Abstract. Six species of Pleuroweisieae, Anoectangium aestivum (Hedw.) Mitt., Molendoa sendtneriana (B.S.G.) Limpr., Hymenostylium recurvirostrum (Hedw.) Dix., Gymnostomum aeruginosum Sm., G. valerianum (Bartr.) Zander and Eucladium verticillatum (Brid.) B.S.G., including several with extensive synonymy, are present in Middle America. Four species also found in Europe and Asia, are polytypic, separable by unique combinations of modalities in mostly clinal character states. Infraspecific taxa are not distinguishable because of highly plastic phenotypes. Certain morphological variation is associated with a large-small stature gradient. Weak geographic segregates of two species are disjunctive between the West Indies and eastern Asia. The Pleuroweisieae is probably a phylogenetically heterogeneous group. Two combinations in Gyroweisia are synonyms of Husnotiella obtusifolia, comb. nov.

This synopsis of the Middle American species of Pleuroweisieae is a preliminary study of herbarium material and type specimens in preparation for a contribution to a proposed (Sharp & Bowers, 1974) bryoflora of Mexico. Much material from outside the “Am 2” and “Am 3” regions of the Index Muscorum (Wijk et al., 1959–69) was studied to somewhat alleviate the common problem (Touw, 1974) of recognition of locally disparate elements that may eventually be reduced to synonymy after revisionary studies. An attempt was made to informally describe and bring together under one name probable environmental and minor genetic variants.

Of the 17 species and 3 varieties of Middle American Pleuroweisieae not treated as synonyms in the Index Muscorum (Wijk et al., 1959–69), only 6 species and no varieties are accepted here in the genera Anoectangium, Molendoa, Hymenostylium, Gymnostomum and Eucladium. Twenty-four basionyms are cited as new synonyms, of which the type specimens of 12 are from Middle America, 7 are from South America, 1 is from the United States, 3 are from Europe and 1 is from the Middle East. All 6 recognized species are found in Mexico, for which 13 species and 2 varieties of Pleuroweisieae were previously listed by Crum (1951), with the recent addition of two species by Zander (1976). Five species are presently recognized for Central America

1 I thank the curators of the herbaria mentioned for loans of specimens, and F. Hermann, R. Magill, G. Pierce and A. J. Sharp for invaluable suggestions and criticism.

2 Clinton Herbarium, Buffalo Museum of Science, Buffalo, New York 14211.
and 3 for the West Indies. All species but one are also found in both Europe and eastern Asia. The new synonymy reduces the number of taxa of Pleuroweisieae that should be recognized for North America north of Mexico, for which 17 species and 3 varieties were listed by Crum, Steere and Anderson (1973), with the addition of one species by Saito (1972). A total of 7 species are now recognized for that area, namely Anoectangium aestivum, Molendoa sendtneriana, Hymenostylium recurviostrum, Gymnostomum aeruginosum, G. angustifolium, Eucladium verticillatum, Gyroweisia reflexa and G. tenuis, and one variety, H. recurviostrum var. commutatum; this variety is of doubtful value (Crum, 1973).

The synonymy in this paper is largely of names with New World types. Additional Old World synonyms, and often additional illustrations, can be found in recent works by Chen (1941), Chuang (1973), Gangulee (1972), Podpěra (1954), Saito (1975), Savicz-Ljubitzkaja and Smirnova (1970), Wijk et al. (1959–69) and others. The extensive synonymy is perhaps the beginning of "large scale reductions" that Crum (1951) suggested would be necessary for certain tropical genera of Pottiaceae.

The species are distinguished by combinations of modes in ranges of variation of each of many euryplastic characters. Polymorphism in many species makes identification difficult, and often more than a few characters must be examined to allow for the occasional absence or extreme modification of one or more significant characters. "Good characters," i.e. those found in a majority of specimens or unique to the species, are given as a range of character states with indication of modality when important. In the polymorphic species there is no one combination of a few stenoplastic characters that will suffice for identification. The morphological and culture studies of Florschütz and Florschütz-de Waard (1974) of tropical species of Campylopus have shown that traditionally important taxonomic features in that genus, such as costal morphology and leaf auriculation, are variable and therefore "unreliable." In the present study of the Pleuroweisieae, unreliability of characters is hopefully circumvented by emphasizing modalities of character expression and the use of combinations of many characters for diagnosis.

As is the case in the Hepaticae (Schuster, 1966, p. 315) an evaluation of the degree to which environmental modification masks genetypic expression in widespread polymorphic species is apparently necessary before infraspecific taxa, if any, can be recognized. The largely clinal, independent and broad variation in characters in the four polymorphous species (see supplemental key) of Pleuroweisieae is probably similar to the multiplicity of biotypes in Rhacomitrium heterostichum (Hedw.) Brid. discussed by Anderson (1963). The weak geographic segregates of Anoectangium aestivum and Hymenostylium recurviostrum noted in the present study are not equivalent to subspecies or varieties, as defined for instance by Semple (1974), and are not given taxonomic status. In a similar manner, geographic variants of Trichostomum cylindricum (Brid.) C.Muell. are discussed but not recognized as taxa by Crum and Anderson (1958) on account of the “... occurrence of intermediates and the lack of complete correlation of distinctive characters.” Briggs (1965) in an experimental study of four species of Dicranum found genotypes with wide phenotypic plasticity and those that were relatively invariant in the same species, however, “... the considerable phenotypic plasticity ... blurs the distinctness of particular genotypes and, therefore, the use of varietal names is not recommended.” Briggs suggested that varietal names may be better reserved for “... morphologically distinct intraspecific populations which are stable in cultivation,” when experimental data are available.
Longton (1974) reviewed the paucity of information on genecological differentiation in mosses and presented data on cultured *Polytrichum strictum* Brid. which indicates that both plastic and genetic responses contribute to phenotypic variation in field populations. Variation, he found, is clinal in *P. strictum* but not so in other species of mosses. Stebbins (1950) noted that phenotypic plasticity is correlated with variable, harsh environments. Of the polymorphic species of Pleuroweisieae, *Anoectangium aestivum* and *Molendoa sendtneriana* are "pollacaulophytes," sensu Watson (1964), capable of surviving in habitats with variable or intermittent water supply. The former species has been regenerated from 19-year old herbarium fragments (Malta, 1921). The other two polymorphs, *Hymenostylium recurvirostrum* and *Gymnostomum aeruginosum*, are hygrophytic calciphiles, often exposed to strong insolation and desiccating winds. The polymorphic species are all perennial, dioicous, often produce abundant sporophytes and often reproduce asexually by fragile leaves and, in some species, by obovoid propagula. They exhibit enormous amplitude and complexity of phenotypic expression that may reflect at least some degree of infraspecific genetic differentiation.

