY)
Iceland
   E. Icel., Egilsstaoir, Eyvindara; Johannsson 12 Aug. 1967. (FLAS)
Bear Island
Mt. Misery; Berggren 1868. (S-PA)

Spitzbergen
Kobbe Bay; Berggren 1868. (MICH, S-PA)

Sweden
Halsingland, Abra, Hofsjatter; Collinder 17 July 1878. (S-PA)
Harjedalen, Storsjo, Lyungalsforsen; Florin 10 July 1931. (S-PA)
Jamtland, Frostvikens; Florin 13 Aug 1925. (S-PA)
Nordbotten, Kiruna Katterjaure; Hulphers 14 July 1944. (S-PA)
Asele Lappmark, Vilhelmina; Moller 20 July 1914. (S-PA)
Lycksele Lappmark, Tarna, N. Storsfjallet; Stenholm 16 July 1924. (S-PA)
Pite Lappmark, Arjeplog; Moller 12 July 1918. (S-PA)
Lule Lappmark, regio Sarjekensis; Jensen & Arnell 3 Aug. 1902. (S-PA)
Torne Lappmark, Abisko; Hulphers 21 July 1941. (S-PA)

Norway
Kongswold; Kindberg July 1885. (S-PA)
Lomseggere; Bryhn July 1879. (S-PA)
Finmarken, mellan Nergaan ob fjellet Aglapp; Maalseludalen; Holmgren 28 July 1868. (S-PA)
Norlands, am Salten Bejeeren; Hagen 3 Aug 1894. (S-PA)
Tromsø, amt Nordreisen; Arnell 29 Aug 1891. (S-PA)
Gausta; Jaederholm, July 1895. (S-PA)

Finland
N. E. Le Poroeno, Vallinkorva; L. & H. Roivainen 1 Aug 1961. (BP, UAC)

Soviet Union
Siberia, Yakutia, Lowlands of the Lena River, Buchta Tiksi; Kildushevsky 12 Aug 1955. (LE)
Kola Peninsula, Khibiny Mnt.; Shelyakov 1768a. (LE)
Tilajak, Konjakovsk Serebryank Mountains, Headwaters of the Iova River; Gorchakovski 9 June 1953. (LE)
Middle Urals, Denezhkin Kamen; Teklemiushev 10 July 1928. (LE)
Novaya Zemlya, Guba Krestova; Brotherus 9-10 Aug 1901. (LE)
Turukhansk District, Jenesei Inlet, Dudinka River, Matiyev 253. (LE)
Siberia, Jenes, Duninka; Arnell 7 Aug 1876. (C,NY)
Lapponia ponojensis; Ponoj; M. Brenner 17 July 1863. (LE)

Lectotype: Insulae Spetsbergensis, Wahlenbergs Bay. Leg: A.J. Malmberg. 1861. (S-PA)


Amblystegium polare (Lindb.) Lindb., Musci Scand. 33. 1879.


Hypnum palustre var. polare (Lindb.) Husn., Musc. Gall. 411 1894.


Hgyrohypnum polare (Lindb.) Broth., Nat. Pfl. 1(3):1041. 190


Lectotype: Siberia, Lena, Kumashsur, 70° 30' N; Nilsson-Ehle 1898. (S-PA)


Hgyrohypnum polare var. falcatum (Bryhn) Broth., Laubm. Fennosk. 499. 1923.

Hgyrohypnum palustre var. polare (Lindb.) Moenk., Laub, Eur. 737. 1927.

Hgyrohypnum palustre var. ehlei (Arn.) Grout, Moss Fl. N. Am. 3:88. 1931.

Hygrohypnum polare var. pseudostramineum (Lindb.) Podp., Consp. 573. 1954.


Names treated elsewhere as synonyms, but for which the literature was unavailable for assessment during this study.


Amblystegium polare var. pseudostramineum (Lindb.) Hess. Medd. Groenland 43:179. 1911.

Plants variable, forming densely woven, appressed turfs or loosely woven patches. Color golden-yellow to yellowish-green, rarely bright-green. Stems (1) 2-6 (13) cm. long, prostrate, ascending or erect. Unbranched or if branched, then usually from near the base or the main stem, less commonly from above, in all cases the branches tend to become fastigate. Stem cross section revealing an incomplete, outer row of thin walled, inflated cortical cells, beneath which lies 2 to 3 rows of small, brownish, incrassate cortical cells, which in turn enclose a broad medullary zone of large, thin-walled and hyaline cells; central strand well developed, becoming discolored with age, in older stems the inflated outer cortical cells are collapsed and evident only through the thickened, concave inner walls. Rhizoids few, dark brown, arising from the base of ventral stem leaves, smooth walled.
Leaves variable, closely spaced to distant; attitude of the leaves upon the stem differing little from the wet to dry condition, usually loosely appressed imbricate to loosely spreading; shape variable, ovate-lanceolate, oblong-lanceolate, elliptic or broadly elliptic; (0.9) 1.1-1.6 (2.1) mm long x (0.6) 0.75 - 1.0 (1.1) mm wide; straight to falcate; shallowly to deeply concave, rarely almost plane, plicate or not plicate; apex highly variable, almost plane, shallowly concave and gradually tapering to an acute or apiculate point or deeply concave-cucullate with an oft recurved apiculus, sometimes so deeply concave that the apiculus is directed toward the adaxial leaf base; margins plane, entire except for a slightly crenulate apiculus, sometimes slightly inrolled near the apex, margin in falcate leaves sometimes inrolled making the leaf tubulose in the upper half; costa very stout, single, percurrent in the apiculus or ending shortly below the apex, rarely forked, never short and double.

Aerolation variable; median leaf cells fusiform to long linear flexuose; (33) 40-50 (65) µm long x 5-6 (8) µm wide; cells becoming shorter toward the apex, usually rhomboid, sometimes oval; basal cells becoming shorter and wider, somewhat incrassate, becoming yellow with age, pits few to many; alar cells numerous, quadrate to short rectangular, usually thin-walled and hyaline, forming a well defined group, rarely becoming brownish with age.

Plants dioicous; male and female plants similar, perigonia and perichaëtia poorly known. Perigonal leaves variable; outer perigonal leaves rounded obtuse, to 0.4 mm. long, ecostate; inner perigonal leaves ovate-lanceolate, occasionally abruptly acuminate, finely serrulate at the tip, convave imbricate, ecostate or with a faint single
costa reaching slightly over \( \frac{1}{4} \) the leaf length. Outer and middle perichaetal leaves broadly ovate, tapering to an obtuse tip, ecostate; inner perichaetal leaves long lanceolate, to 3.0 mm. long, gradually tapering to an acuminate apex, apex becoming frayed with age, 2 to 4 deep plicae; costa single, strong, ending shortly below the apex.

Sporophyte incompletely known; seta 10 to 12 mm. long, smooth, gradually tapering into the 1.0 to 1.6 mm. long capsule; capsules not constricted below the mouth; peristome unknown; spores 15 to 29 um., finely papillose, light yellowish green.

**Hygrohypnum polare** may be distinguished by the stout, percurrent costa in association with the outermost, incomplete row of inflated, thin-walled cortical stem cells (Fig. 61h). No other species of *Hygrohypnum* exhibits this character combination.

Though easy to recognize, *Hygrohypnum polare* varies in the expression of leaf shape, leaf symmetry, leaf concavity, the nature of the leaf apex and internode length.

Leaf shape varies from ovate-lanceolate (Fig. 60a), to oblong-lanceolate (Fig. 60d), or elliptic (Fig. 60j) and broadly elliptic (Fig. 60b). Rarely, small leaves may be ovate. Leaf symmetry varies from straight to strongly falcate (Fig. 60g). Falcation has rarely been seen in leaves of shapes other than ovate-lanceolate. As in *Hygrohypnum luridum*, falcate leaves have no taxonomic value, for straight and falcate leaves do occur in alternating groups on the same stem.

The leaf apex regularly terminates in a small, obtuse, sometimes crenulate apiculus. The degree to which the leaf apex tapers and the amount of concavity exhibited by the leaf varies widely. Ovate lanceolate leaves usually taper gradually to an acute apex with the apiculus at the extreme tip (Figs. 60a & c). These leaves vary from almost plane
to deeply concave, such that the apex appears like the bow of a boat. In oblong-lanceolate to elliptical leaves the concavity is frequently so severe that the apex is rounded cucullate and the apiculus is directed toward the adaxial leaf base (Fig. 57j & Fig. 61b).

Leaf attitude varies little between the wet and dry conditions. Falcate leaves excepted, leaves are usually loosely imbricated to slightly spreading. Imbricated leaves which are also deeply concave are, in effect, julaceous (Fig. 60 h).

Internode length varies within individual stems and between different stems. As a consequence leaves may be crowded to widely spaced.

Lindberg (1867) described *Hygrohypnum polare* var. *pseudostamineum*. This taxon was characterized by elongated, sparsely branched stems and distant leaves whose apices are weakly secund. The holotype (H-SOL) collected by Malmberg has sidely spaced, broadly elliptic, cucullate leaves and a vague resemblance to *Calliergon stramineum*. The variety is rejected for many specimens of the species are as sparsely branched and have as crowded or as distant leaves as the supposed variety. Further, with crowded, distant, falcate and straight leaves can be seen in the type specimen of the variety.

*Hygrohypnum luridum* var. *ehlei* (Arn.) Wijk et Marg. was originally described as *Amblystegium ehlei*. This study has shown that the Arnell taxon is a peculiar variant of *Hygrohypnum polare*. The alleged variety cannot be allied with *H. luridum* for the stem cross section reveals an incomplete hyalodermis of inflated, thin walled cells. Such stem cells occur only in *H. polare* and *H. ochraceum*. *Hygrohypnum ochraceum* cannot be considered for as Arnell (1913) correctly noted the leaves of his taxon possessed a strong single costa which ended in the leaf apex, a
character not present in *H. ochraceum*. Arnell (1913) also noted that the stem leaves of his variety were "haud secunda", while the branch leaves were "apicalia curvata-falcata". Present observations show that the leaves are more lanceolate and more severely falcate-circinate than the species as a whole. As in other species, straight and falcate leaves do occur on the same stems. The straight stem leaves noted by Arnell differ from the leaves of typical *H. polare* only in their less apparent concavity, but the apex is as crenulate as in the species itself. The alar cells of both stem and branch leaves are slightly less distinct than in the species as a whole. It is interesting to note that all the specimens that could be interpreted as the so called variety come from the Lena River drainage in Siberia. None is as yet known from the Jenesei or Ob river areas or from comparable areas in Scandinavia or North America. Further, the severely falcate leaves of these plants bear an interesting resemblance to some species of *Drapanocladus*. The typification of the variety is ambiguous. Arnell (1913) cited two localities as the sources of the specimens on which he based his taxon. The localities are:

Siberia, in valle flum. Lena, Kumachsur, 70° 30' lat. sept., Nilsson-Ehle 1898 and Siberia, in valle flum. Lena, Bulun, 70° 43' lat. sept., Nilsson-Ehle 1898. At S-PA there are 4 specimens agreeing with the data for the Kumachsur location and one at H-BR. The lone specimen from H-BR and 3 of the 4 S-PA specimens bear the collecting date of 19 July 1898, whereas the remaining S-PA specimen is dated 26 July 1898. A single specimen from the Bulun cite dated 19 Sept. 1898 is at S-PA. None of the Kumachsur specimens appear to be clear duplicate of one another yet they are unquestionably the same variation of *H. polare*. A single specimen from Kumachsur at S-PA has been appropriately designated as the lectotype.
In literature not available for this study, Bryhn (1902) described *Hygrohypnum polare* var. *falcatum*. At H-BR there is a specimen bearing this name that was collected by G. Simmons in 1898 from Faulkefjord in N. V. Gronland and identified by N. Bryhn. Other specimens bearing this varietal epithet have been located, but none have borne a Bryhn determination nor have any but the above mentioned specimen and another Simmons collection from Ellesmere Is. borne collecting dates prior to 1902. It seems reasonable to assume that the specimen from N. V. Gronland is the one on which Bryhn based his variety. Upon this assumption the variety is judged to be a falcate leaved variant of *H. polare* and not worthy of taxonomic rank.

Numerous workers (Lindberg, 1867; Schimper, 1876; Limpricht, 1904; Roth, 1905; Brotherus, 1923; Moenkelmeyer, 1927; Grout, 1931 and Martensson, 1956) have remarked that the sporophyte of *H. polare* was virtually unknown. Details of the capsule and peristome are unknown, however, it seems to have been overlooked that Limpricht (1904) noted that E. Nyman collected fertile material in Sweden's Lule Lappmark district on 27 July 1891. As Limpricht noted the sporophytes are old and partially decayed. However, it is more important to know that the species is not completely sterile. It is hoped that Scandinavian workers will endeavor to locate fertile material. A measure of the elusiveness of these structures can be measured by their apparent absence from the adjacent and intensively studied Tornetrask.

The questionable occurrence of *Hygrohypnum polare* in continental Europe and North America and its confusion with strong, single costate forms of *H. luridum* is well known in the literature (Boulay, 1872; Renaud, 1883, Husnot, 1894; Amman, 1912 and Parriot, 1952). Husnot's
troublesome exsiccati Musci Galliae #592 has played a central role in the problem. Collected in the Pyrennes from the outlet of Lac Vert near Luchon, the exsiccata was distributed as Hyphnum palustre var. laxum. The only specimen of this exsiccata available for study is at S-PA. The specimen is unquestionably Hygrohypnum polare. However, certain stems bear leaves that are readily mistaken for H. luridum, for they are not cucullate in the apex and the costa tapers to a slender point that ends well below the apex. The various names and comments that have been applied to this exsiccata by Boulay, Husnot, Amann and Parriat are easily attributable to the typical and aberrant leaves on the specimen. Growth in this southern most station of an otherwise northern species no doubt accounts for the somewhat aberrant form. The presence of Hygrohypnum polare in continental Europe is clearly established by Lisowski's Bryotheca Polonica numbers 298, 670, 671 and 818 from the Tatras. Similarly, H. polare is widely scattered in arctic North America and recent report (Brassard, 1975) places the species in central Labrador.

The only species of Hygrohypnum with which H. polare may be confused is H. luridum. The confusion is confined only to those strong, single costate forms of H. luridum. The most important difference resides in the presence of the inflated cortical stem cells of H. polare.

Lindberg (1867) cited two specimens collected on Spitzbergen by Malmgren in 1861 as the basis for Hyphnum polare, the basionym for Hygrohypnum polare. One specimen was cited from "Kobbe Bay 6", and another from "Wahlenbergs bay inter Bryum ventricosum". Lindberg did not specify a holotype and inconsistent citation on specimen labels has further complicated typification. Three collections, two of which exist as pairs of duplicates, for a total of five specimens at either S-PA or
H-SOL, can be attributed to Malmgren. One collection, duplicated at S-PA and H-SOL, bears handwritten labels written by the same hand and bear the name "Robbe bay". The name is quite contrary to the name in Lindberg's description of *Hypnum polare*. The specimen has falcate leaves. The only known specimen from Wahlenbergs bay is at S-PA. The specimen bears a printed label bearing Malmgren's name, the date 1861 and Insulae Spitzbergensis. Written by a hand different from that on the "Robbe bay" specimen is the phrase "Wahlenbergs bay". Though *Bryum ventricosum* is present in the packet, its presence there is not noted on the packet as indicated in Lindberg's description. The specimen is a good representative of *Hygrohypnum polare* with straight leaves.

A third Malmgren collection from Spitzbergen and dated 1861 is duplicated at S-PA and H-SOL. These duplicates bear labels written in the same hand as occurs on the "Robbe bay". Of significance is the statement on each packet; "Augusta bay inter *Bryum ventricosum*". The phrase "inter *Bryum ventricosum*" corresponds to Lindberg's reference to the Wahlenbergs bay specimen, whose actual label does not carry the remark. Remarkably, the Augusta bay specimen contains no *Bryum* of any sort. Morphologically, the Wahlenbergs bay and Augusta bay specimens are similar.

Although both straight and falcate leaves occur in *Hygrohypnum polare*, most specimens have straight leaves. The Wahlenbergs bay collection at S-PA with its straight leaves best represents the most frequent form in the species and is thus chosen as the lectotype for *H. polare*. 
Fig. 60a - k. Variation in the leaf shape and the habit of the shoots of *Hygrohypnum polare*.

a - g, j - k. Variation in leaf shape.

h - i. Variation in the habit of the shoots.

Scale:

a - g, j - k; [_____1mm_____]

h - i; The shoot is approximately 1 cm long
Fig. 61 a - h. Cellular details of the foliage leaves and the stem of *Hygrohypnum polare*.

a, b. Leaf apices.
c, d. Median leaf cells.
e. Marginal leaf cells
f, g. Alar cells.
h. Stem cross section.

Scale:

a, f - h;  

b - e;
Fig. 62. *Hygrohypnum polare*
Exsiccati Examined

Bauer, Musci Europaei exsiccati #648 as *Hygrohypnum polare* (BRNM, UCA, H)
Husnot, Musci Galliae #592 as *Hypnum palustre* var. *laxum*. (S-PA)
Lisowski, Bryotheca Polonica
Fasc. X, #298. (S-PA, H, CANM, BP, LE)
Fasc. XXV, #670. (S-PA; H, CANM, BP, LE)
Fasc. XXXI, #818. (S-PA; H, CANM, BP, LE)
Fasc. XXV, #671 as *Hygrohypnum polare* var. *falcata* (CANM, BP, LE)

Selected Specimens Examined

Canada

British Columbia
Lake Lindeman; Williams 17 May 1898 as *Hypnum polare*. (NY)

Labrador
Churchill Falls, Bridge Camp area; Brassard 5178. (NFLD)

Yukon Territory
Southern Ogilvie Mtns., One Eighty Lake; Horton 2816 (ALTA)

Northwest Territories

Ellesmere Island
Beitstadfjord; Simmons 10 June 1899 as *Hypnum polare*. (H-BR)
Bedford Pen. Is., Cape Sabine; Simmons 17 Aug. 1898 as *Hypnum polare*. (H-BR)
Cape Rutherford; Simmons 21 Aug. 1893 as *Hypnum polare*. (H-BR)
Craig Harbour; Dutilly 1232 as *Hygrohypnum polare*. (MICH, NY)
Head of Tanquary Fjord; Brassard 1536. (UAC, NY, MICH)

Baffin Island
Cape Searle; Steere 33. (USA)
Head of Clyde Inlet; Wynne-Edwards 9264. (NY)
Slidre Fjord; Troeslen 14 July 1952 (DUKE)

United States

Alaska
Mt. McKinley National Park, Deep Canyon; Murie 8 July 1951. (NY)
Brooks Range, Franklin Mountains, Schrader Lake-Peters Lake area just N. of Mt. Chamberlain; Steere 18926. (NY)

Greenland
N. V. Gronland, Faulkefjord; Simmons Aug. 1899. (H-BR)
Hurry Inlet; Dusen 7 Aug. 1899 as *Amblystegium polare*. (H-BR, NY)
Godhavn; Holmen 14400. (S-PA, NY)
Svartenhuk Peninsula, Simiutap kua; Holmen 17103. (NY, S-PA)
Martlek; Berggren 1870 as *Hypnum polare*. (S-PA)
Head of fjord south of Marmorlik; Holmen 16087. (S-PA)
Thule; Fristrip Sept. 1954. (NY, S-PA)
Nothøf Land, T-§; Holmen 19181. (S-PA, NY)
Arsuk; Laqulaury, (S-PA)
Disco Land, Hammersdal; Porsild 340. (S-PA)
Peary Land, S, coast of Independence Fjord; Holmen 7158. (S-PA)
Scoresby sund, Charcots Land; Holmen 18891. (S-PA, NY)

Spitzbergen
Kobbe Bay; Malmberg 1861 as Hypnum polare. (H-SOL)
Augusta Bay. Malmberg 1861 as Hypnum polare. (S-PA,LECTOTYPE)
Wahlenbergs Bay; Malmberg 1861 as Hypnum polare. (S-PA)

Murchison Bay, Celsa bug; Wulff 28 Aug. 1899 as Amblystegium polare. (S-PA, NY)
Kap Foster, Baslandet; Wulff 20 July 1899 as Amblystegium polare. (S-PA)
Kung Karl's Land, Johnsen'sberg; Anderson & Hesselman 17 Aug. 1898 as Amblystegium polare. (S-PA)
Prince Charles Foreland; Beggren 1868 as Hypnum polare. (NY)

Norway
N. Opdal, in Drivan; Lindberg 1 Aug. 1882 as Amblystegium polare. (H-SOL)

Sweden
Lule Lappmark, Jokkmokk; Nyman Aug. 1893 as Amblystegium polare. (S-PA)
Torne Lappmark, Karesuando; Martensson 27 July 1949. (NY,S-PA)
Torne Lappmark, Abiskojokk; Jaederholm 15 July 1917 as Limnobium polare. (S-PA)

Finland
Lapponia ov., Dolgaga guba prope Svjaetoi; Brotherus July 1872. (NY)

Poland
Montes Tatri Ali in valle Kociot Mieguszowiecki, Lisowski 28 Aug. 1956 as Bryotheca polonica #298 as Hygrohypnum polare

France
Haute Garrone, Lac Vat pres Luchon; Husnot, in Musci Galliae 592 as Hypnum palustre var. laxum. (S-PA)

Soviet Union
Siberia, Jenesei, Plachino; Arnell 23 July 1876 as Amblystegium polare. (H-SOL)
Siberia, Jenesei, Tolstoi; Arnell 1 Sept. 1867 as Amblystegium polare. (H-SOL)
Siberia, Ural Mountains, Tobolsk; Sukatschew 30 June 1909. (H)
Siberia, Vostocschye Sajany, the upper part of the Uda R.; Bardunov 11 Aug. 1961. (S-PA)
Novaya Zemlya, Matoschkin Schar; Ekstram 1905. (S-PA)
Novaya Zemlya, Karmakul Bay; Ekstram Aug. 1895 as Amblystegium polare. (S-PA, NY); as Hypnum polare
Rossia Arctica, Terra Franz Josef, insula Aagaard; Savicz 657. (S-PA)
Rossia arctica, Insulae Vise; Savicz 1500. (S-PA)
Asia arctica, Kap Tscheljuschin; Kjellman 19-20 Aug. 1878 as *Amblystegium polare*. (S-PA)
Kola Peninsula, Lap. murmania, flus Harfofka; Brotherus July 1877 as *Amblystegium polare*. (H-SOL)

Great Britain
Scotland
West Ross, north side of Beinn Dearg; Wallace 1 August 1952.
(cited from Wallace 1972)
Hygrohypnum ochraceum (Turn. ex Wils.) Loesk., Moosfl. Harz. 321. 1903.