The widespread species *Weissia controversa* Hedw. is known to exhibit polymorphy (Grout, 1938-39) complicated by intergeneric hybridization (Crum, 1973). A cytotype, *W. sharpii* Anderson and Lemon, has a distinctive, sympatric range, apparent reproductive isolation and weak morphological differences (Anderson & Lemon, 1973). Several other weakly distinguishable species and varieties of *Weissia*, such as *W. andrewsii* Bartr., *W. glauca* Bartr. and *W. controversa* var. *longiseta* (Lesq. & James) Crum, Steere & Anderson, form a sympatric satellite complex, mainly southern in distribution in North America, that may be similar in some respects to the variant geographic segregates of *Hymenostylium recurvirostrum* and of *Anoectangium aestivum*. The north-southcline in population variability in *W. controversa* sensu lato is quite like that reported in *Selaginella* species by Tryon (1971). Polyploidy that might shelter adaptationally valuable recessive traits in the gametophyte (Longton, 1974) is not evident in the Pleuroweisieae, as *n = 13* is the chromosome number consistently recorded for *Eucladium verticillatum*, *Gymnostomum aeruginosum* and *Hymenostylium recurvirostrum* as well as for Asian species of *Anoectangium* (Cave, 1956–64; Fritsch, 1972; Kumar & Garg, 1974; Moore, 1970).

**Morphology**

Description of variation in characters, of morphological extremes and of modal expressions of clinal series and character combinations, is exemplified by the nomenclatural types or in the lists of specimens examined. Many expressions that intergrade or are minor segregates in the New World are recognized at the species level in Europe and Asia by recent authors, as noted in the text. The amount of variation in character expression is often used here as a character itself in the circumscription of species, though of little use in the identification of individual specimens, which must be done on the basis of presence of a majority of significant characters.

Descriptors of character states used here are generally the same terms of recent authors (Kawai, 1968; Kawai & Walther, 1969; Saito, 1975) for types of character expression in the Pottiaceae. However, typological terms that may imply discreteness are not used here for intergrading character states with apparently the same morphogenetic origins. Categories of combinations of characters, such as coastal cross section types (Kawai, 1968), are little used; instead, a modality in character combinations is
emphasized for each species. The number of portmanteau characters is hopefully
reduced. For instance, “obscure upper laminal cells,” a phrase often used in keys as a
descriptor of Gymnostomum aeruginosum, is interpreted here as a composite attribute
of several characters with variable expression: shape, number and degree of crowding
of laminal papillae, and uni- or bi-stratose condition of the marginal cells. Modality of
color character expressions can be judged from the described range of variation and frequency
of expression of character states. A few characters are emphasized that previously
have been little used in the taxonomy of the Pleuroveisieae, including description of
lamina insertion on the costa, differentiation of ventral costal epidermis and character-
istics of upper laminal papillae and areolation.

Longton (1974) noted a clinal decline in plant growth in Polytrichum strictum,
associated with severity of climate, including mean length of stems, dry weight and
number of leaves. Other characteristics, including tomentum abundance and shape of
lamellar papillae, were constant. Some correlation in variation of characters in the
Pleuroveisieae occurs on a gradient of plant size, especially evident in the polymorphic
species. The many exceptions, however, indicate some independence in phenetic
expression of character combination. The extremes of this gradient are not recognizable
taxonomically due to the lack of geographic segregation and the clinal nature of the
large and small size expressions. Reduced forms are often difficult to identify because
of the occasional absence of taxonomically significant characters. Plants of small stature
appear to be distributed largely in arctic, alpine or desert areas; their size is possibly
due in part to restriction of microenvironmental boundaries by desiccating winds.
Several morphological elements exhibit a tendency to reduction in size, absence or
modification of appearance associated with reduction of overall plant stature. In small
plants of Pleuroveisieae the stem is narrower and often fragile, the central strand is
smaller or absent, the cortical cell walls are often less thickened, the differentiated
eeder layer is less often present, the tomentum is often absent or very thin, the
branches are fewer and the axillary hairs are shorter and of fewer cells. In addition
the leaves are shorter and less twisted when dry, the apex is often more obtuse, the leaf
shape is oval to ligulate and the leaf base is less often differentiated in shape. The costa
ends more commonly below the leaf apex and is, in cross section, more rounded in
shape, the ventral stereid band is reduced in size or absent, the guide cells are fewer
in number and the dorsal stereid band is reduced in size, though seldom absent. In
some species the upper laminal cells are more commonly bistratose and somewhat
smaller in size. The basal laminal cells are differentiated in a smaller area, except in
specimens with very thin cell walls. The perichaetial leaves are shorter and the area
do differentiation of prosenchymatous cells smaller, except in Molendoa and Aneoct-
tangium, in which it is larger. The sporophyte is smaller overall, the capsule more
commonly ovoid, the exothecial cells shorter in length, the annulus less differentiated
in size (although in most species it is only weakly differentiated to begin with). In
general, character state combinations are correlated at least modally in the circum-
scription of species, in the large-small stature gradient, and in minor geographic
seggregates but are otherwise practically independent.

The trend in plants of small stature is towards reduction of morphological elements,
however, the bistratose condition of the upper laminal cells is an apparent elaboration,
as is the tendency of smaller plants of Hymenostylium recurvirostrum towards dimor-
phism of marginal and median upper laminal cells (Fig. 41). In plants of relatively
large stature some species exhibit additional elaborations. In H. recurvirostrum, the
leaves show a tendency to dentition or serrulation of the upper margins (Fig. 42) and to decurrent lower margins, while the costa is occasionally excurrent in a stout, cylindrical mucro. The costa of *Molendoa sendtneriana* becomes broad and flattened, with numerous guide cells. The very closely related, robust Old World species *M. hornschuchiana* (Hook.) Lindb. ex Limpr. exhibits, in varying degrees of differentiation, serrulation of the leaf base by protruding walls of marginal rhomboidal cells, similar in appearance to the serrulation on the upper margins of occasional specimens of *H. recurvirostrum*.

Both the acceptance of geographical species and a priori erection of taxa based on characters found satisfactory in distantly related groups, but not empirically studied, have contributed to the past recognition of the numerous names here placed in synonymy. In regard to the latter problem, leaf shape and number of stereid bands in the costa have been most commonly misapprehended. The outline of the leaf, especially of the apex, is extremely variable in many species of Pleuroweisieae. An acute, versus a blunt, apex has been long considered important in distinguishing such synonym pairs as *Anoectangium aestival*um and *A. euchloron*, *Gymnostomum aeruginosum* and *G. calcareum*, *Molendoa sendtneriana* and *M. tenuinervis* in Europe and *A. incurvans* and *A. obtusifolium* in Middle America. Variation in leaf shape, especially of the apex, is probably a common environmental modification in widely distributed species of mosses capable of colonizing environmentally harsh habitats. Leaf shape is apparently more constant and thus more reliable as a taxonomic criterion in moss species restricted to mesic sites, especially in the pleurocarpous families. Leaf stance and degree of contortion, used by previous authors in species diagnoses for synonyms of *Anoectangium aestival*um and *Hymenostylium recurvirostrum*, is also probably greatly affected by environmental conditions, though perhaps to differing extents in minor genetic variants. Experimental studies of *Dicranum* (Briggs, 1965) suggest that ‘... falcato-secund leaves are a xeromorphic feature developed under conditions of low relative humidity of the air.’

The presence or absence of a ventral stereid band in the costa has long been considered of major importance in separating subfamilies of the Pottiaceae, but there has been unwarranted reliance upon the constancy of this character for the separation of species. The term “stereid band” in the present paper is used to describe differentiated areas of thick-walled cells in the costa, with degree of differentiation clinal within an amplitude unique to the species. Species with wide range in degree of differentiation may in individual specimens show a complete lack of ventral stereid cells, as attested by Saito (1975), even a lack of thin-walled cells that might be interpreted as homologous. In view of this, the potential for ventral stereid band development is here considered a more significant character than is the degree of differentiation. *Anoectangium aestival*um never has a differentiated ventral stereid band. However, in most other species of Middle American Pleuroweisieae, the ventral stereid band is variable in presence, often absent in small plants or those with very thin cell walls. In part, this will explain the many combinations in *Anoectangium* in the synonymy of *Molendoa sendtneriana*, as *Molendoa* has been commonly distinguished by the presence of two stereid bands. In the present descriptions of costal morphology the cross section is taken at mid-leaf unless otherwise stated, and the terms “ventral” and “dorsal” are used in lieu of “adaxial” and “abaxial,” respectively, as the latter are easily confused in reading.

Branching patterns (sensu Stotler, 1972; Schuster, 1966) are apparently terminal
excepting lateral fertile branches and new, flagellate, axillary branches in *Anoectangium aestivum*.

Saito (1975) considers axillary hair characters, including number of uniseriate cells and differentiation in color of basal or terminal cells, important in distinguishing between certain tribes and genera of Pottiaceae. He describes five Japanese species of Pleuroweisieae, which also occur in Middle America, as having axillary hairs of hyaline cells, 8–10 cells in length, except *Molendoa sendtneriana*, which has axillary hairs 17–20 cells in length. No such uniformity exists in the New World distribution of the five species. Differentiation of a brownish, thicker-walled basal cell or uniseriate pair of cells is occasional or common in all species but one. The number of uniseriate cells comprising the hair varies with the stature of the plants; the smaller plants of *Anoectangium aestivum* and *Molendoa sendtneriana* often have hairs only three cells in length. The basal cells of the axillary hairs may be variable in differentiation, occasionally on the same stem, the more mature hairs with brown basal cells, those near the stem apex entirely of clear cells. Intermediately differentiated axillary hairs are sometimes observed, with the first and second cross walls above the hair insertion thickened and brownish in color.

Incrassate laminal cell walls are characteristic of some montane or island populations of species of Pleuroweisieae, including facies of *Anoectangium aestivum* in the Appalachian Mountains of the United States and *Hymenostylium recurvirostrum* in the West Indies. In the former, this phenomenon is associated with local morphological stenoplasticity, but in the latter with local phenetic variability.

The laminal ornamentation of species of Pleuroweisieae is generally highly developed in dry or alternately dry and wet habitats and often only weakly developed or rarely absent in evenly or very wet sites, judging from the often meager information on herbarium labels. The degree of thickening of the upper laminal cell walls apparently influences, to some extent, the papillae morphology. The number of salients or processes per papilla were observed to vary in many species in a continuum from 1 (“simple papilla”) in thin-walled specimens to 2 (“bifid”) to 3 (“trifid”) to several (“multifid” or “multiple”) in thick-walled plants. Plants with thinner cell walls are more apt to have superficially bulging upper laminal cells that “crowd” the papillae into positions over the centers of the lumens, in which case the processes are sometimes fused into multifid papillae due to apparent crowding, not wall thickening. Plants with thin cell walls have papillae usually less massive than those found in thick-walled specimens of the same species. However, such character attributes as papillae size, position and degree of fusion are apparently under some degree of genetic control, resulting in modalities of expression unique to each species. As examples, the laminal papillae are usually multifid and centered over the cell lumens in *Anoectangium aestivum* (Fig. 15) and *Gymnostomum valerianum* (Fig. 65), usually simple and centered in *Hymenostylium recurvirostrum* (Fig. 43), often low, plate-like, crowded, bi-trifid and scattered in *Molendoa sendtneriana* (Fig. 25–26), and often simple, hollow, crowded and scattered in *G. aeruginosum* (Fig. 59), these last, when large, appearing as “o-” or “c-shaped” papillae in optical cross section.

Laminal papillae are characteristic of the family Pottiaceae, but little is known of their function. Loeske’s (1926) survey showed that, in the same species, plants with large papillae are found in rather dry places while those with small papillae are in wetter areas. Haberlandt (1914) indicated that papillae or bulging surfaces of laminal cells may act as planoconvex condensing lenses that focus light into the interior of the
cell, and the protrusion of the cell walls out of a covering film of water may allow the gathering of light otherwise lost through reflection. However, Burrage (1971) and Martin and Juniper (1970) noted that surface hairs of vascular plants have a high reflectance in visible light, though less in the infrared. Goebel (1905) stated that laminal papillae of mosses act as effective capillary apparatus for the imbibition of water, but, according to Holloway (1971) and Martin and Juniper (1970), superficial hairs and rough leaf surfaces of vascular plants, even after the removal of cuticular wax, have great water repellent properties through the trapping of air films beneath water droplets. Burrage (1971) stated that leaves with rough or hairy surfaces have thicker boundary layers of air than do smooth leaves.

**Geographic Relationships**

Of the six species of Pleuroweisieae recognized for Middle America, *Gymnostomum valerianum* is a rare endemic, *Molendoa sendtneriana* is infrequent but widespread in the Northern Hemisphere and South America (Fig. 1), restricted to arctic and montane-alpine habitats, *Anoectangium aestivum* is frequent in the tropics but restricted to montane or island stations elsewhere, *Eucladium verticillatum* is present across the Northern Hemisphere and in Africa, and the remaining two species are widespread in temperate and tropical areas worldwide.

*Anoectangium aestivum* and *Hymenostylium recurviostrum* exhibit east-west disjunctions of variant populations between the West Indies and eastern Asia, especially Japan. Discussions of the similarity of the bryofloras of Japan and Mexico (e.g. Sharp & Iwatsuki, 1965) and of eastern Asia and North America (e.g. Iwatsuki & Sharp, 1967, 1968) have emphasized disjunction of species and vicariad species. However, Crum and Anderson (1958) noted the disjunction of variant populations of *Trichostomum cylindricum* (Brid.) C.Muell. between the Southern Appalachian Mountains of the United States and Europe. It is perhaps premature to suggest a likely explanation for these infraspecific disjunctions; however, local isolation in mountain or island groups seems to have been a common factor. Disjunction at the infraspecific level is difficult
to evaluate on account of differing attitudes on the part of specialists towards the
taxonomic status of weak segregates.