Synonymy

Hygrohypnum ochraceum (Turn. ex Wils.) Loesk., Moosfl. Harz. 321. 1903.


nom.nud.in syn.


Hynum ochraceum var. complanatum Milde, Bryol. Siles. 376. 1869.

Hynum ochraceum var. flaccidum Milde, Bryol. Siles. 376. 1869.

Hynum ochraceum var. uncinatum Milde, Bryol. Siles. 376. 1869.

Amblystegium ochraceum (Turn. ex Wils.) Lindb., Musci Scand. 33. 1879.


Amblystegium ochraceum var. flaccidum (Mild.) Braithw., Brit. Moss. Fl. 3:59. 1898.


Limnobium *simplicinerve* (Lindb.) Roth, Eur. Laubm. 2:651. 1905.

39f.6. 1905.


*Drepanocaldus furcatus* Roth et Bock, Hedwigia 48:176. 6f.7. 1909.


(Type at S-PA)


*Hygrohypnum ochraceum var. obtusifolium* Spindl. Hedwigia 50:182. 6. 1911.
Hygrohypnum ochraceum var. simplicinerve (Lindb.) Spindl.  
50:184. 6. 1911.


Hygrohypnum dilatatum fo. triste Podp., Vysledky VI. 47. 1912.


Hygrohypnum ochraceum var. flaccidum (Mild.) Amann, Fl. Mouss. Suisse. 2:361. 1912.


Hygrohypnum ochraceum fo. complanatum (Mild.) Moenk., Susswasserfl. 154. 1914.

Hygrohypnum ochraceum fo. filiforme (Limpr.) Moenk., Susswasserfl. 154. 1914.

Hygrohypnum ochraceum fo. obtusifolium (Spindl.) Moenk., Susswasserfl. 154. 1914.

Hygrohypnum ochraceum fo. uncinatum (Mild.) Moenk., Susswasserfl. 154. 1914.


Hypnum pseudolycopodoides Kindb. ex Nichols, Bryologist 19:40. 1916. (Type at S-PA)


Hypnum crassicostatum (Kindb.) Grout, Bryologist. 33:71. 1935. nom. invalid. in synon.

Hygrohypnum ochraceum fo. filescens (Loesk. in Bauer) Podp., Consp. 575. 1954.

Hygrohypnum ochraceum fo. theresianum (Roth) Podp., Consp. 575. 1954.

Nomen nuda


Names of nomen nuda for which the literature has been unavailable for verification.


Names of taxa of which the literature has been unavailable for assessment.

Amblystegium ochraceum var. complanatum (Mild.) Moell., Bot. Not. 1907. 144. 1907.

Amblystegium ochraceum var. complanatum Moell., Fort. sk. vaxt 2 Moss 41. 1907.

Amblystegium ochraceum var. filiforme (Limpr.) Moell., Bot. Not. 1907. 144. 1907.

Amblystegium ochraceum var. flaccidum Moell., Fort. sk vaxt 2 Moss. 41. 1907.

Amblystegium ochraceum var. ovatum (Kaal.) Moell., Bot. Not. 1907, 144. 1907.
1911.

Hygrohypnum dilatum fo. trieste (Podp.) Podp., Vysledky VI.
47. 1912.

Hygrohypnum ochraceum var. ovatum Kall. ex Moell., Bot. Not.
1907. 144. 1907.

Hygrohypnum ochraceum fo. trieste (Podp.) Podp., Cas. Moravsk.

Hygrohypnum ochraceum var. trieste (Podp.) Podp., Skom. Klub.

1876.

1902.

Plants variable; soft or coarse, forming small tufts or extensive mats or swollen tuffs as much as 10 to 15 cm \(^2\), tightly woven or loosely entangled and easily fragmenting; color bright shiny yellow green, dull yellow-green, bright or dull-green, dull olivaceous-green with or without rusty mottling, dirty brown, rarely blackish or blackish-green. Stems 2-15 (20) cm long, variously prostrate and creeping or ascending near the apex; stem tips straight or hooked; stems generally foliose throughout, leaves in older extremities of long stems frequently shredded or absent. Branching irregular, usually widely spaced, in short stems branches are sometimes crowded, long stems are sometimes almost completely unbranched, on other occasions long stems are almost pinnately branched. Stem cross sections revealing 2 to 3 rows of small, thick-walled, yellowish to reddish-brown cortical cells, enclosed by a single outer row of hyaline,
thin walled and often inflated epidermal cells; medullary cells larger, hyaline and thin walled, sometimes becoming thicker walled and discolored with age; central strand well developed. Rhizoids of variable occurrence, apparently humidity dependent, reddish-brown, arising from the base of ventral stem leaves.

Leaves variable among different plants or within individual stems or branches, usually ovate lanceolate or lanceolate, infrequently ovate, rarely broadly ovate; (0.7) 1.0 - 1.8 (2.5) mm long x (0.2) 0.5 - 0.8 (1.2) mm wide; attitude upon the stem variable, crowded or distant, loosely imbricate to spreading, straight or falcate, falcate leaves may have one margin infolded along one side as a wing, or the leaf may be sharply folded along the midline in the upper half of the leaf whereupon the folded portion is then sharply turned to one side or the other, at other times falcate leaves may be concave caniculate, especially in the upper half, straight leaves are shallowly concave to plane; upon drying leaves may become somewhat crisped or not at all, in those leaves that are folded through the midline in the upper half the folded portion tends to curl through several turns upon drying, in leaves that attain larger dimensions there is a tendency for them to undergo shrinkage upon drying, which is accompanied by a tendency to wrinkle and a suggestion of plication; leaf margins entire, except where minutely denticulate or serrulate in the apex; apex acute to long tapering acuminate, obtuse or bluntish; leaves concave to plane; sometimes appearing decurrent by virtue of the persistent cortical stem cells; costa variable, almost absent, short and double, usually long and double with one or both arms reaching midleaf or beyond, or single to midleaf or beyond or single with 1 to 3 lateral forks, generally coarse throughout.

Aerolation variable; median leaf cells fusiform to long linear
flexuose; (30) 37-83 (120) μm long x (4) 5-6 (8) μm wide; cells generally shorter toward the apex; marginal leaf cells becoming shorter toward the apex; toward the base becoming longer or shorter and wider, throughout the middle of the leaf the marginal leaf cells may become shorter, but little wider or longer and narrower than the adjacent median leaf cells; cells toward the leaf base variable generally becoming wider, but variously becoming longer, shorter or changing little in length; basal cells incrassate, pits few to none; alar cells variable, quadrate, rectangular, sometimes linear, thin walled or incrassate, hyaline, almost never discolored, forming an irregularly defined group of cells which occur as 2 to 3 rows of cells which lie along the margin, the row of cells on the margin grades from quadrate at the point of insertion to rectangular to linear at a distance of 4 or 5 cells above the point of insertion, the second and third rows of cells are more vairable and often tend to grade into the adjacent cells.

Plants dioicus; male and female plants similar though the males are more slender; perigonia ovoid; outer perigonial leaves scale like, ecostate, entire; middle and inner perigonial leaves ovate with an abruptly acuminate apex, to 0.9 mm long, entire, ecostate, concave-imbricate, squarrose recurved in the upper half; outer and middle perichaetial leaves ovate and gradually to abruptly acuminate in the apex, squarrose in the upper half, concave below, margins entire except minutely serrulate in the apex, costa variable, short and double, absent; inner perichaetial leaves long tapering lanceolate, to 3.5 mm long, erect, entire except sometimes minutely serrulate in the apex, plicate, costa variable, single, long and double or absent.

Seta 16 to 31 mm long reddish-brown, smooth, erect or slightly arched;
capsule typical for the genus; annulus present, of 2 to 3 rows of cells, deciduous.

Preistome typical for the genus; endostome with 1 to 3 cilia between adjacent segments; spores.

*Hygrohypnum ochraceum* is a polymorphic, yet very distinctive species, which may be distinguished from other species in the genus by the dioecious sexuality, the outer layer of inflated cortical stem cells (Fig. 66a) the variable costa (Fig. 64 a-l) and the nature of the alar cells (Fig. 66 b-e).

The study of herbarium specimens and living cultures have shown that *Hygrohypnum ochraceum* varies in leaf shape and size, the nature of the leaf apex, costal structure, the marginal leaf cells, leaf symmetry, internode length and habit.

The leaf shape usually varies from ovate-lanceolate (Fig. 64a) to lanceolate (Fig. 64k). Ovate leaves (Fig. 64j) frequently occur and so broadly ovate leaves (Fig. 64i), but the latter are rare.

The leaf apex is acute. However, the tip may be sharp (Fig. 65) or blunt (Fig. 65c). The margin of the leaf apex adds further diversity to the leaf by varying from entire to minutely denticulate to serrulate (Figs. 65a and c). All of these variations may occur among the leaves on a single stem.

Through differing in detail, the costa of *Hygrohypnum ochraceum* is as variable as that of *H. luridum*. The costa is usually double with one or both arms reaching midleaf or slightly beyond. However, it may also be short and double, short and single, single to midleaf or beyond, single with 1 to 3 lateral forks or sometimes almost absent. All of these variations may occur frequently among the leaves of a single stem.
The marginal leaf cells occurring through the middle of the leaf exhibit a remarkable variation. They may be longer, shorter or little different from the adjacent median leaf cells. In some cases the long marginal leaf cells are reminiscent of *Hygrohypnum bestii* (Fig. 64d).

The alar region is generally differentiated as a group of quadrate to linear cells forming 2 to 3 rows of cells extending along the margin of the leaf for a distance of 4 to 6 cell lengths above the point of leaf insertion (Fig. 66 b-ë). The marginal row of alar cells characteristically varies acropetally from quadrate through short rectangular to rectangular or even linear (Figs. 66 b-d). The inner rows of differentiated alar cells are less regular in their form. In some cases the basal cells become enlarged and thin walled. In such cases the basal cells and alar cells merge with little differentiation between them, save for the row of marginal cells (Fig. 66e).

Leaf symmetry and size, internode length, and overall appearance have played important roles in the recognition of apparent subspecific taxa. Each of these characters is variable and each may influence the other.

The leaves of *Hygrohypnum ochraceum* vary from straight to falcate uncinate. As in the case of *H. luridum* and *H. polare*, the variation between straight and curved leaves may occur between different plants or within individual plants. Within individual plants stem segments bearing straight leaves have been observed giving way to falcate or circinate leaves or vice versa (Fig. 63c). In other cases stems have been observed bearing straight leaves, while branches bore falcate leaves.

The falcate nature of the leaves of *Hygrohypnum ochraceum* varies. In some specimens with small leaves the leaves are concave-caniculate and the falcation is evident throughout the leaf (Fig. 63b & d). Such
leaves are firm and retain their appearance whether wet or dry. In other cases the lower half of the leaf is more or less ovate-concave and straight. The upper half of the leaf is infolded along its midline and then decidedly falcate (Fig. 64g). The folding in the upper half imparts a caniculate appearance to the leaves. Upon drying such leaves may twist through several turns of this folded upper half (Fig. 63e). In other falcate leaves one side of the leaf may be infolded as a wing and the leaf is then curved away from the side of the fold (Fig. 64d).

Straight leaves vary in two ways. They may either be loosely imbricate-spreading (Fig. 63c), or they may be somewhat complanate (Fig. 63a).

Leaves that occur along a gradient of increasing length and width also exhibit an increased flaccidity. A measure of this softness is the conspicuous side to side or lateral shrinkage that accompanies dessication in larger leaves. The shrinkage results in crisping or wrinkling. In those large falcate leaves which become folded and twisted in the upper half, the twisting becomes especially pronounced (Fig. 63e).

The internode length varies from short, such that the leaves are crowded imbricate (Fig. 63c) to long, such that the stem is clearly visible between adjacent leaves (Fig. 63a). Plants that have been grown in culture have uniformly responded by increasing the internode length beyond that attained under natural conditions. The reciprocal reaction of internode shortening was not observed.

Among the plants bearing falcate leaves leaf size, internode length and leaf shrinkage and crisping upon drying may looked upon as increasing parallel to one another. Among many specimens almost continuous variation can be observed from small, firm, closely spaced
falcate leaves to larger, flaccid, widely spaced leaves which are markedly shrunken and crisped when dry. Remarkable, specimens from opposite ends of this spectrum that have been studied in culture have responded by producing less falcate to almost straight, complanate leaves with long internodes.

As number 645 of Bauer's Musci europaei exsiccati Loeske described *Hygrohypnum ochraceum* var. *filescens* as "forma filescens, foliorum apicibus valde brevibus." Limpricht's original description of *H. ochraceum* var. *filiforme* (Krypt. Fl. Schles. 1:63. 1876) was unavailable for examination. However, Limpricht's (1904) recharacterization of the plant-stated "sehr lang fluthend, fadenformig, mit fast drehund beblattern, sehr dunnen, verlangerten Aesten. Blatter kurz zugespitzt...." The leaf apex has already been shown to be a variable character. Very long stems or branches do not necessarily have to have long internodes. Examination of two specimens of the Bauer exsiccata has shown that the very long stems also have variously elongated internodes and straight or falcate leaves. This taxon is rejected for it is based on variable features.

Each of the criteria employed by Milde (1969) to characterise and distinguish *Hypnum ochraceum* var. *flaccidum* and *H. ochraceum* var. *complanatum* are based on variable features. The two taxa were seen to share "Stengel lang," and leaves "breit-lanzettlich" or "breit-lanzettformig" and "locker abstehend" or "locker beblattern." Variety *flaccidum* was described as "blatter uberall allseitig abstehend, einfarbig braun, "whose leaves were "lang zugespitzt," whereas var. *complantatum* was described as "blatter fast zweireihig gestellt, locker stohend abstehand, nirgends einseitwedig, saftig, grun, einfarbig," with leaves "kurzer zugespitzt." Color varies widely within individual plants and throughout the species. A complanate and/or spreading attitude on the leaves has been produced in culture from
plants otherwise bearing falcate leaves. Since the two taxa based on variable characters they are rejected.

Milde (1869) also described *Hypnum ochraceum* var. *uncinatum* on the basis of the "stengel an der spitze hakenformig einwartzgekrummt, Blatter einseitwendig, langlich, lanzugespitzt, stumplich, roth und grun geschecht." Numerous specimens exhibit variation of this basic form, but as was pointed out earlier, leaf falcation is a highly variable feature and cannot effectively be used delimit a taxon.

Lindberg in Hult (1886) placed much weight upon "nervo semper simplici crassiusculo" in his characterization of *Amblystegium simplicinerve*. Collected by Hjelt & Hult from the Ounasjoki River near Rovaniemi in Finland (at H-SOL) the holotype clearly exhibits as many leaves bearing short and double costae as it does strong single costae. The attitude of the leaves also varies from flacate to straight and imbricate. The plant is an average example of *Hygrohypnum ochraceum*.

Neither the type description nor any specimen of *Hygrohypnum ochraceum* fo. *ovatum* (Kaal.) C. Jens. have been available for examination during this study. Jensen's (1939) brief description clearly remarks on the ovate nature of the leaves and the short, broad leaf apex. Both of these features are variable. Should the type of this taxon become available it is likely that it will be shown that it is no more than a form of *H. ochraceum*.

Spindler (1911) provided neither a formal description nor a clear reference to a holotype for his *Hygrohypnum ochraceum* var. *obtusifolium*. However, at H is a Spindler specimen present at duplicates, which bear the name *H. ochraceum* nov. var. *obtusifolium*. The plants are usually dark and encrusted with soil and algal particules. The leaves are broad and their apices obtuse, but otherwise there is nothing unusual about the plants.
The type description of *Hygrohypnum dilatatum* ver. *triste* Podp. has not been available for study. However, a lone Podpera collection bearing this name dated 1909 from S-PA proved to be a flaccid, falcate leaved form of *Hygrohypnum ochraceum*.

The only other species of *Hygrohypnum* with which *H. ochraceum* could be confused is *H. luridum*. Such confusion can occur only through their superficial similarity for they are fundamentally very different. The following chart will point out the important differences.

<table>
<thead>
<tr>
<th></th>
<th><strong>H. ochraceum</strong></th>
<th><strong>H. luridum</strong></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sexuality</td>
<td>Dioicous</td>
<td>Autoicous</td>
</tr>
<tr>
<td>Annulus</td>
<td>Present</td>
<td>Absent</td>
</tr>
<tr>
<td>Stem cross section</td>
<td>Outer cortical layer inflated and thin walled.</td>
<td>All cortical cells small, thick walled.</td>
</tr>
<tr>
<td>Alar cells</td>
<td>2 to 3 vertical rows of quadrate to rectangular or linear cells increasing in length acropetally. Of-thin walled, seldom discolored, never excavated.</td>
<td>Generally many small, quadrate to short rectangular cells, usually incrassate and discolored, sometimes excavated.</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>Variously acute, acuminate, entire or denticulate or serrulate, sometimes obtuse.</td>
<td>Always acute and entire, margins sometimes inrolled as to differentiate a pseudoapiculus.</td>
</tr>
</tbody>
</table>
Fig. 63 a–e. Variation in the habit of leafy shoots of *Hygrohypnum ochraceum* and comparisons between the wet and dry conditions in the shoots

a. A shoot with widely spaced, complanate leaves.
b. The ventral view of a shoot with strongly falcate leaves.
c. A shoot with falcate and straight, narrowly lanceolate leaves.
d, e. A shoot with strongly falcate leaves as seen in the moist (d) and dry (e) conditions.

Scale: These shoots are approximately 1.2 cm long
Fig. 64.a - 1. Variation in the leaf shape of *Hygrohypnum ochraceum*.

Scale: [--- 1mm ---]
Fig. 65 a - i. Cellular detail of the foliage leaves of *Hygrohypnum ochraceum*.

a - c, f. Leaf apices.

d, e. Marginal leaf cells.

g - i. Median leaf cells.