**Relationships**

I agree with others (Andrews, 1922; Hilpert, 1933; Steere, 1945) that the Pleuro-
weisieae is probably a heterogeneous assemblage. This treatment follows the interpre-
tation of Saito (1975), which is largely equivalent to the Eucladioideae of Chen
(1941). Though actual relationships can be better understood only after study of the
Pottiaceae as a whole, certain similarities based on many characters relate most species
of Pleuroweisieae to those of other tribes. *Hymenostylium recurvoirostrum* has striking
gametophytic resemblance to species of *Leptodontium*. *Gymnostomum valerianum*
(and the closely related *G. angustifolium* of the eastern United States, Alaska and
eastern Asia) may be related to species of the Trichostomoideae as is evidenced by the
subtubulose upper leaf and multiple, centered papillae. *Molendoa sendtneriana* and
*G. aeruginosum* both have many characteristics in common with *Didymodon*. A
phylogenetic relationship based on reduction of the annulus and peristome, such as is
evident in the genus *Husnoiota* (discussed in the section on excluded species), may
apply to *Leptodontium viticuloides* and *Hymenostylium recurvoirostrum*, and to
*Gyroweisia tenuis* and *Gymnostomum aeruginosum*. The past emphasis on peristome
morphology for primary diagnostic characters in supraspecific classification is agreeably
defended by Crosby (1974); however, the relationships of eperistomate taxa and of
taxa with reduced peristomes, though not in obvious reduction series, may be better
understood through thorough analysis and comparison of gametophyte characters.

**Key to Pleuroweisieae in Middle America**

1. Perichaetia borne on short lateral branches; perichaetial leaves usually highly differ-
entiated, upper laminal cells different from those of stem leaves ........................................... 2

1. Perichaetia borne terminally on elongate stems or branches; perichaetial leaves dif-
ferentiated below middle, upper laminal cells similar to those of stem leaves ........................................... 3

2. Urn narrow-mouthed, smooth, not collapsed when dry; gametophytes not glau-
cous, upper ventral surface of leaf very narrowly and deeply grooved along costa,
ventral superficial cells of costa rectangular, costa in cross section (Fig. 16) with
one stereid band and lamina inserted ventrally, upper laminal cells subquadrate,
especially homogeneous in size and shape except when thick-walled, laminal
papillae (Fig. 15) usually multiple and centered over lumens .... *Anoectangium aestivum*

2. Urn often wide-mouthed, often rugose and collapsed below when dry; gameto-
phytes often glaucous, upper ventral surface of leaf flat to broadly grooved
along costa, ventral superficial cells of costa quadrate to rectangular, costa in
cross section (Fig. 27) with two stereid bands or ventral stereid band absent in
small plants, lamina inserted laterally, upper laminal cells subquadrate to tri-
angular, rather heterogeneous in size and shape, laminal papillae (Fig. 25-26)
usually broad and simple to granular or irregular, scattered over lumens ....

3. Capsules peristomate; leaves usually serrulate on lower margins, basal laminal cells
highly differentiated, usually well defined as a group, hyaline, thin-walled, bulging-
rectangular ............................................................................................................................................... 4

3. Capsules gymnostomous; leaves entire to weakly denticulate on lower margins, basal
laminal cells not strongly differentiated, hyaline to clear yellow-brown, often rather
thick-walled, usually short-rectangular, seldom bulging ....................................................................... 4

4. Operculum usually adherent to columella after dehiscence of capsule; stem
central strand usually absent; costa in cross section usually without a differen-
tiated epidermal layer of cells ventral to the ventral stereid band, lamina inserted
ventrally, upper laminal cells usually highly heterogeneous, subquadrate marginally to apically, enlarged and rectangular medially, cell walls often thickened (occasionally trigonous) at the corners, laminal papillae usually simple and not crowded  

**Hymenostylium recurvirostrum**

4. Operculum deciduous; stem central strand often present, costa in cross section with a differentiated epidermal layer of cells ventral to the ventral stereid band, lamina inserted laterally or up to a 90° angle, upper laminal cells essentially homogeneous in size and shape, subquadrate, cell walls usually thin or evenly thickened, laminal papillae various, but crowded when simple  

5. Leaves when dry spreading-incurved from the base and obscurely catenulate, oblong- to linear-lanceolate, 1.7–3.0 mm long, distantly coarsely dentate in upper ½–⅓, costa percurrent to shortly excurrent, laminal papillae (Fig. 65) usually large, massive, multiple, centered over lumens  

**Gymnostomum valerianum**

5. Leaves when dry appressed-incurved to weakly spreading, ligulate to oblong-lanceolate, mostly 0.5–0.8 mm long, entire above, costa usually ending 2–5 cells below the apex, laminal papillae (Fig. 59) usually simple to granular, low, often crowded, apparently scattered over lumens  

**Gymnostomum aeruginosum**

**SUPPLEMENTAL KEY TO STERILE MATERIAL WITH ENTIRE LEAF MARGINS**  
(POLYMORPHIC SPECIES)

1. Lamina ventrally narrowly and deeply grooved along costa, which is superficially about 2 cells broad above  

**Anoectantigum aestivum**

1. Lamina ventrally plane, concave or broadly grooved along costa, which is superficially 2–4 or more cells broad above  

2. Plants often glossy, stem central strand usually absent, leaves usually strongly keeled, often recurved when wet, margins often recurved on one or both sides, costa usually excurrent in a broad, often marginally “scalloped” mucro (Fig. 40), ventral cells usually narrowly rectangular in surface view, in cross section (Fig. 44–45) usually without ventral epidermal layer of cells ventral to ventral stereid band, lamina inserted ventrally, upper lamina seldom bistratose on the margins, cells often larger and becoming rectangular medially, walls often much thickened (to trigonous) at corners, laminal papillae (Fig. 43) usually not crowded, not obscuring cell lumens  

**Hymenostylium recurvirostrum**

2. Plants dull, stem central strand often present, leaves plane to weakly keeled or ventrally concave, seldom recurved when wet, margins plane to weakly recurved, costa seldom excurrent, ventral cells often quadrate in surface view, in cross section usually with epidermal layer of cells ventral to the ventral stereid band, lamina inserted laterally or up to a 90° angle, upper lamina often bistratose on the margins, cells not medially differentiated, walls thin to evenly thickened or weakly thickened at corners, laminal papillae usually crowded, obscuring cell lumens  

3. Plants often glaucous, leaves usually crowded, plane to weakly keeled, apex when rounded not apiculate, costa usually ending 1–3 cells below apex to percurrent, seldom excurrent, upper laminal cells usually heterogeneous in size and shape, subquadrate to triangular, occasionally transversely elongated in patches, walls usually evenly thickened, occasionally sinuose, upper laminal papillae (Fig. 25–26) low, broad and simple to irregular, plate-like or granular, solid  

**Molendoa sendtneriana**

3. Plants not glaucous, leaves usually not crowded, plane to ventrally concave, occasionally weakly keeled, apex when rounded sometimes apiculate, costa usually ending 2–5 cells below apex, upper laminal cells essentially homogeneous in size and shape, walls usually thin, straight, upper laminal papillae (Fig. 59) usually small, simple to granular, sometimes hollow  

**Gymnostomum aeruginosum**

**TAXONOMIC TREATMENT**

1869.  