Scale:

```
   a - c, f;    100um
   d, e, g - i; 100um
```
Fig. 66a–e. The stem anatomy and the variation in the alar cells of *Hygrohypnum ochraceum*.

Scale:

a;  

100um 

b–e;  

100um
Fig. 67. *Hygrohypnum ochraceum*
Exsiccati Examined

Allen, Mosses of the Cascades Mountains, Washington
139b. (MICH, NY, MIN, USA, TENN)
140 as Hypnum palustre. (NY, H. ochraceum in part)

Austin, Musci Appalachiani #437 (NY)

Bauer, Bryotheca Bohemica
#69 as Hypnum ochraceum. (C, LE, S-PA)=
#267 as Hypnum ochraceum. (C, H, LE, S-PA)

Musci europ. et. amer. exsiccati #2186. (BRNM)

Musci europaei exsiccati
#644 as Hygrohypnum ochraceum var. complanatum fo. latifolia Roth. (BNM, H)
#645. (BRNM, H)
#646. (BRNM, H)
#647. (BRNM, H)
#1283. (BRNM)
#1284. (BRNM)

Brotherus, Bryotheca Fennica #85 as Hygrohypnum ochraceum. (LE)

Grout, North American Musci Pleurocarpi
#111. (CANM, H-BR, MO, NY S-PA, UC, UBC)
#111a. (H-BR, NY, USA, MICH, TENN, UC, MIN, MO)
#240. (H-BR, NY, USA, MICH, TENN, UC, MIN, MO, WTU)
#278. (S-PA H-BR, NY, USA, MICH, UC, MIN, MO)
#299. (H-BR, USA, MICH, TENN, UC, MIN, MO)
#380. (H-BR, NY, USA, TENN, UC, MIN, MO)
#386. (H-BR, NY, USA, MIN, TENN)
#467. (S-PA, NY, USA, MICH, TENN, UC, MIN, MO)

North American Musci Pleurocarpi Supplement #62. (MIN, UC)

Husnot, Musci Galliae. #496. (NY, S-PA)

Kerner, Flora Exsiccata Austro-Hungarica #3511 as Hypnum ochraceum.
(C, LE, S-PA, BP, H, NY)

Limpricht, Bryotheca Silesiaca
#91. (BP, LE, S-PA)
#348. (BP)
#349. (BP, LE, NY, S-PA)

Lisowski, Bryotheca Polenica
Fasc. XI, #320, (BP, H, S-PA)
#321. (H)
#322. (BP, H)
Fasc. XIV, #393. (BP, H, LE, S-PA)
#394. (BP, H)
Fasc. XX, #549. (BP, S-PA)
Fasc. XXX, #792. (BP, S-PA)
#793. (BP)
Fasc. XXXI, #821. (BP, H, S-PA)
#822. (S-PA)

Macoun, Canadian Cryptogams #141 as Hypnum palustre. (USA)

Canadian Mosses
#397. (CANM, H, MICH, MO, NY, LE, UBC)
#490. (MO)

Canadian Musci
#360. (MICH, MIN, UC, USA, TRTC, S-PA)
#396. as Hygrohypnum alpestre. (C)
#898. as Hypnum palustre. (USA)
Matouschek, Kryptogamae exsiccatea
  #1287 as Hypnum ochraceum. (C, H, LE, S-PA)
  #1288 as Hypnum ochraceum var. filiforme. (H)
Migula, Cryptogamae Germaniae, Austriae at Helvetiae exsiccatea
  #270 as Hypnum ochraceum. (C)
  #271 as Hypnum ochraceum var filiforme. (C, MIN)
  #375 as Hypnum ochraceum. (C)
Muller, Westfallen Laubmoose #244. (BP, S-PA)
Noguchi and Hattori, Musci Japonica #705. (S-PA)
Petrak, Flora Bohemiae et Moraviae exsiccata Lfg. 4, Nr. 175 as
  Hypnum ochraceum var. uncinatum. (C)
Pilous, Musci czechoslovenici exsiccati
  #84. (H)
  #111. (H)
  #142. (H)
  #168. (H)
  #239. (H)
  #428. (H)
  #690. (H)
  #705. (H)
  #707. (H)
  #757. (H)
  #1184. as Hygrohypnum ochraceum var. uncinatum. (C,H)
Piper, Musci Occidentali-Americani #79 as Hypnum palustre. (USA)
Rabenhorst, Bryotheca europaea
  #693. (S-PA)
  #693b. (S-PA)
  #693c. (S-PA)
  #693e. (S-PA)
  #844 as Limnobium ochraceum. (C)
Slezske museum v Opaue-Museum Silesiae, Sectio Botanica Opava,
  Musci et Hepaticae exsiccati #94 as Hygrohypnum ochraceum.
  (C, BP, S-PA)
Sullivant and Lesquereux, Musci Boreali Americani
  Ed. I, #305, (MICH, NY)
  Ed. II, #452. (MICH, NY, NYS)

Selected Specimens Examined
Canada
  British Columbia
    Queen Charlotte Islands, Moresby Is., S. side of Takakia Lake;
    Schofield 25200. (UBC)
    Queen Charlotte Islands, Graham Is., head of Dawson Inlet;
    Schofield & Vaarama 24619. (UBC)
    Mt. Seymour Provincial Park; Schofield 19948. (UBC)
    Prince Rupert Area, Hays Mt., Kaien Is.; Schofield and Sharp
    25840. (CANM, UBC)
    Vancouver Island, Port Renfrew, San Juan Point; Schofield 13730
    (UBC, TENN, NY)
    Caribou District, Mt. Ishpa; Boas 654. (CANM, UBC)
    Kokanee Glacier Prov. Park; MacFadden Aug. 1924. (UBC, TENN, USA)
    Vancouver Island, Burman Lake; Boas 218. (UBC)
British Columbia (continued)
Revelstoke Area, Big Bend of the Columbia River, Selkirk Mtns.; MacFadden 3863. (CANM, UBC)
Wells Gray Prov. Park, Battle Mtn., S. of Fight Meadows; L. and T. Ahti 14154. (H, UBC)
Garibaldi Prov. Park, Sentinel Glacier Area; Schofield 32947. (CANM, UBC)
Mt. Cheam; Macoun 12 Aug. 1901. (CANM)
Griffin Lake; Macoun 10 Aug. 1889. (CANM)
Rogers Pass; Macoun #370, 2 Aug. 1890. (CANM)

Alberta
Jasper Natl. Park, Tonquin Valley; MacFadden 3871. (CANM)
Little Slave Lake; Macoun 1872. (CANM)
Waterton Lakes Natl. Park, N. shore of Cameron Lake; Hermann 20560. (NY)

Ontario
Muskoka Dist., Muskoka R., High Falls; Hand 758. (CANM, TENN)
Algoma Dist., Agawa Bay, Lake Superior Prov. Park; Ireland 4791. (CANM, USA)
Thunder Bay Dist., S side of St. Ignace Is., Garton 7028.
Algonquin Park, Brewer Lake; Cain 764. (TENN, TRTC)
Sarnia; Macoun 11 Aug 1891. (NY)
Bruce Peninsula, Sauble Falls; Moxley 24 May 1936. (NY)
Haliburton Dist., Irondale; Cain 5000. (TRTC)

Quebec
NE of Luskville, Luskville Falls; Ireland & Ley 10018. (CANM)
Parc du Mont Tremblant, E. of Lac Monroe; Hermann 16747. (CANM)
Gaspe Bay, near Fort Prevost; Crum and Williams 10831. (CANM)
Graciefiel, near Blue Lake; Crum 8271a. (CANM)
Mont St. Hilaire; Dupret 8 Sept 1906. (CANM)
Montmorency River; Macoun 520. (CANM)
Argenteuil Co., Lakefield near La Chute; Cook 10. (CANM)
Comte de Matane, Lac a' Foin; Boivin & Blaind 693. (MICH)
Rimouski Co., Pointe au Pere; Lepage 13535. (USA)
Beauceville; Anselme 15 July 1943. (TRTC)

Nova Scotia
Annapolis Co.\^ Kejimkujik National Park, Mill Falls of Mersey R., Ireland 12473. (ALTA, CANM)
Inverness Co., Cape Breton Highlands Natl. Park, Buelach Ban Falls; Ireland 11848. (CANM)
Colchester Co., Upper Brookside, NE of Truro; Smith 2 July 1931 (MICH)
Antigonish Co., near James River Station, Glen Bard; Grout 6431. (MICH)
Kings Co., White Rock Dam; Erskine 53c2462. (NSPM)

New Brunswick
Albert Co., Fundy Natl. Park, road to Marven L.; Ireland 11247. (ALTA, CANM)
Queens Co., Caanan Forks; Moser 1889. (CANM)
Madawaska Co., Little R., Habeeb 21 June 1944. (NY)
Bass River; Fowler 30 May 1870. (NY)

Newfoundland
Waterford R. at Browning Park; Damman 6. (CANM)
Broad Cove; Waghorne 1034. (CANM)
Beechy Cove; Waghorne 20 Aug 1895. (NY)
Labrador
Battle Harbour; Waghorne 410. (CANM)
L'Anse au Clair; Waghorne 31 July 1893. (NY)

Yukon Territory
Bonanza Creek; Williams 9 June 1899. (NY, USA)
Hunker Creek; Macoun 26 July 1902. (S-PA)

United States
Alaska
Adak Is.; Jordal 2759. (USA, TENN)
Yakutat; Stair 4928. (TENN)
Amchitka Is., near Cyril Cove; Sjacklette 7178. (MICH)
Attu Isl., near Massacre Bay; Jordal and Miller 2986. (MICH)
Mt. McKinley Natl. Park, Eilson; Sherrard A22. (USA)
Juneau, Montana Creek; Hermann 22087h. (USA)
Sitka; Macoun 26 Sept 1891. (NY)
Anchorage, Fire Lake; Lepage 9-6-48. (NY)
Cape Lisburne; Steere & Crum 20540. (NY)

Washington
Jefferson Co., Olympic Natl. Park, Mt. Olympus; Becking 5309992. (WTU)
Grays Harbor Co., Westport; Foster Aug. 1909. (WTU)
Mt. Rainier Natl. Park, Paradise Valley, Frye 27. (WTU)
Yakima Co., Mt. Adams; Lawton 5176. (WTU)
Chelan Co., Stevens Pass Area; Frye 3252. (WTU)

Oregon
Hood River Co., Mt. Hood Natl. Forest north of Bennett Pass; Lawton 3226. (WTU)
Newport, at Stocker Mill; Daughtery 8 Aug. 1921. (WTU)
Clackamas Co., SW slope of Mt. Hood; Hermann 18705. (WTU)
Klamath Co., Crater L. Natl. Park; Mueller 6672. (HSC)
Union Co., Wallawa Mtns., SE of Union; Hermann 18872. (USA)
Wallawo Co., SE of Imnaha, Hat Point; Hermann 18932. (USA, NY)

California
Trinity Co., Coffee Creek near South Fork; Norris 9361. (HSC)
Siskiyou Co., Marble Mountain Wilderness Area; Spjut 1194. (HSC)
Eldorado Co., Echo Lake; Conard 5 Sept 1947. (MICH)
Shasta Co., Lassen Natl. Park near Summit Lake; Koch 1923. (MICH)
Mono Co., H.M. Hall Natural Area; Catcheside 47120. (MICH)
Plumas Co., Plumas Natl. Forest, N. fort of Feather R.; Koch 1893. (NY)
Mariposa Co., Big Tree Grove

Idaho
Boundary Co., Bonner's Ferry; Frye 9 Sept. 1928. (WTU)
Lemhi Co., N. of Gibbonsville; Frye 1 Sept. 1939. (WTU)
Kootenai Co., Hope; Sandberg Aug 1892. (NY, USA)
Custer Co., Sawtooth Wilderness Area, Forks of Baron Creek; Morton 8584. (USA)

Montana
Mineral Co., Henderson; Frye 20 Aug 1925. (WTU)
Glacier Natl. Park, Logan Pass; Hermann 20654. (WTU)

Utah
Above Salt Lake; Evans 15 Aug. 1924. (NY)
Wasatch Mtns. N. of Ogden R., Kelley 4 Aug. 1925. (NY)
Nevada
Elko Co., Humboldt Natl. Forest, SW of Mountain City, Lawton 2710. (NY, TENN, UBC)

Arizona
Apache Co., Mt. Baldy; Phillips & Haring 9071. (MICH)

Wyoming
Fremont Co., W. of Dubois, Two Roger Pass; Frye 22 June 1931. (WTU)
Carbon Co., Medicine Bow Mtns. SE of Morgan; Hermann 17809. (USA)
Teton Co., Teton Natl. Pk., Cascade Canyon; Cain 4547. (UAC, TRTC)
Yellowstone National Park; Roell 2 Sept. 1888. (LE)

Colorado
Larimer Co., Rocky Mtn. Natl. Park; Longs Peak; Kiener 7310. (MICH)
Gilpin Co. near Tolland; Grout, July 1914. (USA)
Mount Axtell Area; Tidestrom 8 Aug. 1910. (USA, S-PA)
San Juan Co., San Juan Mtns., SSW of Silverton; Hermann 23303. (NY)

Michigan
Keweenaw Co., near Horseshoe Harbor; Steere Sept. 1935. (MICH)
Alger Co., Au Train Point; Steere 471. (MICH)

Minnesota
Cook Co., Grand Marais, Rosebush Falls; Holzinger 28 July 1902. (NY, S-PA)

Pennsylvania
Cambria Co., near Summit; James Aug. 1859. (TENN)
Monroe Co., Pocono Forks; James Nov. 1868. (TENN)
Pike Co., Saw Creek near mouth of Big Bushkill; Glime 30 July 1965. (MICH)
Chester Co., W. of Oxford; Stair 6/1/47. (MICH)
Montgomery Co., Evansburg; Taylor 2501. (MICH)
Bradford Co., Bennett Brook; Burnett 18 Aug 1895. (NY)

New York
Greene Co., E. of Haines Falls Village; Hermann 14440. (TENN, TRTC)
Essex Co., Mt. Marcy Trail; Smith 17 Aug 1934.
Yonkers; r. Howe. (MICH, S-PA)
Lake George, Huletts Landing; Jelliffe 21 June 1889. (NY)
Sand Lake; "C.H.P." 1865. (NY)
Penn Yan Saw Mill; Rumstead. (NY)

Vermont
Manchester Co., Downer's Glen; Thompson 2 Sept 1934. (MICH)

New Hampshire
Marlow, near Sand Pond; Allen & Stair 8/3/39. (MICH)
White Mountains, near Mt. Madison; Taylor 2496. (MICH)
Mt. Belknap, Gilford; Carter 5 Sept. 1904. (USA)

Maine
Mount Katahdin, cliff at Falls above Camp Baxter; Allard 5171 (MICH)
Cumberland; Collins 2500. (MICH)
Acadia Natl. Park, Mt. Desert; Taylor 3357. (MICH)
Oxford Co., Canton Point; Parlin 11581. (NY)

Massachusetts
Berkshire Co., Plantain Pond Britton 13 Aug. k901. (NY)
Essex Co., Amesbury; Huntington 4. (NY)

Connecticut
New Haven, Wintergreen Falls; Allen 15 June 1878. (NY)

Rhode Island
Greystone; Collins 2138. (MICH)

Maryland
Garrett Co., NNW of Oakland, Swallow State Falls Forest, Hermann 14917. (USA)
New Jersey
   Rosemont; Best 1894.  (NY)
Virginia
   Giles Co., Mountain Lake; Sharp V267.  (NY)
West Virginia
   Blackwater Falls; Smith 5 July 1878.  (NY)
Greenland
   Disco Island, Diskofjord Kuanit; Porsild 949.  (NY)
   Kvarak vid Fredersksdal Marti; Vahl.  (H-BR)
Great Britain
   Cornwall, near Penzance; Curnow Sept. 1863.  (S-PA)
   Lancaster, Todmorden; Schimper 1865.  (S-PA)
   York, Hebden Bridge; Hunt May 1865.  (H, S-PA)
Wales
   North Aber; Wilson May 1863.  (S-PA)
   Cum Idwal; Yong 1932.  (S-PA)
Scotland
   Braemar; Head of Far Easedale; Binstead Oct. 1924.  (H)
Ireland
   Killarney; Lindberg July 1873.  (H)
France
   Vogeses; Pierrot Juli 1884.  (S-PA)
   Haute Savoie, Bord du hac du Breveu; Guinet Auot 1888.  (S-PA)
Austria
   Salzburg, Gastein; Swanziger.  (S-PA)
   Tirol Achenseeohf; Suse Aug. 1895.  (S-PA)
   Steiermark, bei Schladming; Breidler 5/9/1884.  (S-PA)
   West Tirol, Moosbachthal bei St. Anton am Arlberge; Schiffner 7.8.1907.  (BP, S-PA)
Germany
   Thuringer, Overhof; Rose.  (S-PA)
   Berchtesgaden; Suse 1 Sept. 1895.  (S-PA)
   Bayerischen Wald (Hauptberg); Freiberg 25 Oct. 1955.  (S-PA)
   Harz; Hespe 240.  (S-PA)
Belgium
   Bouillon; Cardot 10 Julliet 1881.  (H)
Czechoslovakia
   Vysoke Tatry, vallis Vel Studena; Vajda 13 July 1961.  (BP)
   Tatra Minor, prope Luchy; Vajda 10 Oct. 1965.  (BP)
Poland
   Silesia septentia, Montes Jeseniky; Duda 30 July 1950.  (BP)
   Sudety Mountains, as Bryotheca Polanica Fasc. XIV #393  (BP)
   Montes Carcontici, as Bryotheca Polonica #320.  (BP)
Hungary
   Carpath. Meridion, In rupibus irrigatis rivi Riu mare Gura Zlata, montes Retyezat; Vajda 12 July 1968.  (BP)
Spain
   Hispanien centr. Sierra de Credos; Levier 12 Aug. 1878.  (NY, S-PA)
Portugal
   Minho Prov., V-la Celova de Cerveira eutre Beuporta e campos vale volla do a norte flutuando presa sos granitos nos cursos de qua aqua corrente; Leha 20078.  (S-PA)
Faroes
   Sydiro Traugesvaag; Jensen 12/8/1896.  (H, S-PA)
   Bordo, Gravendal; Jensen 17 May 1896.  (H, S-PA)
Iceland
Lladara, Nord Isl.; Davidsson 30 June 1903. (S-PA)
Tunga Fos; Peddersen 25 June 1886. (H)
N. Isls., Eyjafjorden; Davidsson 21 Aug. 1897. (H, S-PA)

Bear Island
Beeren Eiland, Nordhamnen; Bergren 1868. (C, H, S-PA)

Norway
Gudbrandsdalen; Berggren June 1865. (S-PA)
Gausta; Jaederholm July 1895. (S-PA)
Telemark, Bo Lifjell; Stormer 30 Aug. 1937. (S-PA)
Troms, Nordreisa, Nyholmen; Arnell 22 Aug. 1891. (S-PA)
Rogaland; Hakelier 20 June 1958. (S-PA)
Hardanger; Greir 2 Aug. 1894. (S-PA)
Nord Trondelag; Hulphers 1 Sept. 1934. (S-PA)
Nordland; Arnell 20 July 1869. (S-PA)
Finmarken; Zetterstedt 6 Aug. 1868. (S-PA)

Sweden
Skane; Gronvell Juli 1887. (S-PA)
Halland; Hjarne 14 May 1942. (S-PA)
Oestergotland; Dusen 21 June 1889. (S-PA)
Vastergotland; Hulphers Juli 1930. (S-PA)
Bohuslan; Thedenius Juni 1883. (S-PA)
Dalsland; Larson 7 Sept. 1916. (S-PA)
Narke; Waldheim 6 June 1931. (S-PA)
Sodermanland; Florin 25 Aug. 1929. (S-PA)
Vastmanland; Tarnlund 14 Sept. 1944. (S-PA)
Varmland; Johannsson 30 June 1928. (S-PA)
Dalarna; Moller 13 July 1909. (S-PA)
Halsingland; Collinder June 1878. (S-PA)
Medelpad; Collinder 18 Sept. 1889. (S-PA)
Harjedalen; Einander 9 Aug. 1892. (S-PA)
Jamtland; Seth 21 July 1895. (S-PA)
Angermanland; Arnell 30 July 1906. (S-PA)
Norrbotten; Moller 5/8/12. (S-PA)
Asele Lappmark; Hulphers 15 July, 1943. (S-PA)
Lycksele Lappmark; Hulphers July 1933. (S-PA)
Lule Lappmark; Hulphers Juli 1935. (S-PA)
Torne Lappmark; Ekstrand 5 Aug. 1880. (S-PA)

Finland
Helsingfors; Lindberg 30 June 1868. (S-PA)
Tavastia australis; Collin July 1887. (S-PA)
Osterbotten; Lackstrom 5 July 1873. (S-PA)
Lapponia Keminsis; Hult 12 July 1877. (S-PA)
Kuusamo; Brother 14 July 1883. (S-PA)
Utsijokk; Hult 30 July 1870. (S-PA)
Kemin Lappmark; Ulvinen 11 Aug. 1962. (S-PA)
Karelia australis; Fagerstrom 25 Aug. 1964. (S-PA)
Savonia borealis; Kotilainen June 1917. (LE)

Spitsbergen
Green Harbour; Berggren 1868. (H, S-PA)

Soviet Union
Guba Vologda, distr. Totemsk; Korezagin 29 July 1926. (S-PA)
Siberia, Jenesei, Asinova; Arnell 4/7/1876. (H, H-BR, LE, NY, S-PA)
Syd-Kamchatka; Hulten 10/9/1921. (S-PA)
Siberia, in valle flum Lena, Kumachsur; Nilsson-Ehle 26 July, 1898. (LE, H, S-PA)
Soviet Union (Continued)

Transbaikalia distr. Taxhita, Yamarovka; Mikhno 20 July 1905 (H-BR)
Amur Region, Zei in jugo Tukuringz; Kuseneva 315. (H-BR)
Altai distr., Birsk; Kursky 26 June 1909. (H-BR)
Lapponia tulomensis, prope Alexandrovsk; Savicz, Savic & Nykolsky 28
(S-PA)

Jenisei, Mjelnitsa; Arnell 12 July 1876. (S-PA)
Jenesei, Plachino; Arnell 23 July 1876. (S-PA)
Jenesei, Patagovskoye; Arnell 25 July 1876. (S-PA)
Jenesei, Antisferova; Arnell 27 July 1876. (S-PA)
Jenesei, Tolstoiyos; Arnell 18 Aug. 1876. (S-PA)
Jenesei, Alinskoye; Arnell 9 July 1876. (S-PA)
Lapponia imandrae, in alpp. Umtek; Kihlman 24 July 1892. (S-PA)
Lapponica murmanica; Brotherus Juli 1885. (S-PA)
Lapponia varsugae, Pjalitsa; Kihlman 16 Aug. 1889. (S-PA)
Lapp. or., Jokonga; Brotherus July 1872. (S-PA)
Karelia lodogensis, Svanlahte; Huuskonen 28 July 1937. (S-PA)

Mongolia

Orchon; Lewin 17 Aug. 1891. (H-NR)

Japan

Twashiro Prov., Mt. Bandai; Usmatsu May 1908. (H, MICH)
Eniwa Prov., Mt. Tburi; Takewaki 2/11/1921. (S-PA, H)
Shinano Prov., Mt. Shirouma; Ishiba 17 Aug. 1909. (H-BR)

Holotype: Germany, Geroldsau prope Baden-Baden; Schimper 1854. (BM)


Hypnum eugyrium (B.S.G.) Sull. et Lesq., Musci Bor. Am. 66. 1856.


Amblystegium eugyrium (B.S.G.) Lindb., Musci Scand. 33. 1879.


Amblystegium eugyrium var. mackayi (Schimp.) Braithw., Brit. Moss Fl. 3:62. 1898.

Hygrohypnum mackayi (Schimp.) Loesk., Moosfl. Harz. 321. 1903.

Limnobium mackayi (Schimp.) Roth, Eur. Laubm., 2:648. 56f.5. 1905.

Hygrohypnum eugyrium var. mackayi (Schimp.) Broth., Nat. Pfl. 1(3): 1040. 1909.

Names treated as synonyms elsewhere, but for which the literature was unavailable for assessment during this study.


Names of certain taxa for which the literature was examined, but
found inadequate for effective assessment of the taxon in the absence of the type specimen.


Plants forming loosely, often easily fragmenting patches or tufts, sometimes tightly woven, color variable, yellow-green, pale green, bright green, often exhibiting a golden-brown to deep metallic red mottling, plants frequently becoming a dark red, reddish-brown or brown with age, most plants exhibit a striking satin-like lustre or sheen. Stems (1) 2-4 (6) cm long, prostrate or ascending near the tip, older extremities may become denuded with age, stems initially green or yellow-green, but becoming red or reddish-brown with age. Branching irregular, branches mostly ascending, sometimes almost erect; often the older, but still foliose portions of both the stems and branches become clogged with silt and sand. Stem cross sections revealing 3 to 5 rows of small, thick walled cortical cells, color varying with age, the epidermal cells frequently slightly less darkly pigmented than the adjacent cortical cells, further the outer tangential wall of the epidermal cells is often slightly thinner walled; medullary cells are initially thin walled and hyaline, but become somewhat incrassate and discolored with age; central strand present.

Rhizoids few to none, arising from the bases of ventral stem or branch leaves.

Leaves variable; ovate, oblong-lanceolate to lanceolate, straight or falcate; (0.8) 1.1 - 1.8 (2.0) mm long x (0.3) 0.5-0.8 (1.2) mm wide; leaves generally crowded or among plants or stems with lanceolate-falcate leaves somewhat distant, variously appressed or loosely imbricate or loosely spreading; attitude changing little from the wet to the dry condition; leaves generally quite concave though slightly less so in some
more lanceolate leaves; leaf base usually clasps the stem; margins variable, entire or a few small teeth on the apex, plane or variously folded or inrolled, one side may often be infolded as a wing, in which case that side of the leaf which exhibits the fold is situated closest to the dorsal side of a more or less prostrate stem or branch or both margins may be inrolled in the upper half creating a tubulose condition which is common among more lanceolate leaves; the overall leaf configuration is decidedly modified by the clasping leaf base; Apex variable, acute, abruptly or gradually long tapering, margins often inrolled slightly below apex giving the impression of an apiculus, entire, or with a few teeth in the extreme tip; costa usually short and double, frequently double with one or both arms reaching midleaf, rarely single to mid leaf or beyond and/or forked.

Aerolation variable; median leaf cells fusiform-flexuose or linear flexuose; 30-80 um long X 4-6 um wide, separating into two groups geographically, North American plants usually 45 to 75 um X 4 to 5 um., European plants usually 30 to 62 um. X 4 to 5 um.; cells becoming shorter or changing little toward the apex; cells toward the base variable, becoming shorter or longer, but increasing in width only slightly; basal cells generally strongly pitted; alar region composed of 6 to 12 enlarged or inflated, usually excavated, quadrate to rectangular cells, which form a clearly defined group, the cells hyaline or become bright dark red or reddish-brown with age, the marginal alar cells are always thin-walled while the inner alar cells are regularly incrassate and occasionally pitted, the pigmentation upon aging of the incrassate cells may become so intense as to obscure the cell lumina.

Plants monoicous; perigonial leaves broadly ovate, up to 0.8 mm long, abruptly accuminate; inner perigonial leaves deeply concave-imbricate, margins entire or sometimes weakly serrulate in the apex, ecostate; outer
and middle perichaetial leaves ovate to broadly ovate, generally tapering gradually to a long point, apex entire or frequently coarsely serrate, erect or slightly spreading, the upper half twisting upon drying; inner perichaetial leaves erect long linear lanceolate, tapering to an acute or acuminate, entire or coarsely serrulate apex, 2 to 4 weakly to strongly developed plicae, costa variable, absent, short, double and faint, double to midleaf, infrequently single to midleaf.

Seta 13 to 26 mm long, yellowish brown, to red, smooth, when wet erect to slightly arcing, twisting when dry.

Capsule typical for the genus.

Peristome typical for the genus, annulus large to 2 to 3 rows or cells, dehiscent; spores 12 to 20 um; finely papillose; 2 to 3 slender, finely papillose-cilia.

Hygrohypnum eugyrium is a very clearly defined species. Several features are useful in diagnosing the species, the most important of which is the nature of the alar cells. The alar cells are characteristically quadrate to rectangular and inflated (Fig. 69 h-i). In no other species is the genus are the alar cells so regularly inflated. In most cases the alar cells are also conspicuously excavated. When young the alar cells are hyaline, but age they acquire a very characteristic red or reddish brown color. The walls of the marginal alar cells are thin (Fig. 69h). However, the interior alar cells regularly become incrassate with age and frequently pitted (Fig. 69i). Leaves selected for examination of the alar cells should be taken only from well developed stem or branch segments.

The lustre exhibited by H. eugyrium is frequently useful as a field or dissecting microscope character. The apparent nature of the cell wall
material on the leaf surface and the areolation pattern seem to impart an almost satin-like sheen to many plants.

The stem cortex of most species in the genus is composed of several rows of small, thick walled, usually darkly pigmented cells. Among those species with such stems, *Hygrohypnum eugyrium* varies slightly. Often the outer most layer of cortical stem cells is slightly less pigmented than inner cortical layers. Further, the outer tangential wall of the outer most row of cortical cells is thinner than its inner tangential wall or either of its radial walls (Fig. 69g). Limpricht (1904), Roth (1905), Brotherus (1923) and Nyholm (1965) also noted this phenomenon.

The leaves of *Hygrohypnum eugyrium*, like those of other species in the genus, are variable. The leaf shape varies from ovate (Fig. 68g), oblong-lanceolate (Figs. 68d & h) and lanceolate (Fig. 68f). The attitude of the leaves upon the stem varies from appressed or loosely imbricated (Figs. 68e) to spreading (Fig. 68e). The leaf base may be plane or strongly clasp. Strongly clasping leaf bases are often accentuated in strongly falcate leaves. The leaf margin is entire except in some weekly serrulate leaf apices. The margin may be variously plane, infolded along one side as a wing (Fig. 68g) or variously inrolled along both sides (Fig. 68j). The leaves may be plane or concave. The varying degrees of marginal infolding or inrolling may accentuate the overall concavity. The apex is acute, varying from abruptly to gradually long tapering. The apex may be modified through the influence of the inrolling of the leaf margin and the amount of leaf concavity. In cases where one or both margins are inrolled the apical acuity may appear sharper than it really is (Fig. 68f, g & j). In plants where both margins are inrolled the inrolling often ceases just below the apex thus imparting an apiculate appearance to the leaf (Fig. 68g & h).
The costa of *Hygrohypnum eugyrium* is variable. Usually it is short and double. Occasionally it may be double with one or both arms reaching midleaf or rarely single to slightly beyond midleaf with one or two lateral forks.

The median leaf cells seem to indicate that the species may be responding to some disruptive selection pressure. The median leaf cells range from 30 to 80 um long X 4 to 6 um wide over the world wide range of the species. North American plants vary from 32 to 80 um X 4 to 6 um but usually lie between 45 to 75 um X 4 to 5 um. European plants, on the other hand, range from 30 to 75 um X 4 to 5 um usually occurring between 30 and 62 um X 4 to 5 um. The lengths of the median leaf cells clearly overlap, but the mean lengths seem to be offset from one another.

Schimper (1855, 1876) and Grout (1931) attempted to relate ovate and oblong leaves to a stem position and lanceolate leaves to branches. The present study was unable to substantiate these observations. Both leaf forms have been observed along individual stems and on different branches attached to a common stem.

Schimper (1876) described *Hypnum eugyrium* var. mackayi based on a Mackay collection from Tork Waterfall near Killarney, Ireland in 1865. One specimen bearing these data is at S-PA. In the Schimper herbarium at BM is a second specimen bearing slightly different data. The label reads "Hypnum mackayanum," in mollibus ad cataractum, Turk Waterfall prope Killarney, leg initio Juli 1865. No collector is indicated. Also present in the Schimper herbarium are Holmgren, Nowell and Lamy collections as cited in Schimper's description. The two small fragments comprising the Mackay collection are unusual for the plants are small in terms of the many specimens examined in the present study and the leaves are strongly falcate. Schimper characterized the variety as a robust plant, less soft
than the parent variety and bearing broadly oblong, less acuminate leaves. So too were the leaves described as secund or slightly so or erect spreading, though slightly deflected laterally. The specimen at BM for which no collector was clearly indicated agrees with the Schimper description. The large leaves of the so called "Hypnum mackayanum" are about 1.6 to 1.7 mm long. Such lengths are well short of the known 2.0 mm maximum. Other specimens bearing far smaller leaves agree in all other characters recognized by Schimper. Therefore, Hygrohypnum eugyrium var. mackayi (Schimp.) Broth. is not recognized by this study. The specimen at BM bearing the nomen nudum "Hypnum mackayanum" is designated as the lectotype of the variety. This may be redundant, for the specimen may be the holotype, a fact that cannot be established clearly in the absence of a collector's name.

The type description of Limnobium eugyrium var. nervosum Roell (1907) was examined. It is the basionym for Hygrohypnum eugyrium var. nervosum (Roell) Podp. The original description makes no reference to a specimen and the description is, itself, insufficient to effectively assess the taxon.

Hygrohypnum eugyrium ssp. subeugyrium var. occidentale (Card. et Ther.) Grout is a form of Hygrohypnum luridum. Examination of the apparent holotype at NY collected by Wm. Trelease from Muir Glacier, Alaska reveals the specimen to be a julaceous, oblong-lanceolate leaved form of H. luridum. It is quite typical of western North American H. luridum and is easily recognized by its numerous small, quadrate and incrassate alar cells and the stronger, single costa.

Schimper (1855) described Limnobium eugyrium from his own collection taken in 1854 at Geroldsau waterfall in Baden-Baden in southwestern Germany. The specimen was reported to contain an admixture of Brachythecium
velutinum. Both S-PA and the Schimper herbarium at BM have specimens answering this description. A careful examination of them reveals that the specimen at S-PA is a fragment from the one at BM. The duplicity of the specimen is further substantiated by their possession of similar admixtures of Plagiochila. The specimen in the Schimper herbarium at BM is redesignated the holotype and the one from S-PA is treated as an isotype.

*Hygrohypnum eugyrium* has been confused frequently with *H. luridum* and vegetative material of *Sematophyllum marylandicum*. Several features presented in the following chart and discussion may clarify the differences among the three taxa.

<table>
<thead>
<tr>
<th></th>
<th><em>H. eugyrium</em></th>
<th><em>H. luridum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Alar cells</strong></td>
<td>Alar cells quadrate to rectangular, regularly in-flated and excavated; often becoming brown or metallic red with age.</td>
<td>Alar cells quadrate to short rectangular, sometimes exca-vated, rarely inflated; remain-ing hyaline or becoming yellowish-brown with age, rarely becoming dark reddish brown.</td>
</tr>
<tr>
<td><strong>Leaf apex</strong></td>
<td>Sometimes bearing a few, small teeth.</td>
<td>Always entire.</td>
</tr>
<tr>
<td><strong>Stem Cross section</strong></td>
<td>Outer layer of cortical cells less pigmented than inner ones. Outer tangen-tial wall of outer row of cortical cells thinner than inner tangential walls or adjacent radial walls.</td>
<td>Pigmentation and wall thick-ness of cortical cells uni-form.</td>
</tr>
<tr>
<td><strong>Capsule</strong></td>
<td>Annulate.</td>
<td>Exannulate.</td>
</tr>
</tbody>
</table>

Various stem and leaf characters permit one to distinguish *Hygro-hypnum eugyrium* and *Sematophyllum marylandicum*. As pointed out in the preceding chart the outer layer of cortical stem cells of *H. eugyrium* is differentiated from the inner cortical cells. The cortical stem
cells of *S. marylandicum* have uniform wall thickness and uniform pigmentation. Typically, the straight leaves of *S. marylandicum* are lanceolate and loosely imbricated to spreading upon the stems. The apex of the leaves of *S. marylandicum* may taper abruptly or gradually to an acute, entire point. Pronounced leaf concavity in the straight leaves of *S. marylandicum* gives them a boat shaped configuration. In the leaves of *H. eugyrium* the frequency with which one leaf margin or another variously inrolls gives an overall impression of asymmetry to the leaves and as such a boat shaped concavity is not apparent. The leaf apices of *H. eugyrium* frequently exhibit a few small teeth. The alar cells of the two species are often quite similar, but in young leaves of *S. marylandicum* there is a row of 2 or 3 inflated cells extending from the leaf margin across the base at the point of insertion. This feature seems less apparent in older leaves.
Fig. 68a - j. Variation in the habit of the shoot and leaf shape of *Hygrohypnum eugyrium*.

a - c, e. The habit of the shoots in the moist condition.

d, f - j. Variation in leaf shape.

Scale:

a - c, e;

d, f - j;  \[1\text{mm}\]
Fig. 69 a - i. Cellular detail of the foliage leaves and the stem of *Hygrohypnum eugyrium*.

a - c. Leaf apices.
d. Marginal leaf cells
e - f. Median leaf cells.
g. Stem cross section.
h, i. Alar cells.

Scale:

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a - c  100um
d - f  100um
g - i  100um
```
Fig. 70. *Hygrohypnum eugyrium*
Exsiccati Examined

Austin, Musci Appalachiani #438 as *Hypnum eugyrium*. (CANM, MICH, USA, UBC)

Bauer, Musci Europ. et Ameri. Exsiccati #1885 as *Hygrohypnum eugyrium*. (BRNM, NY)

Musci Europ. Exsiccati #643 as *Hygrohypnum eugyrium*. (BRNM)

Farlow Herbarium, Reliquiae Farlowianae #586 as *Hypnum eugyrium* (MICH, UC, USA)

Grout, North American Musci Perfecti #55 as *Hygrohypnum eugyrium* var. mackayi. (C, CANM, MICH, UC, USA, TENN, F)

#295 (C, CANM, MICH, MIN, UC, USA, TENN, F)

North American Musci Pleurocarpi

#61 as *Hygrohypnum eugyrium* var. mackayi. (MICH, MO, UC, USA, TENN)

#129 as *Hygrohypnum eugyrium* var. mackayi. (CANM, MO, UC, USA, TENN)

#323. (CANM, MICH, MIN, MO, UC, USA, TENN)

Husnot, Musci Galliae #693 as *Hypnum eugyrium*. (G)

Lisowski, Bryotheca Polonica Fasc. VII #217 as *Hygrohypnum eugyrium*. (BP, CANM, S-PA, LE)

Macoun, Canadian Mosses #496 as *Calliergon circulifolium*. (USA)

Canadian Musci #535 as *Hypnum eugyrium*. (MO, UC, USA)

Museo Hist. Natur. Vindobonensis, Kryptogame exsiccate #2600 as *Hygrohypnum eugyrium* var. mackayi. (BP, C, LE, NY, F)

Rabenhorst, Bryotheca Europaea #650 as *Limnolium eugyrium*. (NY)

Sullivant & Lesquereux, Musci Boreali-Americani

Ed. I, #303 as *Hypnum eugyrium*. (MICH)

Ed. II, #450 as *Hypnum eugyrium*. (MICH, NY, UC, F)

Verdoorn, Bryophyta Arduennae Exsiccata, Nov. Belg. Indigena #17 as *Hygrophyum eugyrium* var. mackayi. (MO, NY, UC, F)

Selected Specimens Examined

Canada

Quebec

Gaspesian Park, Gaspe Nord, slopes of Mt. Albert; Crum & Williams, 10681. (CANM)

Terrebonne Co., Vicinity of Mt. Tremblant Lodge, Crum 9834. (CANM)

New Brunswick

Victoria Co., S. of Grand Falls; Hand 55-011. (CANM)

Albert Co., Fundy National Park, Dickson Falls; Ireland 10735. (CANM)

Grand Manan Is.; Dunham June 1914. (NY)

Bass River; Fowler. (NY)

Newfoundland

Top Sail Harbour; Waghorne 11 Oct 1890 as *Hypnum eugyrium*. (CANM)

Chance Cove & Greene Island; Waghorne 25 Sept. 1890 as *Hypnum eugyrium*. (CANM)

Nova Scotia

Cape Breton Island, Inverness Co., Big Southwest Brook; Schofield & Crum 4884. (CANM)

Kings Co., Black Hole; Schofield 10949. (CANM)
Nova Scotia (continued)
Victoria Co., Cape Breton Highlands National Park, trail to Framey Peak; Ireland 11726. (CANM)

United States

Georgia
Walker Co., Cloudland Canyon, E. of Trenton; Anderson 12958 (DUKE)

North Carolina
Swain Co., Great Smokey Mountains National Park, Kanati Fork; Anderson & Robinson 8893. (CANN)
Transylvania Co., Horsepasture Creek, Bohaynee Rd.; Anderson 13023. (CANN)
Macon Co., White oak Bottoms. SE of Rainbow Springs; Robinson 12919. (CANN)
Yancey Co., Middle Creek; Anderson & Robinson 9604. (CANN)
Jackson Co., Upper Falls Whitewater River; Anderson 8697 (DUKE)

Tennessee
Sevier Co., Great Smokey Mountains National Park, Roaring Fork, Mt. Le Conte; Sharp 34509. (TENN)
Blount Co., Great Smokey Mountains National Park, Cades Cove; Sharp 4056. (NY)
Carter Co., Roan Mtn.; Sharp 5 May 1934. (TENN)

Virginia
Madison Co., Shenandoah National Park, near Limberfoot; Ireland 899. (CANN)
Albemarle Co., Shenandoah National Park, Jones Run Creek; Ireland 2166. (CANN)
Greyson Co., White Top Mountain; Vail & Britton 29 May 1892 (MICH)
Rockingham Co., Shenandoah National Park, Big Run Trail; Schnooberger 3505. (MICH)

West Virginia
Greenback, Iron Bridge; Gray M-963. (TENN)
Tibbs Run; Millspaugh 4 July 1892. (NY)

Maryland
Frederick Co., NW of Bethel, Catochin Mountain; Hermann 14286. (USA)
Garrett Co., SW of New Germany, Whiskey Hollow; Hermann 17614. (USA)

Pennsylvania
Bradford, Headwaters of Bennett Brook; Burnett 26 Aug. 1894 (NY)
Carbondale, Stoney Brook; Rau. (NY)
Huntington Co., Masseyburg; Becking 57070142. (CANM)

New York
Hamilton Co., SW of Long Lake Village; Hermann 16886. (MICH)
Marathon; Austin 1869. (NY)
Essex Co., Olmsteadville, Bigby Pond; Beals 7-11 Oct. 1917 (NY)
Renssalaer Co., Sand Lake; Peck 1866. (NY)
Ulster Co., Phonoecia; Haring 29 June 1936. (NY)
Connecticut
   Near New Haven, Sargent's Brook; Allen 29 May 1880. (NY)
Vermont
   Stratton; Grout 1 Aug. 1901. (TENN)
New Hampshire
   Jaffrey, Farlow; June 1903. (MICH)
Maine
   Piscataquis Co., N. of Milo, N. end of Schoodic Lake, Hermann 19132. (USA)
   Camden; Crockett 18 June 1902. (USA)
   Oxford Co., Buckfield; Parlin 10027. (NY)
   Mt. Desert Island, Seal Harbor; White 1 July 1892. (NY)
Ohio
   Hocking Co., Old Mans Cave, Benton Township, NE of South Bloomington; Crum 1 Sept. 1968. (MICH)
Faroes
   Syders, near Famien; Jensen 8 May 1896 as *Hypnum eugyrium* var. mackayi. (CANM, LE)
Great Britain
   Wales
   Merioneth; Rhodes 2060. (TENN)
   Bangor; Schimper. (S-PA)
   Carnarvonshire, Aber; Wilson 5 June 1861. (MICH)
England
   Westmoreland, Potterfellow; Waddell Dec. 1885: as *Hypnum eugyrium* (CANM)
   Yorkshire, Cantley; Nowell 5 June 1861 as *Hypnum eugyrium*.
      (BM-Schimper, S-PA)
   Cornwall; Schimper. (S-PA)
Scotland
   Braemar; Richards July 1910 as *Hypnum eugyrium*. (S-PA)
Ireland
   Killarney, Turk Waterfall; leg. unspecified but presumed to be Mackey 1865. as "Hypnum mackayanum". Holotype of *Hypnum eugyrium* var. mackayi. (BM-Schimper, Osotype at S-PA)
Sweden
   Smaland, Bankeryd Alefors; Arven 2 June 1896. (BP, S-PA)
   Ostergotland, Motala ja Leweeuda pa straaklipps; Mosen 22 Sept 1871. (S-PA)
   Dalsland, Jerbo sn Hult vid grainen vid Svingen pra sten; Larsen 9 June 1919. (S-PA)
Poland
   Plurium ad saxa arenacea in rivula Solinka inter monter Diziat et Jawarnik; Lisowski 24 April 1956 in Bryotheca Polonica Fasc. VII #217. (CANM, S-PA)
Germany
   Baden Gerolsauer Wasserfall; Schimper 1854. as *Limnobium eugyrium*. (HOLOTYPE in Schimper Herb. at BM; ISOTYPE at S-PA)
   Harz, Theseburg, in Bovetal; Quelle 9 Sept 1900. (B)
Austria
Steiermark, I. Keppeldorfer Bache bei Angare; Breidler 15 May 1890. (BP)

Hungary
Carpathian merid., In rupibus irrigatis rive Riu mare prope Zlata montes Retyezat; Vajada 12 July 1968. (BP)

France
Pierres souvant inoundres – Pres de Bouchot Gerbamont (Vesges); Pierrat June 1881 as Hypnum eugyrium in Musci Galliae #693. (G)

Haute Vienne, in saxas humidis ad molendarium prope Saint-Priest-Taurion; Lamy. (BM-Schimper)

Japan
Honshu, Okayama Pref. Eita-gun, Usheroyama; Igi 514. (NICH)
Honshu, Nigata Pref., Leg. ? 6 June 1951. (NICH, accession #112073)

Lectotype: Newfoundland, Exploits; Waghorne 16 Dec 1893. (NY)


Hygrohypnum eugyrium var. miquelonense (Ren. & Card.) Grout, Check List Pleuroc. Moss N. Am. 16. 1929.

Plants rigid to soft, variously forming tightly woven, appressed mats or loosely woven patches or cushions. Color variable, stem or branch tios dark metallic red, bright green, yellow-green, becoming various shades of red with age, reddish-brown, maroon-red, reddish-black or brownish-black, sometimes the transition from older more darkly pigmented extremities is quite abrupt. Stems (1) 2-5 (6) cm long, oldest extremities mostly denuded, save for a few persistent leaf bases, leaves progressively shredded toward the stem bases in Japanese material; branching irregular, branches usually less than 2 cm long, foliose throughout. Stem cross section revealing 3 to 4, sometimes 5 rows of small thick-walled, yellowish to yellowish or reddish-brown cortical cells; medullary cells larger, remaining thin-walled or becoming incrassate with age; central strand
poorly developed or absent; rhizoids reddish, arising from the bases of ventral stem leaves or sexual inflorescence.

Leaves variable; shape narrowly ovate to ovate or oblong to oblong-lanceolate, (0.9)1.0 -1.5 (2.0) mm long X (0.3) 0.5 - 0.7 (0.8) mm wide; falcate, secund or straight, symmetrical or sometimes asymmetrical in the apex, in strongly falcate leaves the upper half of the leaf folds along the midline and curves sharply and ventrally beneath the stem, in some cases one side of the leaf is infolded as a wing; concave, shallowly so in broad leaves, deeply so in more lanceolate leaves such that the apex appears boat shaped, more or less canaliculate in falcate leaves; leaf apex variable, tapering gradually or abruptly to an acute or slightly acuminate point, sometimes as a consequence of leaf concavity the leaf margin inrolls just below the apex thus accentuating a small apiculus on some acuminate apices, abruptly acute apices are regularly blunt and finely denticulate; margins entire save for a few teeth at the tip of acuminate apices or the acute, but blunt and denticulate apices; costa usually short and double, sometimes weak or almost absent, rarely single to midleaf; leaf attitude changing little from the wet to dry condition, falcate-imbricate to straight, loosely imbricate, sometimes slightly complanate.

Areolation variable; median leaf cells long linear flexuose (40) 45 - 80 (114) μm long X (4) 5 - 6 (7) μm wide cells becoming shorter toward the apex; cells toward the base generally becoming shorter and wider, often strongly pitted and exhibiting a yellowish pigmentation; alar cells variable, forming an irregular group of quadrate, short rectangular or irregular, strongly incrassate, yellowish or reddish-brown cells or a basal row of enlarged, incrassate cells surrounded by a few quadrate or irregular cells; plane or frequently excavated.
Plants autoicous; middle and inner perigonial leaves ovate, to 0.8 mm long, acute to acuminate, sometimes slightly squarrose, margins entire except for a few teeth in the apex, ecostate, basal cells sometimes pitted; outer and middle perichaetial leaves broadly ovate to ovate-lanceolate, squarrose in the upper half, ecostate, plicate; inner perichaetial leaves ovate lanceolate to long linear triangular lanceolate, to 5.0 mm long, erect, margins entire save for a few fine teeth in the apex, deeply plicate; costa variable, ecostate, short and double, or single to midleaf.

Seta yellowish-red to reddish-brown, 13 to 22 mm long, usually 17 to 20, smooth; capsule typical for the genus.

Peristome typical for the genus; annulus present, endostome with 1 to 3 well developed cilia between adjacent segments; spores 11 to 19 um in diameter, colorless to yellow green, finely papillose.

*Hygrohypnum subeugyrium* is most easily recognized by the regular occurrence of a few minutely denticulate to finely serrulate leaf apices among others that are entire (Fig. 73 a-c) in association with the quadrate to rectangular, enlarged and incrassate and:often excavated alar cells (Fig. 73 d, g-i).

*Hygrohypnum subeugyrium* varies in leaf shape, the shape of the leaf apex, the symmetry of the leaves and their attitude upon the stem or branches, the leaf concavity and the development of the alar cells.

Leaf shape varies from narrowly-ovate (Fig. 71d) to oblong lanceolate (Fig. 71e). Ovate leaves are generally straight, but longer and narrower leaves are straight or falcate. Ovate leaves are usually broadly and shallowly concave, whereas the narrower leaves are sometimes quite deeply concave such that the leaf apex is almost boat shaped (Fig. 71c). Frequently,
one side of the leaf is inrolled as a wing (Figs. 71 a & b).

The nature of the leaf apex is extremely important in recognizing the species. However, the apex is variable and discretion must be used in assessing it. To insure that the necessary characters are seen the worker must examine the apices to ten to 25 leaves. The apex varies from gradually to abruptly acute or somewhat acuminate (Figs. 72 c & b) to abruptly acute with a blunt point (Fig. 72a). Those acute apices with the blunt point are regularly finely denticulate. The margins of other apices vary from entire to having few fine teeth at the very tip of the apex (Fig. 73b). Among American and Scandinavian plants the whole spectrum of variation regularly occurs in individual plants. Among these plants the species is diagnosed immediately by the acute, but blunt apex with the finely denticulate margins. The acute, but blunt and finely denticulate margins has not been observed, as yet, in Japanese material. Identification of Japanese material must rely upon the few fine teeth occurring directly in the apex.

The alar cells are basically quadrate to short rectangular and incrassate, but the group they form is irregular in form and extent. In some cases they form an irregular group of quadrate cells (Fig. 73d), while in others there may be a row of much enlarged cells extending across the leaf base similar to some species of Semtophyllum (Figs. 73 g & h). In the latter case the row of enlarged basal cells is surrounded by a few quadrate or irregular cells (Figs. 73 g & h). Contrary to Renauld and Cardot's description, the alar cells may be weakly excavated (Fig. 73i). Many of the inner alar cells are quite pitted.

The attitude of the leaves upon the stem is also quite variable. In some cases, especially in Scandinavian material, the leaves are somewhat
complanate (Fig. 71 g & h). In other cases, the leaves are decidedly falcate, (Fig. 71i), particularly in Japanese plants (Fig. 72 g & h). Rarely, the stem and branch tips may be hooked.

Hygrohyponentum purpurascens Broth. is united here with H. subeugyrium. On the assumption that these two taxa were different they were originally studied independently. Attempts to separate them in preliminary keys and a reexamination of tentative descriptions for each revealed that they agreed in almost every essential character. Agreement may be found in color, stem anatomy, leaf size and shape, median leaf cell size and shape, alar differentiation, seta color and length, endostomal cilia and spore size.

Perhaps the most striking feature of Hygrohyponentum purpurascens was the maroon red pigmentation evident in all specimens. However, numerous specimens of H. subeugyrium from eastern North America and Scandinavia exhibit very nearly the same color. Considering the variability in color in other species, color does not appear sufficiently reliable to maintain the species.

The nature of the leaf apex of Hygrohyponentum subeugyrium and H. purpurascens offers the only morphological feature with which the two could be separated. The acute, but blunt and finely denticulate apex has not been observed in Japanese material. In view of the greater similarity with respect to other characters the leaf apex does not seem sufficient to maintain them as separate. It is worth noting that very few specimens of H. purpurascens have been available for study and that as Deguchi (1973) noted, Japanese bryologists have tended to overlook this taxon. It seems reasonable to speculate that as additional specimens become available the acute, but blunt and finely denticulate apex may well be present, in Japan. The holotype of Hygrohyponentum purpurascens
Broth. is at H-BR.

In the original description Renauld and Cardot (1896) described *Hygrohypnum subeugyrium* in terms of *H. eugyrium* and *H. luridum*. Although all the specimens of *H. subeugyrium* that have been examined during this study have come from material mistakenly determined as *H. eugyrium*, the relationship between the two taxa is a remote one and the choice of *subeugyrium* as a specific epithet mistakenly implies a closer relationship. The following chart and discussion will hopefully point out the important differences between *H. subeugyrium*, *H. eugyrium* and *H. luridum*.

<table>
<thead>
<tr>
<th></th>
<th><em>H. subeugyrium</em></th>
<th><em>H. eugyrium</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf apex</td>
<td>Acute, sharp or blunt, almost entire or finely dentate or serrulate.</td>
<td>Sharply acute, entire or sometimes with a few teeth.</td>
</tr>
<tr>
<td>Alar cells</td>
<td>Quadrate to short rectangular, incrassate forming a basal row surrounded by quadrate or irregular cells.</td>
<td>Quadrate to rectangular, regularly inflated and excavated.</td>
</tr>
<tr>
<td>Cortical stem cells</td>
<td>Cells uniformly small, thick walled, evenly pigmented.</td>
<td>Outer tangential wall of the outer most row of cortical cells slightly thinner walled and less pigmented than other walls and other cells.</td>
</tr>
<tr>
<td>Leaf insertion</td>
<td>Do not clasp the stem.</td>
<td>Usually clasp the stem.</td>
</tr>
</tbody>
</table>

The median leaf cells of *H. subeugyrium* vary from 42 to 114 um long, but generally range from 60 to 75 um. However, a significant number of cells are between 80 and 95 um. This contrasts *H. eugyrium* in which the median leaf cells range from 30 to 80 um with most cells lying between 40 and 62 um. In Europe most median leaf cells of *H. eugyrium* occur between 30 and 62 um, whereas those of *H. subeugyrium* are usually between 60 to 90 um.

Although Renauld and Cardot (1896) compared *Hygrohypnum subeugyrium*...
with *H. luridum*, the similarity between the two taxa is not great. The leaf apex of *H. luridum* is never toothed, or is it ever blunt. Renauld and Cardot (1896) described the capsule of *Hypnum subeugyrium* as exannulate, which would ally it with *H. luridum*. However, they were mistaken, for an annulus may be found in young operculate capsules of *Hygrohypnum subeugyrium*. The annulus is evidently lost very soon after capsule dehiscence.

The nomenclature of *Hygrohypnum subeugyrium* has been somewhat confused, for Renauld and Cardot described the species on two different occasions under two different names. Renauld and Cardot (1893) originally described the plant as *Hypnum eugyrium var. miquelonense* in a footnote in a list of North American mosses. The type locality was given as Miquelon, but no specimen was cited. The only known specimen bearing the varietal name is at NY. The specimen, collected by Delamare, bears no collecting date and only these brief data: "Newfoundland, St. Pierre Miquelon, Langlad." In the absence of a clear reference to a specimen it can only be speculated that the Delamare collection is the holotype. However, it is significant that the fragmentary specimen clearly agrees with the description and the assumption has been made that if the specimen is not the holotype, then it is at least representative of the variety.

Renauld and Cardot (1896) were apparently unaware that *Hypnum subeugyrium* was the same as *Hypnum eugyrium var. miquelonense*. Their description of *H. subeugyrium* was based on a Waghorne collection of 1893 from Exploits, Newfoundland. The only known specimen agreeing with this reference is at NY. The collecting date is given as 16 Dec. 1893. The Waghorne and Delamare specimens are clearly one and the same taxon. Unfortunately, it seems unlikely that the Waghorne specimen at NY is the
holotype. Renauld and Cardot (1896) described the plant as exannulate. However mistaken this observation was, it could not have been made from the NY specimen for it is completely sterile. Until a bonafide holotype is established the Waghorne specimen of 16 Dec. 1893 at NY is designated the lectotype.

Selected Specimens Examined

Canada

Ontario

Nipissing Dist., Lake Timagami, Paradise Bay; Cain 3121 as Hygrohypnum eugyrium. (CANM)
Nipissing Dist., Lake Timagami, Gull R.; Cain 3139 as Hygrohypnum eugyrium. (UAC, UBC)
Nipissing Dist., Lake Timagami, Gomphidius Bay as Hygrohypnum eugyrium. (NY)

Quebec

Terrebonne Co., N. of St. Jovite, near Mt. Tremblant Lodge; Hermann 15730 as Hygrohypnum eugyrium. (USA)

Newfoundland

Exploits; Waghorne 16 Dec. 1893. as Hyphnum subeugyrium. (NY, likely holotype, tentative lectotype)

Nova Scotia

Cape Breton Island, valley of Barracois; Nichols 1496 as Hypnum alpestre. (NY)

St. Pierre Miquelon

Leg.: D. Delamare as Hypnum eugyrium var. miquelonense. (NY, likely holotype, but tentatively designated the lectotype)

United States

Tennessee

Great Smokey Mountains National Park, Rainbow Falls, NE side of Mt. LeConte; Steere 10678 as Hygrohypnum eugyrium. (MICH)
Cooke Co., Rich Butte Mtn.; Sharp 39177 as Hygrohypnum eugyrium. (MICH, TENN)

New York

Hamilton Co., Raquette River, SW of Long Lake Village; Hermann 16911 as Hygrohypnum eugyrium. (CANM)

New Hampshire

White Mountains; James July 1857 as Hypnum eugyrium. (UBC)

Great Britain

Scotland, Argyll Co., Loch Sumart, Morvern; Wallace & Crundwell 1/7/1954 as Hygrohypnum eugyrium. (CANM)

Sweden

Vastergotland

Ostads sn. Alanda; Larsson 12 Sept. 1930 as Hygrohypnum eugyrium. (S-PA)
Sweden (continued)

Vastergotland

Undenas, sn. Granvik, NV. om Hyttehamn; Hakelier 5 June 1966 as *Hygrohypnum eugyrium*. (S-PA)

Bramhulte sn. Tosseryd; Soderberg 19 Aug. 1920 as *Hygrohypnum eugyrium*. (S-PA, UBC)

Bohuslan

Spekerods sn. Lundby; Larsson 6 June 1915 as *Hygrohypnum eugyrium*. (S-PA)

Narke

Hidings sn Svenskyttan; Hakelier 7 May 1959 as *Hygrohypnum eugyrium*. (S-PA)

Halland

Fjaros, Algarda; Stenholm 27 July 1922 as *Hygrohypnum eugyrium*. (S-PA)

Dalsland

Vassbrotau; Larsson 19 Oct. 1914 as *Hygrohypnum eugyrium*. (S-PA)

Forsbacka; Larsson 20 June 1916 as *Hygrohypnum eugyrium*. (S-PA)

Vassbotten; Larsson 27 July 1937 as *Hygrohypnum eugyrium*. (S-PA)

Odeberg sn. Radenefors; Bergstrom 27 July 1920 as *Hygrohypnum eugyrium*. (S-PA)

Japan

Prov. Shinano, Mt. Shirouma; Iishibia 17 Aug. 1949 as *H. purpurascens*. (Holotype, H-BR)

Prov. Tse, Mt. Kamogataka; Yasuda 8/6 1922 as *H. purpurascens*. (H-BR)

Hondo, Mt. Odaigahara; Takaki 3 Aug. 1948 as *H. purpurascens*. (S-PA)

Honshu, Nara Pref. Mt. Misen; Nakajima 24221 as *H. purpurascens*. (H)

Shikiku, Ehime Pref., Omogo; Hattori 124 as *H. purpurascens*. (NICH)

Aki Prov., Mt. Ege, Saeki-gun; Koyama 2059 as *H. purpurascens*. (NICH)

Nara Pref., Odigahara, valley of Nagoya-dani; Mizutani 541 as *H. purpurascens*. (NICH)

Korea

Mt. Sokri; 870 m on wet rocks; Hong 2787, 21 Dec. 1960. (NICH)
Fig. 71 a - i. Variation in leaf shape and the habit of the shoot of *Hygrohypnum subeugyrium* in Europe and North America.

a - f. Variation in leaf shape.

g - i. Variation in the habit of the moist shoots

Scale:

a - f;  