**FIG. 2–16**
Basionym: Gymnostomum aestivum Hedw., Spec. Musc. 32. 1801.

Type(?): Dominican Republic, ex herb. Montagne anon., s.n. (MICH, NY).
Anoectangium tenellum (Mitt.) Par., Ind. Bryol. 41. 1894.
Zygodon jamaicensis C.Muell., Bull. Herb. Boiss. 5: 558. 1897. Type: Jamaica, Contenti Road, Harris 10088 (FH— isotype).
Anoectangium jamaicense (C.Muell.) Par., Ind. Bryol. Suppl. 13. 1900.
Anoectangium incrassatum Broth. in Bryg., Bot. Tidskr. 36: 279. 1919, syn. nov.

Plants in turfs or mats, yellow-green to dark brown above, light- to red-brown below. Stems seldom branched, occasionally flagellate, to 1.0–3.0 cm long, oval to rounded-triangular, or 5-sided in cross section, with distinct central strand, cortical cells with small lumens and thick or thin walls, epidermis undifferentiated; axillary hairs of 3–10 uniserate, hyaline, bulging cells, occasionally somewhat brownish or only basal 1–2 cells thick-walled and brownish, short cells near point of attachment grading to long-cylindric distally; weakly radiculose to red-brown tomentose. Leaves often distant, occasionally crowded or in comal tuft or series, when dry often spiralled about stem, occasionally secund, appressed to widely spreading from base, incurved to twisted above, when wet weakly to widely spreading and recurved; (0.6–1.0) 1.5–2.0 mm long, ligulate to lanceolate, keeled, ventral surface narrowly and deeply

grooved along costa, occasionally somewhat cucullate at apex, margins plane to occasionally weakly recurved at leaf middle and below, occasionally crenulate above by projecting papillae or bulging leaf cells, seldom weakly denticulate, occasionally irregularly sinuolate; apex broadly obtuse to sharply acute, usually apiculate or mucronate by 1–3 translucent cells, base little differentiated in shape or seldom distinctly ovate, not sheathing stem, not decurrent. Costa subpercurrent by a few cells to usually excurrent as a translucent mucro, ventral superficial cells ventrally narrowly rectangular, smooth dorsal cells elongate, occasionally short-rectangular to quadrate near apex, papillose; in cross section elliptical to reniform, usually weakly to strongly concave ventrally, lamina inserted ventrally, with a single layer of 2(–4) ventral epidermal cells, often only differentiated near insertion of lamina or entirely absent, 2(–5) guide cells, usually strong dorsal stereid band and dorsal epidermal layer occasionally differentiated. Upper laminal cells subquadrate, with thin or evenly thickened walls, usually superficially bulging, but only weakly convex when cell walls are thickened, lumens rounded-quadrate to occasionally ovate or angular, (5–)7–9(–15) μm wide, about 1:1, usually essentially homogeneous in size and shape, but in thick cell-walled collections occasionally elongated to 2:1 longitudinally along upper margins or both longitudinally and transversely in pairs medially, in some collections occasionally protruding from the leaf surface or entirely extraplanar as bistratose patches or transverse rows; papillae usually massive, multiple, centered over the lumens, with mostly 4–6 salients per lumen, but occasionally simple or bifid, crowded, appearing scattered over lumens. Basal laminal cells weakly differentiated near base of costa, yellow-brown, smooth, little wider than upper laminal cells, short-rectangular, mostly 2–4:1, usually thick-walled. Leaves at base of branches small, acute-ovate to deltoid, costate, serrulate, often with rhomboidal laminal cells. Dioicus. Perichaetia terminal on short lateral branches, inner leaves ovate- to oblong-lanceolate, sheathing the seta, 1.0–1.5 mm long, cell walls thin, prosenchymatous. Perigonia terminal 1(–4) on short lateral branches, gemmate. Seta 0.3–0.8 cm long, yellow-brown, twisted clockwise below and occasionally counterclockwise above. Urn 0.5–1.0(–1.5) mm long, ovoid to elliptical, with a short neck, yellow-brown to brown, weakly sulcate when dry; exothecial cells short- to long-rectangular, 2–4(–7):1, usually 15–30 μm wide, thin-walled; stomata phaneropore at base of urn; annulus weakly differentiated, of 2 rows of yellow or reddish, transversely elongated, weakly vesiculose cells. Peristome absent. Spermatia 9–12(–19) μm in diameter, indistinctly to strongly papillose, light brown. Operculum 0.4–0.6(–1.8) mm long, long-rostrate, oblique, of untwisted cells. Calyptra 1.2–1.5(–2.0) mm long, cucullate, smooth.

Habitat. Soil, wet talus, thin soil over rocks, calcareous and non-calcareous rock, shale, volcanic ash and rock, clay, damp cliffs, roadsides, banks of streams and rivers, bluffs, wet soil in spray of falls, walls; at elevations of (300–)1200–2700(–3300) m and as low as 10 m in the West Indies.

Distribution. North, Central and South America, Europe, Asia, Africa and Australasia. In Middle America, in addition to the localities of the types and representative specimens cited, this species has also been reported under synonyms from Mexico in Oaxaca and Tamaulipas (Crum, 1951) and Cuba (Bizot, 1965; Léon, 1933; Welch, 1950).

Bartram (1949a) recognized in Moss Flora of Guatemala five species of Anoectangium: A. compactum and A. euchloron (= A. aestivum), A. incurvans and A. obtusifolium (= Molendoa sendtneriana) and A. arizonicum (= Gymnostomum aeruginosum). The key characters he used in distinguishing the species were leaf shape, especially that of the leaf apex, and the uni- or bi-stratose condition of the upper lamina (characters I find to be variable in most species), the density of laminal papillae and associated opacity of the upper leaf cells (of limited taxonomic value), and coloration of the plants and apiculation of leaves when obtuse (good characters). Taking synonymy into account, Bartram’s identifications of individual specimens in his herbarium (FH) were largely equivalent to my own, except for those identified as “A. arizonicum,” which comprised a rather heterogeneous assemblage of small forms of several species.

I concur with Crum and Anderson’s (1956) referral of specimens from the Southern Appalachians of the eastern United States, previously identified as A. eu-
chloron (Sharp, 1938; Grout, 1938–39), to Gymnostomum aeruginosum. Sharp’s (1938) basic premise of disjunction to the Appalachian Mountains of A. euchloron (= A. aestivum) still holds, however, through the Appalachian populations long known as the synonym A. peckii.

Anoectangium aestivum as treated here includes forms that might be referred to A. stracheyanum Mitt. or A. thomsonii Mitt. of Asia. However, the significant characteristics distinguishing these three species, as given by Saito (1975) or under their synonyms by Chen (1941), are variable and intergrading in Middle America.