9; The shoot is approximately 1 cm long

h - i; Each shoot is approximately 0.75 cm long
Fig. 72a - i. Variation in leaf shape and the habit of the shoot of *Hygrohypnum subeugyrium* in Japan.

a - f, i. Leaf shape.
g, h. The habit of the moist shoots.

Scale:

\[ \text{a - f, i; \hspace{1cm} 1mm} \]

\[ \text{g, h; Each shoot is approximately 1 cm long} \]
Fig. 73a - i. Cellular detail of the foliage leaves of *Hygrohypnum subeugyrium*.

a - c. Leaf apices.
d, g - i. Alar cells.
e. Median leaf cells.
f. Marginal leaf cells.

Scale:

- a - c, d, g - i; [100um]
- e, f; [100um]
Fig. 74. Hygrohypnum subeugyrium
Hygrohypnum montanum (Lindb.) Broth., Nat. Pfl. 1(3):1039. 1909

Lectotype: Mt. Albis, N.H., Dr. James, 1853 (NY)

Hygrohypnum montanum was lectotypified by Broth. in Nat. Pfl. 1(3):1039. 1909.

Lectotype: Mt. Albis, N.H., Dr. James, 1853 (NY)


Amblystegium montanum Lindg., Musci Scand. 33. 1879.


Plants soft, in loosely to tightly woven patches or mats, either prostrate and tightly appressed to the substrate or stems and branches somewhat ascending, growing out of ever increasing amounts of accumulating deposits of sand and silt. Stems and branches characteristically short, rarely exceeding 2 cm long, usually about 1 cm; branching irregular, the branches often equalling the length of the main stem, but not regularly fastigate. Stems and branches mostly foliose throughout, denuded only in very old stems. Color variable, bright or dull green, yellow or yellow-green, or dark brown, only the youngest portions of the plants are green or yellow-green, lower or older portions of the stems or branches are dark brown. Stem cross sections revealing 2 to 3 rows of small, thick-walled, brownish or reddish-brown cortical cells; medullary cells larger; thin or thick-walled, hyaline or becoming discolored with age; central strand uniformly absent. Rhizoids sparse, arising from the base of ventral stem leaves.
Leaves variable; closely spaced in stem or branch apices, becoming slightly more distant below; attitude varying little from the wet to the dry condition, but varying greatly with location on the stem; leaves usually ovate-lanceolate, less often lanceolate, variously straight or falcate or squarrose-canaliculate in the upper half, leaves on the upper side of a prostrate or ascending stem or branch are straight, those on the stem or branch flanks are falcate, those on the side nearest the substrate are straight and ovate in the lower half and squarrose-canaliculate above, the overall aspect of the leaves is an erect spreading one, from the apex to the base of a stem or branch the straight dorsal leaves vary more or less continuously from somewhat appressed to erect spreading; upon drying the leaves shrink laterally, the margins often inrolling, the entire leaf twisting variously, otherwise the overall aspect of spreading to squarrose leaves is little changed from the moist condition; leaves small (0.3) 0.5-0.9 (1.1) mm long X (0.25) 0.3-0.5 (0.9) mm wide; broadly concave in the lower half, often becoming canaliculate in the upper half; margins coarsely serrulate over their entire length or almost entire, often varying among leaves from the same plant, serrulation most conspicuous in the leaf apex, margins decidedly recurved in the lower half or plane; leaves occasionally weakly decurrent at the point of insertion; apex acute to somewhat acuminate; costa slender, usually short and double with one arm reaching mid-leaf, rarely slender and single or short and triple.

Areolation variable; median leaf cells short fusiform to long linear flexuose, rarely other than narrow, walls quite thick, varying from (17) 25-50 (69) um long X (3) 4-5 (6) um wide, but varying continuously between leaves from individual plants and not infrequently within one leaf; leaf cells generally becoming shorter toward the apex, short fusiform to
almost rhombic, rarely some cells in the apex are papillose by overlapping
distal end walls on the abaxial leaf surface; mostly fewer than 5 such
cells per leaf; leaf cells variable toward the leaf base, gradually be­
coming shorter and wider, or changing little in length and becoming
slightly wider in both cases the walls become more incrassate and irregu­larly pitted; alar cells variable, undifferentiated or forming a scarcely
differentiated group of short rectangular or irregular, incrassate,
slightly pitted, sometimes yellowish cells.

Plants autoicous, Perigonial leaves 0.2-0.5 mm long, broadly ovate,
sometimes with a small apiculus or very finely toothed, rounded apex, cells
incrassate, discolored yellow brown, ecostate or faintly single. Perichaet­
tial leaves radiculose; outer and middle perichaetial leaves ovate-lanceo­
late, squarrose recurved in the upper half; inner perichaetial leaves
lanceolate, usually with a long tapering apex, sometimes somewhat squarrose,
costa variable, single and slender or very broad and forking 1 to 3 times
at its terminus, in either case sending well above midleaf or slender and
double reaching midleaf or sometimes absent, plane or very slightly plicate;
margins of all perichaetial leaves coarsely or finely serrulate in the apex.

Seta 10 to 17 mm long, color yellowish-red to red, smooth, variously
twisted when dry, erect or slightly arched when wet; capsule typical for
the genus; annulus of 2 to 3 irregular rows of cells.

Peristome typical for the genus; Endostome with 2 to 3 cilia between
adjacent segments; spores finely papillose, dusky, 10 to 13 µm in diameter.

Hygrohypnum montanum is a very distinctive species. The characters
that are most useful in recognizing the species are slightly variable and
as such are best used in combination with one another. Useful are the very
small, ovate to ovate-lanceolate leaves, the rather prominent serrulation
of the leaf margin (Figs. 76 a–d), the extensive recurvature of the leaf margin in the lower half of the leaf (Figs. 75 a–e, h & i) the absence of a central stand in the stem and the peculiar squarrose recurvature of the ventral stem and branch leaves. Each of these features occur individually in other hygrohypnum species, however only in *H. montanum* do they come together in such a unique combination.

The serrulation of the leaf margin is extremely useful in the recognition of the species. However, the feature should be employed with some caution for it does vary somewhat. The margin can be coarsely serrate or almost entire. It may be serrulate only in the leaf apex or only in the upper half of the leaf, but not in the apex. The feature can vary among leaves from the same stem. Generally, the serrulation is best developed in the leaf apex (Figs. 76 a&b). Nyholm (1965) remarked that the leaf apex of *H. montanum* was similar to that of *H. molle*. Such a similarity is at best superficial. The leaf apex of *H. molle* is normally blunt and the toothing is more denticulate, whereas the apex of *H. montanum* is more acute and the toothing is much sharper. Also, the leaves of *H. montanum* are regularly falcate, whereas those of *H. molle* never are. Lastly, the leaf margins in *H. montanum* are recurved while those of *H. molle* are plane.

The recurvature of the leaf margin is also useful in the recognition of the species, but like the marginal serration, it too is somewhat variable. Most leaves are conspicuously recurved, some are less so and others are virtually plane.

Papillae occur on the perichaetial leaves of some species, but only in *H. montanum* have they ever been observed on vegetative leaves. In a few isolated specimens a few cells in the leaf apex have exhibited papillae created by the overriding, anterior cell walls. The occurrence of these papillae is too infrequent to attach any fundamental significance.
The peculiar correlation between leaf attitude and position on the stem should also be noted (Figs. 76 f&g).

Grout (1931) commented that the stems of *H. montanum* were mostly defoliate. The observations made during this study do not support this. Grout further noted the presence of "leaf like paraphyllia". I have observed pseudoparaphyllia around branch primordia but no paraphyllia.

Grout (1931) stated that the median leaf cells were about 5 um wide x 6-10:1. As pointed out earlier the cells may be both longer and shorter than Grout noted. He also noted that the capsule was constricted beneath the mouth when old and empty. The capsule may or may not be so constricted.

Nyholm (1965) observed that the spores of *H. montanum* ranged from 14 to 16 um in diameter. I have found them to vary from 8 to 14 um with most lying between 10 and 12 um.

Grout (1931) and Iwatsuki and Naguchi (1974) indicate that *H. montanum* occurs in Japan. I have seen no specimens to support this.

*Amblystegium montanum* Lindb. is the legal basionym of *Hygrohypnum montanum* (Lindb.) Broth. Lindberg (1879) clearly based his name of *Hyprnum montanum* Wils. in James (1855), which was in turn based on the Wilson description of an apparent James collection from the White Mtns., New Hampshire. Article 64 of the Seattle Code of the rules of nomenclature rejects the Wilson name as a later homonym of *Hyprnum montanum* Lam in Bridel (1801). Prior to 1879 there was no species of *Amblystegium* bearing the epithet montanum. It is not clear whether Lindberg (1879) made the transfer for taxonomic or nomenclatural reasons. Regardless, Lindberg was the first one to transfer the epithet montanum to an acceptable genus. According to Article 72 of the Seattle Code the author transferring the epithet of an otherwise illegal homonym to a suitable genus should make no reference in the new combination to the author of the homonym. Therefore, the citation
of the Lindberg name should be *Amblystegium montanum* Lindb. and not *A. montanum* (Wils.) Lindb. Wijk et al. (1959) correctly noted this. Broth­
erus (1909) cited the illegal Wilson name as the basionym for his combina­
tion *Hygrohypnum montanum*. This also contradicts Article 72 of the Seattle Code. Wijk et al. (1962) also noted this and corrected the citation as to refer to Lindberg's *A. montanum*. Therefore the new name *Hygrohypnum eumontanum* Crum, Steere & Anderson, though a commendable attempt to clarify the situation, is unnecessary.

It is evident from the literature that neither Wilson, James nor Lindberg clearly designated types for their species. Two specimens are of im­
portance in this regard. At H-SOL there is a specimen with a handwritten label stating "*Hypnum montanum* Wils., S.L. exs. n. 453." This specimen is evidently a fragment of the Sullivant & Lesquereux Musci Boreali Americani #453. It seems reasonable to assume that this specimen served as the basis for Lindberg's concept of the species. At NY there is a specimen also with a hand written label bearing the data "*Hypnum montanum* Wils. mss., Mts. Albis, N.Y., Dr. James, 1853." The collection date of the specimen predates the 1855 publication date of the homonym and the specimen was collected by James in the type locality. Both specimens at H-SOL and NY are clearly *Hygrohypnum montanum*. However, the recurvature of the leaf margin of the specimen from H-SOL is not as well developed as in the specimen at NY. The James collection at NY is therefore selected as the lectotype for the species. It does not seem unlikely that the James specimen may well be the original specimen.
Fig. 75a - i. The habit of the shoot and variation in leaf shape of *Hygrohypnum montanum*.

a - e, h, i. Variation in leaf shape.

f, g. The dorsal (f) and ventral (g) views of a typical shoot in the moist condition.

Scale:

a - e, h, i; \(0.5\text{mm}\)

f, g; The shoot is approximately 0.5 cm long
Fig. 76a - h. Cellular detail of the foliage leaves of *Hygrohypnum montanum*.

a, b. Leaf apices.
c, d. Marginal leaf cells.
e, g. Median leaf cells.
f, h. Alar cells.

Scale:

- a, b, f, h; \[ \text{100\,\mu m} \]
- c - e, g; \[ \text{100\,\mu m} \]
Fig. 77. Hygrohypnum montanum
Exsiccati Examined

Austin, Musci Appalachiani Supply. I #546 as Hypnum montanum (NY, USA)
Bauer, Musci Europaeæ Exsiccatæ #1280. (BRNM, NY, DUKE)
Grout, North American Musci Pleurocarpi #397 (CANM, MIN, MO, NY, TENN, USA) #485 (MIN, MO, NY, TENN, UC, USA)
Sullivant & Lesquereux, Musci Boreali-Americani
  Ed. I, #306 as Hypnum montanum. (NY)
  Ed. II, #453 as Hypnum montanum. (CANM, NY, NYS)

Selected Specimens Examined

Canada
Quebec
  Parc du Mont Tremblant, W. of Lac Poisson; Herman 16766. (CANM)
New Brunswick
  Albert Co., Fundy National Park, trail to Laverty Falls; Ireland 11602 (UBC, CANM, DUKE)
Nova Scotia
  Cape Breton Island, Victoria Co., Cape Breton Highlands National Park, Mary Ann Falls; Ireland 10520 (CANM)

United States
New York
  Hamilton Co., SE. of Long Lake Village, E. of the Gables Cottages; Hermann 14723. (CANM, NYS)
  Mt. Marcy, Avalanche Trail; E.G. Britton 2 Sept. 1892. (NY)
Massachusetts
  Mt. Greyløck; Andrews 1 Oct. 1908
Vermont
  Windham Co., along Rd. between Stratton and Arlington, 0.4 mi. E. Windham-Bennington county line; Jamieson 5284. (UBC)
New Hampshire
  Mt. Washington, outlet of Lake of Clouds; J.A. Allen, O.D. Allen & A.J. Grout 12 July 1880 as Hygrohypnum montanum specimen A. in North American Musci Pleurocarpi #397 (CANM)

Norway
  Ringerike; Bryhn 28 July 1912 in Musci Europææ Exsiccatæ #1280 (NY)
  Sande, Jarlsberg; Kaurin 3 Sept. 1890. (S-PA)

Sweden
  Varmland, Gasborns; Hakelier 23 Oct. 1965. (S-PA)
Hygrohypnum closteri (Aust.) Grout, Bryologist 13: 14. 1910

Lectotype: Musci Appalachiani #439. 1870. (NY)

Hypnum closteri Aust., Musci Appalachiani #439. 1870.
Amblystegium closteri (Aust.) Card. in Par., Ind. Bryol. 1:15. 1903.
Hygrohypnum closteri fo. seruulatum Grout, Moss Fl. N. Am. 3(2):92. 1931.

Plants soft, spindly, forming small loosely woven, easily fragmenting patches. Color dull, dirty green. Stems prostrate, short, seldom exceeding 1 to 1.5 cm in length, frequently denuded, but for a few clusters of leaves near stem and branch apices. Branching irregular, branches prostrate to somewhat ascending, short usually no more than 0.5 cm long. Stems and branches regularly radiculose from the bases of ventral leaves, rhizoids red, smooth walled. Stem cross sections revealing 2 to 3 rows of small, thick walled, brownish cortical cells which enclose larger, thinner walled medullary cells, medullary cells usually hyaline, but frequently becoming discolored with age; central strand present, well developed.

Leaves generally narrowly ovate or lanceolate, though not infrequently ovate lanceolate or ovate; leaf apex acute, but blunt; leaves uniformly straight; (0.3) 0.6-0.9 (1.75) mm long X (0.2) 0.3-0.4 (0.75) mm wide; leaves plane or rarely weakly concave; margins entire and plane; costa usually single reaching 1/2 to 3/4 of the leaf length, much less frequently short and double or single and forked, variously slender or stout; leaves varying in attitude from the wet to the dry condition, when wet the leaves
are loosely patent, when dry they are very wide to crest spreading, shrunk markedly with the margins often somewhat inrolled, the leaves variously twisted.

Areolation variable; median leaf cells fusiform or rhombic, straight or fleuose, sometimes linear flexuose, varying from (23) 30-50 (63) um long X (4) 6-7 (13) um wide, generally varying continuously, the very widest cells occurring only in the largest stem leaves; apical leaf cells becoming shorter, differing little in shape; basal leaf cells variable, becoming shorter, longer or wider or changing little; alar cells variable, usually little different from adjacent basal cells, or as a few gradually widened, quadrate or rectangular cells, generally exhibiting no color differentiation with age.

Plants autoicous; perigonia and perichaetia occurring individually or in uni- or bisexual pairs, conspicuously radiculose from the base; perigonia ovate; outer perigonial leaves small transverse ovate from a truncate base, ecostate, margins entire; inner perigonal leaves ovate with a slightly tapering apex, exostate, margins entire, deeply concave imbricate; outer perichaetial leaves triangular, sometimes slightly reflexed at the tip, margins entire and plane; inner perichaetial leaves triangular lanceolate, reaching 1.5 to 2.0 mm long, straight erect, plane not plicate. all perichaetial leaves strongly single costate.

Seta erect to slightly arched, 7-10 (20) mm long, yellowish or yellowish-red, smooth, slightly twisted when dry; capsule typical for the genus; operculum conic with a small terminal papillum, rarely becoming slightly rostrate.

Peristome typical for the genus; annulus deciduous, of one to two rows of cells; inner peristome with 1 to 3 well developed cilia between adjacent segments; spores dusky yellow, finely papallose, (12) 13-17 (20)
This small, incompletely understood, but distinctive species, may be easily recognized by the small, spindly growth habit, the usually small, lanceolate leaves with their acute, but flunt apices and the strong, single costa reaching 1/2 to 3/4 of the leaf length (Fig. 78'a,b,e-g). Particularly unusual is the very distant leaf spacing coupled with the spreading nature of the leaves. (Figs. 78 c&d).

Certain infraspecific variation seems to correlate with geography. Throughout the species' range the seta length varies from 7 to 20 mm. The seta length of specimens from New England, New Jersey, New York, and Pennsylvania is generally shorter, in the range of 7 to 11 mm. Only a single fertile specimen is known from the southern range limits in North Carolina. In that specimen the seta length varies from 16 to 20 mm. It has also been observed that the median leaf cells of specimens from North Carolina are on the average slightly longer than those of northern specimens. However, it must be noted that these apparent discontinuities may well be artifacts of collection for there are only 12 known localities for the species and scarcely 50 specimens. These are far too few specimens from which to draw rigid generalization.

In general, there is no appreciable difference in the size of stem and branch leaves. Occasionally the stem leaves in some of the more vigorous specimens may reach nearly twice the length of branch leaves, in the range of 1.5 to 1.8 mm long. The costa of these long leaves may frequently assume a reddish color.

Grout (1931) described *Hygrohypnum closteri fo. serrulata* based on the apparent presence of a serrulate leaf margin. The holotype and the only
known specimen of the form was collected in 1898 by Burnett from Bolivar Run, Pennsylvania. Examination of the holotype from DUKE reveals not the slightest suggestion of marginal toothing in the leaves. No appreciable difference between the alleged form and other specimens of the species could be discerned. It is concluded that the form does not warrant taxonomic recognition.

Renauld and Cardot (1894) described *Amblystegium holzingeri* on the basis of a Holzinger collection from Rock Creek on the banks of the Potomac River near Washington D.C. The holotype of this species has not been available for study. However, careful study of the type description and the excellent illustration clearly show that the Renauld taxa is the same as *Hygrohypnum closteri*.

For want of adequate collecting data in the type description Grout (1931) excluded *Hypnum malacocladum* Card. & Ther. from his treatment of *Hygrohypnum*. The type description cites a single specimen in the Debat herbarium as the holotype. Examination of the illustration accompanying the type description and a specimen from the Debat herbarium, now at S-PA, indicates that *Hypnum malacocladon* is identical to *Hygrohypnum closteri*.

The position of *Hygrohypnum closteri* in the genus is unclear. The lanceolate to narrowly ovate leaves with their typically strong, single costa would seem to ally *H. closteri* with *H. luridum* and more remotely with *H. polare*. However, the absence of any appreciable alar differentiation is *H. closteri* reduces the likelihood of a real affinity between *H. closteri* and *H. luridum* and/or *H. polare*. The leaves of *H. closteri* regularly are spaced distantly along the stem and are spreading. Elongated internodes usually are associated with specimens having grown under less than optimum conditions, whereas in *H. closteri* the condition appears to
be the norm. Further, spreading leaves often occur in other species throughout the genus, but the spreading leaf attitude is one of a variety of leaf attitude that might be exhibited. In *Hygrohypnum closteri* the normal condition is one of spreading leaves.

The absence of any appreciable leaf concavity also isolates the species, for the species comprising the central core of the genus exhibit conspicuous concavity. The typical concavity found within the genus in conjunction with shorter internodes imparts a loosely imbricate to jucaceous appearance to the stems. This feature is clearly absent in *H. closteri*.

The linear dimensions of the median leaf cells of *H. closteri* lie well within the limits for the character in most other species in the genus. However, the general impression one receives from the areolation is that of *Amblystegium*.

The blunt, though acute leaf apex of *Hygrohypnum closteri* is unlike the more pointed leaf apices frequent among the allies of *H. luridum*. Blunt or obtuse leaf apices are frequent in the genus, but only among those species with much wider leaves than those of *H. closteri*.

The inner perichaetial leaves of *H. closteri* are straight and strongly single costate. Although they are shallowly concave, they do not exhibit the conspicuous plicae evident in the inner perichaetial leaves of most other *Hygrohypna*.

The habitually straight leaves of *H. closteri* are unusual among *H. luridum* and its allies for their leaves are usually falcate or straight.

In 1870 Austin issued *Hypnum closteri* as Musci Appalachiani #439. Grout (1931) designated this exsiccate as the lectotype. In neither case did Austin or Grout select a single specimen as the type. As a result of this study a single specimen of this exsiccate from NY has been appropriately designated as the lectotype. The specimen requires some comment. The
specimen consists of two fragments. One fragment clearly shows the distant erect spreading leaves of the dry plants. The second fragment is somewhat troublesome for there is some variation in leaf shape. Certain leaves are unusually ovate for the species and though the leaves are widely spaced they are rather appressed. As a consequence the fragment looks, in part, superficially like a spindly specimen of *Hygrohypnum molle*. However, the areolation, the shape of the leaf apex and the entire leaf margins clearly show it to be *Hygrohypnum closteri*, particularly when such parts are contiguous with perfectly normal appearing *H. closteri*. Grout (1903) also noted the superficial similarity with *H. molle*.
Fig. 78a - g. The habit of the shoot and the variation in leaf shape of *Hygrohypnum closteri*.

a, b, e - g. Variation in leaf shape.

c, d. A shoot in the moist (d) and dry (c) condition.

Scale:

a, b, e - g; [0.5mm]

c, d; The shoot is approximately 0.5 cm long
Fig. 79a - g. Cellular detail of the foliage leaves of *Hygrohypnum closteri*.

a, b. Leaf apices.
c, d. Median leaf cells.
e. Marginal leaf cells.
f, g. Alar cells.

Scale: [100 um]
Fig. 80. *Hygrohypnum closteri*
Exsiccati Examined

Austin, Musci Appalachiani #439 as Hypnum closteri. (NY, UBC, USA)

Selected Specimens Examined

United States

North Carolina
- Polk Co., Green River Gorge; Zander 3049 (DUKE)
- Swain Co., Great Smokey Mountain National Park, Kanati Fork, Newfound Cap; Schofield 8883 as Hygrohypnum coclearifolium. (DUKE)
- McDowell Co., Linville River, Along North Fork River; Anderson & Felton 9568 as Leptodictyum riparium, (DUKE)

District of Columbia
- Rock Creek; Holzinger 11 June 1891 as Amblystegium holizingeri Ren. & Card. (MIN)

New Jersey
- Closter; Austin as Hypnum closteri in Musci Appalachiani #439. (NY-Lectotype, UBC, USA)
- Palisades; Austin 19 Sept. 1866 as Hypnum obtusifolium nom. nud. in sched. (NY)

New York
- Sam’s Point; Austin Aug. 1867. (N)
- Palisades; Austin 15 July 1865 as Hypnum dimorphum Brid. (NY)
- Nangles Brook (spelling?); Austin May, June 1872 as Hypnum closteri. (NY)

Pennsylvania
- Bolivar Run; Burnett 7 July 1897 as Hypnum closteri. (NY)
- McKean Co., Bolivar Run; Burnett 11 Sept. 1898 as Hypnum closteri f. serrulatum. (DUKE-Holotype)

Vermont
- Newfane; Grout 13 July 1900. (DUKE)

Maine
- North Bridgeton; Wilson 14 July 1908 as Hypnum closteri. (NY)

Careful examination of several isotypes (BM, H, JE, S-PA) indicates that the species is best treated as Scorpidium turgescens (Th. Jens.) Loesk. Scorpidium turgescens and the Herzog plant agree in virtually all critical characters; the yellow or rusty-yellow color, the ovate-oblong or broadly ovate leaves, which frequently exceed 3 mm in length, the leaf concavity, the irregular to quadrate or short rectangular, incrassate alar cells, the short, double costa and the concave to cucullate apex bearing an abruptly differentiated, hooked apiculus.

HYGROHYPNUM BRASILIENSE Herz., Hedwigia 67:258. 1927. (Holotype at JE)

The holotype and only known specimen of this species superficially resembles Hygrohypnum alpestre. The deeply concave, oblong leaves of both species are of nearly the same size (2.1 mm X 1.0 in H. brasiliense versus 0.9 to 1.9 mm X 0.4 to 1.0 in H. alpestre). Also similar are the leaf apices with their minutely reflexed apiculi. The abruptly inflated alar cells and the peculiar metallic green sheen of H. brasiliense are similar to H. eugryium. At the same time the metallic sheen is very similar to the sheen observed in the leaves of some species of Sematophyllum. Scrutiny of the hyaline alar cells reveals the presence of an enlarged basal row of 4 to 5 rectangular to crescentic cells which are of regular occurrence throughout the Sematophyllaceae. The very weak, short, double costa and the absence of a central strand in the stem cross-section are also features of the Sematophyllaceae.

The plane, ovate-oblong inner perichaetial leaves are unlike the typically plicate perichaetial leaves of other Hygrohypna.
On the basis of the metallic sheen in the leaves, the nature of the costa and alar cells and the absence of a central strand in the stem, it is suggested that the real affinities of Herzog's peculiar plant reside with the Sematophyllaceae.


This plant does not belong to the genus Hygrohypnum. The plant exhibits a combination of characters that are unlike any recognized species of Hygrohypnum. The narrowly lanceolate leaves, which taper gradually into a sharply acute point, are minutely serrulate. The leaf is attached to the stem across a truncate insertion line. There is none of the abrupt tapering of the leaf base at its insertion that is so common in Hygrohypnum. The leaf angles exhibit no alar differentiation at all. The stem cross sections reveal that a central strand is absent and that the thick-walled medullary cells are surrounded by only two layers of small thick walled cortical cells. The relationships of this enigmatic little plant have yet to be established.


Examination of the holotype and the only known specimen of this Herzog species reveals that it does not belong to Hygrohypnum. The holotype is at JE. For a detailed discussion of this species see the discussion of Hygrohypnum pelichuense.


Neither the type nor any other specimen of this species has been available for study. Comments accompanying the type description render
some room for speculation as to the real nature of the taxon. The broadly ovate to suborbicular leaf shape with the broadly obtuse apex suggests either *H. smithii* or *H. duriusculum*. If the apical cells are, in fact, ovate, then there is a distinct resemblance to *H. smithii*. That the costa is always short and double is more like *H. duriusculum*. The lax, subquadrate to oblong alar cells suggest some poorer forms of *H. duriusculum* as the alar cells of *H. smithii* are always rather incrassate. The evaluation of the species will have to await the availability of the holotype.


This Sakurai species and its variety *simplex* must be excluded from *Hygrohypnum*. Examination of the holotypes of both taxa reveal the presence of well developed papillae on the abaxial surfaces of the leaves. These papillae are formed by overlapping anterior end walls. Although such papillae occur on the perichaetial leaves of *Hygrohypnum alpinum* and *H. molle*, they are otherwise unknown in the genus. Perhaps the affinities of this plant reside with the Sematophyllaceae.


*(Holotype at S-PA)*

Theriot (1936) suggested a relationship between his species and *Hygrohypnum smithii*. It is true that both plants exhibit a strong single costa and an obtuse or rounded leaf apex. Further, the elliptical leaf shape noted by Theriot is not too dissimilar from the broadly ovate or orbicular leaf shape of *H. smithii*. However, the rectangular shape of the median leaf cells, clearly illustrated in his paper and visible in the plants, in spite of a heavy incrustation of diatoms, is fundamentally different from the rhombic to linear flexuose areolation of *Hygrohypnum*. 
On this basis, the Theriot plant must be excluded from *Hygrohypnum*.

The true relationships of this taxon are unclear. A number of features seem to indicate affinities with the Bryaceae. It is not entirely clear that Theriot's plant is a pleurocarpous moss. Most of the leafy axes are unbranched, varying from 1 to 3.5 cm long. A few exhibit one or two broken, irregularly placed branches near the base of the stems. Were it not for the fact that those branches arise at an angle of 90° from the stem, one might interpret them as innovations of an acrocarpous moss. The widely spaced leaves seem to suggest growth under highly humid conditions. Curiously, the younger parts of the stem and the costae of younger leaves are reddish. Though obtuse, the leaves seem to resemble the Bryaceae. The margins are strongly recurved and the leaf base is conspicuously decurrent. Were the leaf apex acute or acuminate the similarity with the Bryaceae would be all the more striking. An effective assessment of this plant must await the discovery of fertile material.


If this plant was known only from vegetative material it would be reasonable to unite it with *Hygrohypnum eugyrium*. The two taxa strongly resemble each other through their enlarged, quadrate alar cells and the oblong lanceolate leaves in which one margin is frequently inrolled as a wing. However, the two taxa must be retained as separate and *H. entodontoides* must be excluded from the genus. Although no sporophytes were available for study, Brotherus clearly described the operculum as "planarum longiuscule rectique rostratum." The operulum in *Hygrohypnum* is consistently conic. The affinities of the Brotherus plant lie elsewhere.
1964-1965. (Holotype at FH)

The median leaf cells of the plant are regularly rounded rhombic or slightly fusiform and never more than 30 um long. The basal and alar cells are numerous and rounded quadrate. The overall appearance of the areolation is that of the Crypheeaceae and on this basis the plant is excluded from the genus.

1955.

Neither the type nor any other specimen of this Chinese endemic were available for study. As discussed by Chen (1955), certain features of this plant are unusual. A stem 20 to 25 cm long is uncommon in Hygrohypnum. Only a few floating forms of H. ochraceum have reached such dimensions. The lacerated leaves in Chen's illustration give the impression that the plant has a coarse texture. This might suggest a similarity with H. bestii. However, no data are given about leaf length and the 24 um to 30 um median leaf cells are far too short for H. bestii. Further evaluation must await the availability of the type.

Hygrohypnum glaciale Warnst. ex Bauer, Hedwigia 57:128-129. f.60. 1915.
(Holotype at B)

This plant is united with Hypnum revolutum (Mitt.) Lindb. The revolute leaf margins, the very tiny, but clearly recognizable, quadrate alar cells, the costa and the curvature and tooting of the leaf are clearly that of Hypnum revolutum.
(Isotype at S-PA)

The leaves of H. hedbergii are broadly ovate like many Hygrohypna. However, the leaf margins are coarsely serrulate to serrate and the lamina is traversed by a long, slender, single costa which reaches 3/4 of the leaf length. The regularity and coarseness of the teeth on the leaf margin require that the relationships of this plant be sought elsewhere. A comparison with Plathypnidium is in order.

(Holotype at MAK)

This small sterile plant and its forma subrigidulum Sak. are excluded from Hygrohypnum. Sakurai suggested that the straight, lanceolate leaves bore a similarity with H. luridum, but the absence of any alar differentiation and the very weak costs preclude this. Sukurai also suggested an affinity for H. duriusculum, but the oblong-elliptic to orbicular leaves and the well developed alar cells of this species disagree with Sukurai's plant. The correct systematic position of Sakurai's plants are unknown.

Hygrohypnum lusitanicum (Schimp.) Corb., Rev. Bryol. 40:50. 1913.

Hyphnum lusitanicum Schimp., Syn. 2 ed., 781. 1876. (Holotype at BM)

Schimper (1976) described this plant without benefit of the sporophyte. A fertile collection made by H. Buch from Monte de la Fracha in Spain requires that the species be excluded from Hygrohypnum. The Buch collection agrees in all respects with the Schimper type. However, the rostrate operculum clearly disagrees with the conic operculum of Hygrohypnum.

This plant is united with Brachythecium rivulare B.S.G. Although the forking costa resembles Hygrohypnum, the lax areolation and the alar differentiation are that of a Brachythecium.

Hygrohypnum nicholsii Grout, Bryologist 38:10. 2. 1935.

The holotype of this plant has not been studied, but authentic material collected in the type locality by G.E. Nichols was available from DUKE. The coarsely serrulate leaf margin and the strong, single costa which terminates in a spine-like papilla immediately identifies this plant as Eurhynchium riparioides.

Hygrohypnum novae-caesarae (Aust.) Grout, Moss F.N. Am. 3:94. 1931.

Hypnum micans Wils. in Hook., Brit. Fl. 2:86. 1833.
Chryosohypnum micans Lind. in Sull., Icon. Musci Suppl. 91.
pl. 67. 1874.
pl. 113b. 1902.
Hygrohypnum novae-caesarae (Aust.) Grout, Moss Fl. N. Am. 3:94. 1931.

Several reasons require that this Austin Species be transferred to Sematophyllum. All available fertile specimens clearly exhibit a rostrate operculum. In contrast, the opercula of Hygrohypnum are all conic. The stem of the Austin plant has no central strand. The absence of the central strand is typical of the Sematophyllaceae. The row of three, enlarged basal leaf cells extending across the leaf base from the margin is, again, typical of the Sematophyllaceae. The metallic sheen displayed
by the leaves is also like that in *Sematophyllum*. The costa of the Austin plant is uniformly short and double and very faint. Only in very small or otherwise depauperate specimens of *Hygrohypnum eugyrium* or *H. luridum* is the costa of *Hygrohypnum* as faint. The sharp points of the marginal teeth in the leaves of the Austin plant are unlike the blunt teeth of the irregularity denticulate leaf margins in some species of *Hygrohypnum*. The perichaetial leaves of the Austin plant are plane, while those of *Hygrohypnum* are usually strongly plicate. Therefore, the Austin species is best treated as *Sematophyllum novaë-caesarae* (Aust.) Braithw.


Based upon leaf shape, costa structure, alar differentiation, areolation and the truncate leaf insertion *Hygrohypnum pelichuense*, *H. circinatum* and *H. tequendamense* could be considered the same entity. However, such a relationship among the three taxa is less clear considering the distribution of papilllose leaf cells and a stem central strand. The abaxial surface of the leaf apices of *H. pelichuense* and *H. circinatum* bear blunt papillae formed by the apically overriding end walls of the leaf cells. On the other hand, the leaf cells of *H. tequendamense* are smooth. Further, a strong central strand is present in the stems of *H. circinatum*, but is entirely absent in both *H. pelichuense* and *H. tequendamense*.

Each of these taxa is known only from the holotype or at most two other specimens. Consequently it is difficult to evaluate whatever variability might exist in the central strand and the leaf papillae of these taxa. Therefore, a union of these three taxa must await further study as additional material becomes available. However, it is clear
that the ovate-triangular leaf shape, the truncate leaf insertion, the costa structure, alar differentiation and areolation of the three taxa do not permit their inclusion in the genus *Hygrohypnum*. That *Hygrohypnum pelichuense* does not belong to *Hygrohypnum* is particularly evident in sexual plants. The inner perichaetial leaves of *H. pelichuense* are ecostate, plane, ovate or ovate-lanceolate and taper into a long, almost subulate apex. The absence of plicae and the presence of a long subulate apex clearly differ from the inner perichaetial leaves in other species of *Hygrohypnum*. The real relationships of this Williams species must be sought elsewhere than in *Hygrohypnum*.


The type and only known specimen of this species has not been available for study. The holotype was reported to be at F, but it has not been located in that collection.

*Hygrohypnum poecilophyllum* Dixon, Rev. Bryol. Lichenol. 7(1&2); 113. 1934.

The holotype of this species has not been available for examination. The description compares the taxon with *Hygrohypnum eugyrium* and *H. purpurascens* Broth. (= *H. subeugyrium*). The description of the alar cells as "alares magnae, supernae quadratae, infinae oblongae, omnes pellucidae, saepe purpureae, auriculas majusculus, subexcavatas, instruentes," clearly suggests *H. eugyrium*. The leaf apices are described as "haud acuminata, brevissime subacuta, vel obtusata, perconcava, apice denticulate." The reference to the obtuse apex is slightly out of character for *H. eugyrium*, but is within reasonable possibility. This Dixon species is tentatively treated as synonomous with *Hygrohypnum eugyrium*. 
Krakow 1925 B:277. 1925.

This remarkable and extinct species was described in a fossil flora of Poland. Its inadvertent inclusion in Index Muscorum and its implied extant condition are no doubt due to its description in Polish and a linguistic inaccessability. Dickson (1973) reports that the plant is a fossil of Scorpidium.


The holotype of this species has not been available for study. All available specimens bearing this name have proven to be Hygro hypnum duriusculum (DeNot) Jamieson. However, in the type description the alar cells are said to be hyaline, subinflated and moderately distinct. The alar cells of H. duriusculum are frequently discolored. There is a strong possibility that H. tsurugizanicum is conspecific with H. alpinum, a species whose alar cells are hyaline and subinflated. Until the holotype is available for evaluation, a judgment cannot be made.


Examination of the holotype of this Herzog species indicates that it does not belong to Hygro hypnum. The holotype is at JE. A detailed discussion of this species accompanies the discussion of Hygro hypnum pelichuense.

Hygro hypnum validum Herz., Biblioth. Bot. 87:146. 1916. (Holotype at JE)

Contrary to the specific epithet, this sterile plant does not belong to Hygro hypnum. The coarsely and widely serrated leaf margins are suggestive of the Brachytheciaceae. A more or less uniform zone of quadrate to very
short rectangular cells extends laterally across the leaf base from the costa to the margin of the alar zone. In many cases those cells in the alar zone assume a slightly more lax aspect than those toward the costa. The broad, stout single costa tapers gradually to a point at about 3/4 of the leaf length. The coarse aspect of the costa vaguely resembles *H. ochraceum*. In some cases a small spine-like papilla is discernible at the tip of the costa. The real affinities of this plant are unclear, but may reside with the Brachytheciaceae.
DISCUSSION

In 1853 Schimper segregated *Hygrohypnum* Lindb. (as *Limnobium* Schimp.) from *Hypnum* Hedw. and recognized seven species for the new genus. In a tersely worded diagnosis he separated *Hygrohypnum* from *Hypnum* on the basis of a poorly differentiated and seldom excavated or inflated group of alar cells, broadly ovate-lanceolate to orbicular leaves and a common habitat in and around streams. The short diagnosis left considerable room for some very uncritical interpretation, for by 1909 the genus as treated by Brotherus consisted of 22 rather diverse species. These diverse species variously had round to lanceolate leaves, straight and/or falcate leaves, entire or coarsely serrulate leaf margins, strong, single costae to none at all, undifferentiated, small and quadrate or inflated alar cells and conic or rostrate opercula. It was undoubtedly this heterogeneous assemblage that prompted Løeske's (1910) remark that *Hygrohypnum* was a "biologische Mischgattung." At the inception of the present study the number of recognized species had increased to thirty-nine. Accompanying this increase in recognized species was an increase in the morphological heterogeneity of the genus as evidenced by species having smooth or papillose vegetative leaves, plane or plicate perichaetial leaves and rectangular to linear flexuose median leaf cells. One result of the present study has been the exclusion from the genus of 19 of the 39 species.

The exclusion of so many discordant elements would seemingly render a much more natural, cohesive group of species. Unfortunately, this has not resulted. In spite of a world monograph of the genus, *Hygrohypnum*, like many other pleurocarpous moss genera, is still afflicted with an unclear generic boundary. The most inclusive statement that can be made about the genus is that it is a group of plants occurring on rocks between the high and low water lines in or beside, small, cold, swiftly running mountain
streams and has leaves exhibiting a variable costa. It may be added further that the leaf cells are smooth, the median leaf cells vary from rhombic to linear flexsuose and that the operculum is conic. Though these features serve effectively to exclude various semi-aquatic members of the Brachytheciaceae and Sematophyllaceae from *Hygrohypnum*, they do little toward reducing the heterogeniety of the remaining species, or do much toward the clarification of the generic limits between *Hygrohypnum*, *prepanocludus* and *Calliergon*. Even in this more restricted sense the remaining species of *Hygrohypnum* can be variously subdivided (Hedwig, 1801; Bridel, 1801, 1812, 1827; Sprengel, 1827; Wilson, 1855; Renauld, 1883 and Grout, 1931).

In my opinion, the species of *Hygrohypnum* may be arranged in a linear sequence based primarily on variation in leaf shape, leaf symmetry, alar cell differentiation and the attitude of the leaves upon the stem. Within this basic framework a variety of characters influence the positions of individual species. This classification is graphically represented in figure 81.

The sixteen species treated in this classification system are seen to be divisible into two groups based on leaf shape and leaf symmetry. The most cohesive of the two groups includes *Hygrohypnum alpinum*, *H. duriusculum*, *H. smithii*, *H. bestii*, *H. cochlearifolium*, *H. norvegicum*, and *H. molle*. These species possess straight, orbicular to ovate leaves which are shallowly to deeply concave. Although the attitude of the leaves upon the stems is variable, there is a tendency for the leaves to be loosely imbricated to impart a julaceous appearance to the shoots. In addition, their alar cells are undifferentiated (except in *H. alpinum* and *H. duriusculum*) and except for the dioicous *H. bestii*, all are autoicous. Further, none possess a hyalodermis and all, but *H. bestii*, have a well developed central strand.