In the Americas, there are four geographic races of A. aestivum, which are not sufficiently distinct to be given taxonomic status. “Typical” A. aestivum is characterized by oblong-ligulate to lanceolate leaves, usually bulging (Fig. 16) upper laminal cells with walls thin to thickened, usually homogeneous in shape and size, laminal papillae usually multiple, usually centered over the lumens. This is found in Alaska, western Canada, northwestern and southwester United States, Mexico, the West Indies, Central America and the Andes of South America. A facies including the type of the synonym A. incrassatum is weakly distinguished by the ligulate to oblong, broadly acute leaves with usually superficially flat upper laminal cells and usually thickened walls (Fig. 14), occasionally elongate along the upper leaf margins and the lumens often transversely or longitudinally elongate medially, the laminal papillae low, simple, seldom multiple. This is restricted to the West Indies sympatric with the typical race. The facies “A. peckii,” including the type of this synonym, is weakly characterized by the oblong-lanceolate, narrowly acute leaves, and laminal areolation and papillae similar to those of the facies “A. incrassatum.” It is found in its most easily distinguished form in the Appalachian Mountains of the eastern United States, where the typical race is unknown. Grout (1938–39) suggested that A. peckii is “.... perhaps better regarded as a regional variety. . .,” and Crum, Steere and Anderson (1973) recently reduced A. peckii to the synonymy of A. aestivum. Intergrades between these three regional variants in the Americas are not uncommon, and both “atypical” forms are found elsewhere in the world under different names. Weak discontinuity between Old World species of Anoectangium is also apparent, but insufficient material was examined to warrant a taxonomic judgment on possible synonymy. The facies “A. peckii” is closely matched by many Asian specimens (e.g. NEW GUINEA TERR.: Mt. Wilhelm, Weber & McVean B32220—DUKE—as A. anomalum Bartr.) but facies “A. incrassatum” is less commonly represented (e.g. JAPAN: Miazaki, Nakagō, Hattori, 1946—DUKE—as A. dichroum Card.). The Mexican specimen (PUEBLA: Arsène 4800) discussed by Grout (1938–39) as possibly A. peckii is here referred to Hymenostylum recurvirostrum by the terminal perichaetia and other characters. These American variant populations are probably best considered minor satellite segregates duplicated elsewhere to greater or lesser degree in isolated areas. The upper laminal cell size, 8–10 µm, is slightly greater than average for the typical form, which may indicate cytotypic differentiation of the variants.

An additional morphological variant of A. aestivum, restricted to Mexico and the West Indies, consists of expressions with a tendency for upper laminal cells to protrude superficially, often extraplantar in bistratose patches or rows, discussed by Zander (1976). Unlike other variants, the upper laminal cells and papillae are otherwise similar to those of the typical expression.

Characters of the areolation of A. aestivum in aggregate contribute to an appearance rather different than that of Molendoa sendtneriana. In A. aestivum, the
longitudinal rows of upper laminal cells are more distinct than the transverse rows; however, transverse rowing is more prevalent and distinct than in *M. sendtneriana*. Patches of pairs or rows of rectangular cells are found mainly in plants with only weakly convex superficial cell walls and the rectangular cells are often twice as long as the subquadrate cells. Marginal notching and associated square to short-rectangular “fields” of evenly-rowed cells are only occasionally evident in *A. aestivum*, though common in *M. sendtneriana*. Partial breakage of the lamina or bistratose patches of cells at notches are essentially absent, as are echlorophyllose enlarged cells between notches and the costa.

A collection from Guatemala (QUEZALTENANGO: Hermann 26332) is unusual in the linear-oblong leaves with the base broadened at the insertion and the differentiated basal cells thick-walled, occupying a small juxtacostal area. A large proportion of the axillary hairs have thick-walled brownish basal cells, and sporelings are scattered about the tomentum.

Blunt-leaved forms of *A. aestivum* are somewhat similar to *Barbula cruegeri* in leaf shape, the lamina with usually plane margins and a narrow ventral groove along the costa, and the clear apiculus. However, the latter species differs from *A. aestivum* in the following significant but variable gametophyte characters: leaves short-lanceolate to long-oblong, apex never sharply acute; leaf base often highly differentiated in shape, elliptical to oblong, reaching to the leaf middle, often forming a distinct shoulder at midleaf; upper laminal cells with massive, multiple papillae centered over and covering the lumens, but without sharp salients; basal laminal cells differentiated, usually short-rectangular, 2–4:1, filling the leaf base; costa often swollen above midleaf with highly papillose, quadrate dorsal epidermal cells, but when the dorsal surface cells are rectangular, the costa is usually dorsally scabrous above with projecting cell walls; ventral surface cells of costa quadrate and papillose to elongate and smooth; costa with one or two stereid bands; and, propagula occasionally present. Asexual specimens of *B. cruegeri* with oblong leaf shape, lacking a distinctly differentiated leaf base (e.g. CUBA: Trinidad Mt., Welch, 1948—DUKE—as *A. euchloron*) are most difficult to separate from *A. aestivum*; however, these usually possess one or more expressions of the characters listed above that are not included in the circumscription of *A. aestivum*.

*Anoectangium aestivum* may be confused with *Hymenostylium recurvirostrum* due to the similarity in leaf outline and the carinate upper lamina, as when I incorrectly referred the type of *Leptodontium angustinerve* Thér. (= *H. recurvirostrum*) to *A. compactum* (= *A. aestivum*) (Zander, 1972). Also, the ventral epidermis of the costa is occasionally of rather thick-walled cells giving the appearance of the superficially exposed ventral stereid band typical of *H. recurvirostrum*.

Zander: Pleuroweisieae in Middle America


Anoectangium excelsum (C.Muell.) Par., Ind. Bryol. 38. 1894, syn. nov. Type: Molendoa tenuinervis (Limpr.) Par., Ind. Bryol. 41. 1894, syn. nov.

Hymenostylium incurvans (Schimp. ex Besch.) Broth., Nat. Pfl. 1(3): 389. 1902, syn. nov.


Anoectangium liebmannii var. viride Card., Rev. Bryol. 36: 107. 1909, syn. nov. Type:
Plants in a compact turf, dark to light green above, often glaucous with a mealy bloom, usually light brown below. Stems occasionally branching, (0.3-)1.0-2.0(-5.5) cm, in cross section round, elliptical or rounded-triangular, with a usually strong central strand, this often dark brown or collapsed, cortex usually of small, thick-walled, small-lumened cells, occasionally little differentiated from those of the central cylinder, epidermis usually not differentiated, but rarely of thin-walled, occasionally collapsed cells; axillary hairs usually about 2 per leaf, of 3-11 uniseriate cells, usually all clear and thin-walled, occasionally 1-2 basal cells with distinctly thicker walls, these sometimes brownish in color; light brown to red-brown tomentum often present. Leaves larger and crowded above on stem, occasionally very fragile, when dry appressed-incurved to strict and weakly spreading, occasionally twisted, curled or tubulose, rarely catenulate, when wet spreading to spreading-recurved, variously oval, ligulate, long-oblanceolate to linear-lanceolate in shape, (0.3-)1.0-2.0(-2.5) mm long, ventral surface flat to broadly grooved or seldom weakly keeled along the costa; margins plane above, occasionally somewhat recurved below, seldom recurved to above midleaf, entire or often sinuolate above or rarely weakly serrulate along the leaf base; apex broadly rounded and occasionally somewhat cucullate to narrowly acute; leaf base usually scarcely differentiated in shape, occasionally oval, not decurrent, not sheathing. Costa subpercurrent by 1-3(-6) cells to percurrent, occasionally excurrent as a stout mucro in acute leaf apices, ventral superficial cells above quadrate, bulging and papillose, similar to laminal cells, to short- or long-rectangular, not bulging and smooth or weakly papillose; dorsal superficial cells above quadrate to rectangular, smooth to papillose; cross section round to semi-circular, ventrally flat to bulging convex, lamina inserted laterally, ventral epidermis usually present as one layer of 2-4 cells, ventral stereid band strong to absent, guide cells in one layer of 2-4 cells, dorsal stereid band usually strong, occasionally much reduced, dorsal epidermis usually somewhat differentiated. Upper laminal cells usually heterogeneous in size and shape, subquadrate to rectangular or often three-sided, walls usually evenly thickened, occasionally porose or thickened at the corners or thin-walled and even sinuose, superficially flat to bulging convex, lumens rounded-quadrate to oval or rounded-triangular, (6-)8-10(-15) µm wide, usually about 1:1, occasionally transversely rectangular along the margins or in patches medially, often bi-(tri-)stratose along the margins or in patches medially. Upper laminal papillae low, broad and simple or irregular to granular, scattered, or occasionally massive, multiple and centered over the lumens, usually 3-4 salients per lumen. Basal laminal cells usually differentiated as a rect-
angular group or reaching higher along costa or margins, clear, smooth to weakly papillose, little to distinctly wider than the upper laminal cells, usually 9–12 μm wide, mostly short-rectangular, (1–)2–3(–5):1, walls evenly thickened, occasionally somewhat thickened at corners or porose. Propagula rarely present, only on much reduced plants, obovoid to spindle-shaped, about 35–50 μm long, of 5–9 multiseriate cells, borne on short, hyaline stalks in leaf axils, not abundant. Dioicus. Perichaetium terminal on short lateral branches, inner leaves larger than outer, to 1.7 mm long, ovate and acute to ovate-lanceolate and acuminate, occasionally outer leaves serrulate, laminal cells entirely thin-walled and prosenchymatous to differentiated only below midleaf. Perigonia terminal 1(–4) on short lateral branches, geminate, outer leaves occasionally strongly serrulate. Seta 0.3–0.7 cm long, yellow to brown, twisted clockwise below, sometimes counterclockwise above. Urn often wide-mouthed, 0.6–1.5 mm long, ovoid, short-elliptic or cylindric, yellow-brown, often collapsed and rugose below when old, neck short; exothecial cells thin- to occasionally thick-walled, short-rectangular, usually 18–30 μm wide, (1–)2–3(-5):1, superficially flat to occasionally convex; stomates phaneropore, at base of urn; annulus of 2–3 rows of transversely elongated hexagonal cells, weakly vesiculose. Peristome absent. Spores (7–)9–12(–15) μm in diameter, essentially smooth to lightly papillose, brown. Operculum (0.4–)0.8–1.2 mm, long-rostrate, oblique to occasionally geniculate, cells not twisted. Calyptra 1.0–2.0 mm, cucullate, smooth.

Habitat. Walls, boulder, bluffs, cave wall, rocks, gypsum beds, limestone, dolomite, soil bank, sand, tree, in dry to moist, exposed to shaded places; 350–2750 m elevation.

Distribution. All continents except Africa, Australia and Antarctica. In addition to the Middle American distribution of types and representative specimens, this species has been reported from El Salvador (Winkler, 1965) as Anoectangium obtusifolium. I recently reported (Zander, 1976) Molendoa sendtneriana from Middle America, from specimens agreeing with typical European material. Saito (1972) pointed out that collections from the eastern United States considered to be this species (Iwatsuki & Sharp, 1958) were actually representative of a new species also found in eastern Asia, Gymnostomum angustifolium Saito, that could be distinguished in sterile collections by the linear-lanceolate leaves with a short excurrent costa and massive multiple papillae centered over each lumen of the upper leaf cells. In the New World, true M. sendtneriana has been known only from Arctic America including Greenland, reported either as the typical variety or the var. tenuinervis (Bassard, 1972; Gyöffy, 1912; Saito, 1972; Steere, 1951, 1955, 1965, 1975). Present studies of the Pleuroweisieae in America indicate that M. sendtneriana is widespread though uncommon in mountainous areas of the North, Central and South American cordillera, extending north through Colorado in the United States and disjunct to Arctic America. The known world distribution (Fig. 1) suggests that this species may be found throughout arctic regions and south into other parts of the Southern Hemisphere along major mountain chains.

The axillary hairs are usually shorter in reduced plants, of 3 clear cells, but as long as 10–11 clear cells in large specimens, and the basal 1–2 cells are seldom thicker-walled and brownish. The leaves are rarely catenulate when dry, with the appearance of Didymodon rigidulus Hedw., and in shape are extremely variable. Even in the same collection, leaves from densely compacted plants may be much broader and shorter than those of creeping, mat-forming plants. The leaf margins are occasionally weakly serrulate along the leaf base, but no New World specimens have been seen that match the serration of the leaf base by projecting rhomboid cells of the European species M. hornschuchianum. In collections in which the ventral stereid band is present, the ventral epidermis of the costa is rarely absent in some leaves, giving the appearance of the usual costal structure of Hymenostylium recurvirostrum. The cell walls are rarely thickened at the corners as is common in H. recurvirostrum. The area of differentiation of the basal laminal cells may extend up the leaf margins as is characteristic
of *Tortella*. Robust specimens often have entire, long-lanceolate, acuminate perichaetial leaves grading in morphology to those of small specimens with weakly serrulate to entire, ovate-lanceolate perichaetial leaves. The perichaetial leaves vary from convolute-sheathing to half-sheathing.

There is little evidence in New World *Molendoa sendtneriana* of geographic variants similar to those of *Anoectangium aestivum* or *Hymenostylium recurvirostrum*. European specimens are commonly more robust than American collections and are less likely to have bistratose upper laminal cells. The Eurasian species *Molendoa hornschuchiana*, which differs mainly in the distinctly serrulate margins of the leaf base and the lanceolate, long-acuminate leaf shape, may prove to be an extreme expression of tendencies seen in *M. sendtneriana*, perhaps best reflected in relationship at the varietal level. The same may be true of the Eurasian *Pleuroweisia schleipackei* Limpr., only weakly distinguished from *M. sendtneriana* by the combination of recurved leaves with obtuse apices and recurved margins, thick-walled laminal cells, indistinct central strand in the stem, and ovoid capsule with the calyptra extending little below the operculum (c.f., Brotherus, 1924; Chen, 1941). This genus and species is recognized by such recent authors as Podpéra (1954) and Savicz-Ljubitzkaja and Smirnova (1970). However, Hilpert (1933) suggested that *P. schleipackei* is better placed with *Molendoa*. The single specimen I have seen (u.s.s.R.: Caucasus, Brotherus, 1881—BP) is well within the limits of variation of *M. sendtneriana* including details of the areolation, such as the heterogeneous laminal cells, bistratose in patches and along the margins. The short calyptra illustrated by Brotherus (1924) and Chen (1941) is not matched in American material; however, this may be due to aberration in a single specimen or the scarcity of American collections with calyptrae. If further study indicates that the former Old World species is conspecific with *M. sendtneriana*, the priority of the basionym *Hedwigia hornschuchiana* Hook. (1819) will necessitate name changes for American material.