Figure 81. Possible Relationships Among the Species of *Nygrohyphaea*
The remaining species constitute a second and more heterogeneous group with straight or falcate, ovate to lanceolate leaves. The heterogeneity of this second group is evident in the variation in sexuality, stem anatomy, alar differentiation, shape of the leaf apex, leaf concavity, costa structure and marginal toothing of the leaves.

Of the species in this heterogeneous second group *Hygrohypnum alpestre*, *H. luridum*, *H. styriacum* and *H. polare* display certain features which indicate affinities with the group possessing ovate to orbicular leaves. Although the leaves of *H. alpestre* are oblong or oblong-lanceolate, they are exclusively straight, deeply concave and exhibit a loosely imbricate attitude upon the stem or impart a julaceous appearance to the shoot. It is perhaps significant here to note that the straight leaves and the julaceous habit of the stem of *H. alpestre* was sufficiently similar to *H. molle* to be recognized by Bridel (1812, 1827), Sprengel (1827) and Hampe (1837). The association of *H. styriacum*, *H. luridum* and *H. polare* with the group of broad leafed species is less clear. In each of these three species the leaves vary from straight to falcate. The leaves of these three species may be quite concave. When the leaves of these three species are straight, the straightness in conjunction with the leaf concavity imparts a julaceous appearance to the shoot which gives them a strong resemblance to the taxa in the broad leafed group. In addition, the undifferentiated alar cells of *H. styriacum* compare very favourably with the *H. molle* group. However, the highly unusual pseudo-paroicous sexuality of *H. styriacum* is unlike any other species in the genus. In the non-falcate condition, the concave leaves of *H. luridum* and *H. polare* commonly give the shoot a julaceous appearance. The numerous, quadrate to short rectangular alare cells present in both species clearly differ from the undifferentiated alar cells of most of the broad leafed species. However, it does not seem unreasonable to speculate that the numerous quadrate alar cells
of *H. luridum* or *H. polare* could have developed through the elaboration of the few quadrate alar cells of a plant like *H. norvegicum*. However, where the variable costa, autoicous sexuality and stem anatomy of *H. luridum* add to the apparent similarity between *H. luridum* and the group of broad leafed species, the habitually percurrent costa, the dioecy and the incomplete hyalodermis of *H. polare* make its association with the broad leafed species somewhat suspect.

The position of the five remaining species in the genus is unclear. Efforts to place them in other genera have been unsuccessful. In particular, neither *H. eugyrium* nor *H. subeugyrium* exhibit any character which can clearly exclude them from the genus. Like *H. luridum* and *H. polare*, the leaves of *H. eugyrium* and *H. subeugyrium* vary from straight to falcate and are concave. However, in those specimens bearing straight leaves the leaves are generally loosely imbricated to spreading and rarely impart a julaceous appearance to the shoots. The position of *H. subeugyrium* is considered questionable for three reasons. One, there is a tendency toward a complanate appearance to the leafy shoots, especially in Scandinavian specimens. Secondly, a central strand is absent or poorly developed. Lastly, the species often exhibits a dark metallic red pigmentation which is unknown elsewhere in the genus. Further, the diagnostic value to the denticulate leaf apices of *H. subeugyrium* is also peculiar for this character is quite variable in most other species in the genus. *Hygrohypnum eugyrium* exhibits two features which cast doubt upon its proper inclusion in the genus. The leaves of *H. eugyrium* regularly exhibit a peculiar metallic sheen that is reminiscent of some species of *Sematophyllum*. Secondly, the poorly developed hyalodermis evident on the stem is unusual for *Hygrohypnum*. However, the well developed central strand in the stem and the possession of a conic operculum clearly do not permit the treatment of *H. eugyrium* as *Sematophyllum*. It is also impossible to build a case for excluding *H. eugyrium* on the basis of the inflated alar
cells when \( H. \) alpinum, which also possesses inflated alar cells, is retained.

The isolation within the genus of Hygrohypnum ochraceum, \( H. \) montanum and \( H. \) closteri is much more apparent. Leaf concavity in \( H. \) ochraceum is evident only in falcate leaves. Further, straight leaves in \( H. \) ochraceum are borne on shoots with long internodes. As a consequence neither the loosely imbricated and concave leaves nor the julaceous shoots present in other species are evident in \( H. \) ochraceum. The frequent complanate orientation of the straight more or less plane leaves of \( H. \) ochraceum is known elsewhere in the genus only in \( H. \) subeugyrium, which is, itself, a doubtful member of the genus. The well developed hyalodermis and the dioicous sexuality are also unusual in the genus.

Loeske (1910) created the genus Breidleria to deal with certain semi-aquatic, dioicous hypnaeaceous species which had a hyalodermis and a depressed or complanate attitude of the leaves. Included in this genus were Hypnum pratense, Hypnum lindbergii and Hypnum ochraceum (Hygrohypnum ochraceum). Fleischer (1921), Brotherus (1925), Monkemeyer (1927) and most recently Ando (1973) excluded Hypnum ochraceum (Hygrohypnum ochraceum) from Breidleria as a genus or as section Pratensia of Hypnum. It is very interesting that these workers are in doubt concerning the affinities exhibited by Hygrohypnum ochraceum for the Breidleria group. My experience has shown that the similarity in overall appearance among Hypnum pratense, \( H. \) lindbergii and Hygrohypnum ochraceum is considerable. The plants are regularly of the same magnitude of size. In the falcate leaves of both Hypnum pratense and Hygrohypnum ochraceum the upper half of the leaf is sharply folded and exhibits a similar curling. However, the costa of Hygrohypnum ochraceum is stronger and coarser and the leaf apex is blunter than the corresponding structures in the Breidleria group. Perhaps more detailed studies on this problem would be useful.
Naturally occurring specimens of *Hygrohypnum montanum* never produce stem segments bearing exclusively straight leaves; straight leaves are invariably mixed with falcate leaves. As a consequence one does not see the straight, loosely imbricated leaves readily evident in many broad-leaved species or *H. luridum*. The regular occurrence of the finely to coarsely serrulate leaf margins, the lack of a central strand in the stem and the plane or almost plane inner perichaetial leaves are unlike most other species. Nyholm (1965) remarked on the similarity between *H. montanum* and *Campylium halleri*. Although the two taxa occur in different habitats their similarity may be more than superficial. Both species are of the same magnitude in size, possess plane or weakly plicate perichaetial leaves and entire to serrulate and recurved leaf margins. In experimental culture the leaves of *Hygrohypnum montanum* curiously assume a more or less straight symmetry and a wide spacing. Although this seems to be a general response to culture of specimens bearing falcate leaves it is interesting to note that in such a state *H. montanum* strongly resembles a number of species of *Campylium*. It is suggested that more serious study may reveal a closer affinity between *H. montanum* and *Campylium*.

Intensive experience in the genus clearly indicates that *Hygrohypnum closteri* does not belong in the genus. The leaves of *H. closteri* are ovate and straight and therefore could be allied with the group of broad leafed species. However, the leaves of *H. closteri* are virtually plane, regularly widely spaced along the stem and widely spreading to erect spreading. This condition is unlike any other species of *Hygrophypnum*. *Hygrohypnum closteri* differs further in that its inner perichaetial leaves are never plicate and bear a single costa. Although the areolation lies within the limits of *Hygrohypnum*, its areolation generally gives the impression of an *Amblystegium*. Although the formal exclusion of *H. closteri* from *Hygrohypnum* is justified, it has not been done for two reasons. First, there is no other genus with
which it exhibits clearer affinities. Secondly, the creation of a new genus would neither improve the overall understanding of the Amblystegiaceae nor would it improve the practical problems of identification. For the time being and for the sake of expediency it is provisionally retained within *Hygrohypnum*.

Figure 81 illustrates a spatial representation of a classification of *Hygrohypnum* based on the author's experience.

Based on experience *Hygrohypnum* is understood to be composed of eleven seemingly closely related species about which five species of less clear affinities are distributed. To effect a more objective analysis of the phenetic relationships among the 16 species twenty-four qualitative characters were selected for evaluation. Each character can vary in its expression from as few as two states to as many as eight. The number of character states recognized for each character was based on a subjective assessment of the reality of categorizing the variation exhibited in each character. A total of 89 characters states were recognized. Table 2 represents a comparison of the 16 species with respect to each character. Each species may exhibit two or more character states of any character. No attempt has been made to quantify the relative frequencies of the character states. They are simply noted as present or absent.

The data presented in Table 2 were used to generate a similarity matrix in which each species was compared independently with every other species with respect to all 89 character states. A percentage similarity for each species pair was calculated employing the Coefficient of Jaccard as cited in Sokal and Sneath (1963). The formula is given as:

\[ S = \frac{m}{m + u} \]

where

- \( S \) = the similarity
- \( m \) = the number of positive matches, and
- \( u \) = the number of non-matches
Table 2. A comparison of the species of *Hygrohypnum* and the taxonomically important features within the genus.

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<td>Branching Pattern</td>
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<td>Secondary branches irregularly spaced, procumbent to ascending.</td>
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<td>Secondary branches widely spaced.</td>
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<td>Stem Anatomy</td>
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<td>Epidermis of small thick-walled cells.</td>
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<td>Central stem cells like other medullary cells.</td>
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<td>Central cells small.</td>
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<td>Leaf Attitude Upon the Stem</td>
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<td>Leaf Spacing Along the Stem</td>
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The coefficient of similarity are presented as a similarity matrix in Table 3. These similarity data were then subjected to cluster analysis and ordination. Two types of cluster analysis were used, both of which are discussed by Sokal and Sneath (1963). The results of a weighted pair group cluster are presented in figure 82, and those of an unweighted pair group cluster are presented in figure 83. The ordination analysis was taken from Bray and Curtis (1957). In the ordination low spatial separation is equated with a high degree of similarity. The results of the ordination are given in figure 84.

Comparisons between the two cluster analyses, the ordination and the intuitive classification reveal some very interesting results.

In all four analyses *Hygrohypnum alpinum*, *H. duriusculum*, *H. smithii* and *H. molle* occur in close proximity. It is perhaps significant that they all have straight, concave, broadly ovate to orbicular leaves which vary in attitude upon the stem from somewhat imbricate to spreading. The displacement in the ordination of *H. cochlearifolium* to an outlying position is surprising. Perhaps this is a consequence of the deep leaf concavity typical of the species and the recurvature of the vegetative and perichaetial leaf margins. The proximity of *H. alpestre* to *H. alpinum* in the ordination seems anomalous when *H. cochlearifolium* is displaced from the group of broad leafed species. Both *H. cochlearifolium* and *H. alpestre* are deeply concave, however the oblong-elliptic leaf shape of *H. cochlearifolium* would seem to indicate a closer affinity of *H. alpinum* and its associates than would be shown by *H. alpestre*, a species whose leaves are oblong or oblong-lanceolate.

The exclusion of *Hygrohypnum bestii* from the broad leafed group in the two cluster analyses and its subsequent association with *H. ochraceum* is interesting and not entirely unexpected. Certain characters are strikingly similar. For example, there is the dioicous sexuality, the marginal leaf cells which exceed 60 um and the costal and endostomial structure. Measurements of leaf length and median leaf cell length did not readily lend
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Table 3. Similarity Matrix
WEIGHTED PAIR GROUP CLUSTERING

H. ALPINUM

H. CURTISCOLUM

H. SMITHII

H. COCHLEARIFOLIUM

H. MOLLE

H. BEESTII

H. OCHRACEUM

H. NORVEGIUM

H. STYRIACUM

H. MONTANUM

H. EUGYRIUM

H. SUBEUGYRIUM

H. LURIDUM

H. ALPESTRE

H. POLARE

H. CLOSTERI
Ordination Analysis of Hygrohypnum
themselves to inclusion in the calculation of the similarity coefficient. In spite of this, the values for the two species add measurably to their overall similarity. These characters seem to markedly outweigh the differences in stem anatomy and alar differentiation. It is also of special significance that the lowland Pacific Coastal form of *H. bestii* is almost indistinguishable from some forms of *H. ochraceum* save the hyalodermis and alar cells. However, though the leaves of *H. bestii* may be secund they never show any suggestion of the pronounced falcation or circinate curvature so often evident in *H. ochraceum*. The separation of *H. bestii* and *H. ochraceum* in the ordination seems to be more a function of the relative similarities and dissimilarities with *H. cochlearifolium* and *H. eugyrium*, the two end points on the Y axis of the ordination.

The association of *Hygrohypnum norvegicum*, *H. styriacum* and *H. montanum* is apparent in the ordination and both cluster analyses. If the positions of *H. norvegicum* and *H. molle* are reversed in the intuitive scheme, then the similarity is reflected there as well. Perhaps the exclusion of *H. norvegicum* from the broad leafed group may be a function of its ovate leaf shape, the acute leaf apex and perhaps the occasional recurvature of the leaf margin. It is quite clear that all three species share an ovate leaf shape, undifferentiated alar cells and similar costa structure. In both cluster analyses and the ordination, *H. montanum* stands slightly isolated from *H. norvegicum* and *H. styriacum*. Perhaps this is a consequence of its serrulate leaf margins and the absence of a central strand in the stem. There are, however, certain inconsistencies in this spatial arrangement. For example, the leaf margins of *H. montanum* and *H. norvegicum* may be recurved, whereas those of *H. styriacum* are always plane, but both *H. montanum* and *H. styriacum* may have falcate leaves, whereas those of *H. norvegicum* are always straight. There is also the intercalation of the pseudoparoicous *H. styriacum* between the two autoicous species.
The similarity matrix and both cluster analyses indicate that Hygrohypnum eugyrium and H. subeugyrium exhibit the highest degree of similarity between any two species in the genus. In this regard, it is interesting to realize that all but two of the specimens of H. subeugyrium cited in the list of examined specimens were erroneously identified as H. eugyrium. Their overall similarity becomes readily apparent as one scans Table 2. However, these two species are clearly and readily separable from one another on the basis of their alar cells, stem anatomy and the nature of the vegetative leaf apices.

The association of Hygrohypnum luridum and H. alpestre in the two cluster analyses is not unexpected. If the straight leafed forms of H. luridum are compared to H. alpestre on finds that they have similar branching patterns stem anatomy, leaf attitude on the stem, leaf shape, costal structure, alar differentiation (in part), perichaetial leaves and so on. Their major differences lie in the deep leaf concavity of H. alpestre and its peculiar reflexed leaf apex. Although the margin of the leaf apex may be inrolled in straight leafed forms of H. luridum, the apex is never reflexed. Furthermore, an annulus is present in H. alpestre, but lacking in H. luridum.

Hygrohypnum polare can be treated as a perfectly respectable Hygrohypnum. Yet, it is not at all surprising that the cluster analyses and the ordination should indicate an isolated position for it. In personal communication, the late Kjeld Holmen remarked, "If you feed the characters of H. polare into a computer, the output will be Calliergon. But if a taxonomist shall find out, the result will be quite another." Where the costa is variable in all other species of Hygrohypnum, that of H. polare is stout, single and percurrent. The presence of a hyalodermis and the dioicous sexuality further isolate the species. Among the species of Hygrohypnum, H. polare is most often confused
with *H. luridum*. The leaf shape of the two species overlaps, both may be falcate and they both exhibit numerous quadrate to short rectangular alar cells. As a consequence, strong, single costate forms of *H. luridum* can look remarkably like *H. polare* as the problem of Husnot's Musci Galliae #592 will attest.

If one were to follow the seemingly objective results of the cluster analyses and the ordination one would be compelled to search for a more appropriate genus in which to place *Hygrohypnum polare*. An examination of the genus *Calliergon* reveals that *Hygrohypnum polare* compares well with *Calliergon sarmentosum*. Both of these species have strong, single costae, their alar cells are similar and both frequently have a small apiculus at their leaf apices. Also, both species seem to exhibit a slight similarity in ecological plasticity. *Calliergon* is normally a genus of fen, bog and lake margin habitats. However, Olle Martensson (pers.comm.) remarks that in the Scandes he has encountered *C. sarmentosum* and *C. stramineum* in or beside streams. On the other hand, Elsa Nyholm (pers. comm.) said that her first encounter with *Hygrohypnum polare* was in a fen. Regardless, *Calliergon* is a rather uniform group of species uniformly exhibiting a similar branching pattern, straight leaves and the lack of a hyalodermis. To transfer *Hygrohypnum polare* with its hyalodermis and straight and/or falcate leaves to *Calliergon* would serve only to introduce an aberrant species into an otherwise uniform genus.

The remarkably strong leaf falcation that is evident in some specimens of *Hygrohypnum polare*, especially those from the Lena River basin in Russia, and the uniformly strong, percurrent costa easily suggest a similarity with *Drepanocladus*. The presence of a hyalodermis in *H. polare* and some *Drepanocladus* does much to enhance the similarity. However, no known species of *Drepanocladus* exhibits the concavity of the leaf or leaf apex commonly
evident in \textit{H. polare}. On the other hand, neither \textit{H. polare} nor any other species of \textit{Hygrohypnum} exhibits the long narrowly acuminate leaf apices so frequent in \textit{Drepanocladus}. In view of the fundamental differences between \textit{H. polare} and the genera into which it might be transferred, it is felt that \textit{H. polare} is best left in \textit{Hygrohypnum} until new information is available.

As was expected, the cluster analyses and the ordination support the intuitive notion that \textit{Hygrohypnum closteri} does not belong in \textit{Hygrohypnum}. However, as was noted earlier, there is no known genus with which \textit{H. closteri} exhibits any clearer affinities. In the absence of an appropriate genus into which to place the Austin species, the arbitrary exclusion of the plant from \textit{Hygrohypnum} would not improve our understanding of \textit{Hygrohypnum} or the \textit{Amblystegiaceae}. Therefore \textit{H. closteri} is provisionally retained in \textit{Hygrohypnum}.

The results of this study show that \textit{Hygrohypnum} is still a heterogeneous group of mosses. However, the causes of the heterogeneity have been pinpointed and therefore, can be dealt with as additional information comes to light. As presently understood \textit{Hygrohypnum} is a genus of semi-aquatic pleurocarpous mosses that grow on rocks between high and low water in or beside small, cold, swiftly running mountain streams in the northern hemisphere. In this habitat the genus is recognized by its variable costa. Beyond these features the genus does not lend itself to terse diagnosis.
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