The vast variation in leaf shape in Old World *M. sendtneriana* is illustrated and discussed by Pilous (1958) and is matched by American material. Some other character states and character state combinations matched in both hemispheres include robust plants with long-lanceolate leaves, smaller plants with short-lanceolate leaves, laminal cells unistratose or bistratose along the margins or in medial patches, and ventral superficial costal cells quadrate. Propaguliferous expressions are rarely encountered, but likewise have no apparent geographic restriction. I have seen specimens from the United States (COLORADO: Hermann 23589, 23593, 24569) and the Middle East (TURKEY: Handel-Mazzetti 2024), bearing lateral perichaetia in both areas, and propaguliferous forms have been reported for Europe, as *M. sendtneriana* f. *propagulifera* Podp., and Japan, as *M. sendtneriana* var. *japonica* (Broth.) Iwat. (the latter was recently placed in *Didymodon* by Saito, 1975).

Some examples of unusual combinations of character states include collections with long-lanceolate leaves and quadrate ventral costal cells; ligulate leaves with a broad ventral groove, quadrate ventral costal cells, and upper laminal cells with angular lumens; long-oblong leaves with a broad ventral groove, elongate ventral costal cells, two stereid bands present in the costa, and laminal papillae multiple and massive.

There is some correlation in plants of small stature of the following character states: leaves short, with rounded apex, ventral leaf surface concave, not grooved...
along the costa, laminal cells with thick walls and rather angular lumens, papillae massive, ventral superficial cells of the costa quadrate and ventral stereid band absent.

Many arctic and alpine specimens of *M. sendtneriana* are dark in color, have leaves much reduced in length, with upper laminal cells rather thick-walled, and have the general aspect of species of *Andreaea*. Pilous (1958) discussed the European distribution of such “andreaeoid” collections and proposed a name (invalid, Art. 54, I.C.B.N., 1972) for them at the forma level. I find that there is no morphological or geographical discontinuity that would support recognition of these as a separate taxon.

One collection, MEXICO: *Richards et al.* 710 is very unusual in that the leaves are broadly ligulate, unistratose, the costa ending 7–9 cells below the leaf apex, and the upper laminal papillae are massive, low, granular, centered 1(–2) over and nearly covering each cell lumen. However, other collections from the same locality (e.g. *Richards et al.* 706, 709) show intergradation towards the typical expression. In one of these collections (706) the basal laminal cells are not or little differentiated, but this was also noted in a few other Middle American collections.

The most important characters distinguishing *Molendoa* from *Anoectangium* are the potential of two stereid bands in the costa and the usually heterogeneous upper laminal cells, the latter emphasized by Hilpert (1933) but largely ignored in recent taxonomic treatments. Certain other differences in areolation are less striking but show distinctive tendencies of variation. The areolation of the upper lamina of *M. sendtneriana* is characteristically of square to short-rectangular fields of cells, the cells (and their walls) in longitudinal parallel rows, but only weakly arranged in rows transversely with the transverse cross walls usually distinctly staggered. Small patches of pairs of transversely rectangular cells are scattered throughout the fields, often in longitudinal rows several cells in length, each cell about 1:2, in longest dimension about the same as that of subquadrate laminal cells. The fields of cells measure the distance from the margin to the costa in width and usually the distance between the interior notches of the simulate margin in length. The cells between the notches and the costa are occasionally singly echlorophyllose and swollen, similar in appearance to the “nematogonia” illustrated by Correns (1899). Otherwise, in aggregate, the cells bordering the fields are poorly organized. In the area between the marginal notches and the costa, one or more pairs (or trios) of longitudinal rows of cells merge distally into single (or pairs of) rows. The first cell beginning a distal row is often bistratose. In most specimens, the leaf apex is characterized by the merging of longitudinal rows of cells to form fewer, usually obviously staggered rows distally. However, broadly rounded leaves with the costa ending 4–6 cells below the apex often have individual longitudinal rows of cells each diverging distally in the apex into two rows, especially along the margin, the longitudinal rows of cells encircling the end of the costa in the plane of the lamina. The interior marginal notches are often bistratose in otherwise mostly unistratose leaves and often correlate in position with cracks in the lamina. The latter indicates that leaf fragility may be more common than gross observation allows.

*Gymnostomum angustifolium* Saito has not yet been found in Middle America. Its massive multiple laminal papillae centered over the cell lumens are considered important by Saito (1972) in separating this species from *M. sendtneriana*. However, in some specimens from extreme southeastern United States (e.g. FLORIDA: Jackson Co., Mariana, *Anderson & Crum* 13850—DUKE), the laminal papillae are similar to those of *M. sendtneriana*, being granular, weakly centered to scattered, though other collec-
mens of M. sendtneriana are near G. angustifolium in other characters, including the weakly keeled to concave, long-elliptic to acuminate leaf shape, the stout, sharp micro and basal laminal cells which are weakly differentiated. These are referred to M. sendtneriana by the leaf margin bistratose in patches above, the upper laminal cells consistently within the size range of M. sendtneriana, and the laminal papillae 1–4 per lumen. Gymnostomum angustifolium, on the other hand, has unistratose leaf margins, upper laminal cells 10–14 μm in diameter and the laminal papillae occur only 1–2(–3) per lumen.

Didymodon rigidulus Hedw. may be confused with M. sendtneriana on account of the bistratose upper leaf margins, but is distinguished by the lanceolate leaves, often pellucid, with low, simple papillae that are often absent; the bistratose marginal cells are each usually about the same size as the unistratose median cells, seldom appearing as single cells bisected with a cross wall as is usually the case in M. sendtneriana. The dorsal epidermal cells of the costa are often quadrate and spherical propagula are often present, borne on stout, brown branching stalks from the stem.

Partial list of specimens examined.—NORTH AMERICA. GREENLAND. N coast of Independence Fiord, Holmen 7136 (DUKE); Kong Oscars Land, Gásefjorden, Simmons 3884 (DUKE).


CENTRAL AMERICA. GUATEMALA. BAJA VERAPAZ: Jicaco, Sharp 2805 (MEXU, TENN). HUEHUETENANGO: pass above Todos Santos, Sharp 4782 (FH, MEXU, MICH); Zaculeu, Standley 82781 (FH, NY); Chimal, Standley 81672a (FH). ZACAPA: San Lorenzo, Steyermark 43169 (FH).


1934.

Fig. 32-46


*Zygodon eggersii* C.Muell., Hedwigia 37: 235. 1898. Type: Dominican Republic, Isabel de la Torre, Eggers 2819 (MICH—syntype).


*Gymnostomum weidum* Card., Rev. Bryol. 36: 70. 1909. Type: Mexico, Morelos, Cuernavaca, Pringle 10433 (PC—lectotype, FH, NY—isolectotypes); 10533 (PC—syntype, FH, NY—isosyntypes).


Plants in turfs or cushions, sometimes flagellate or filiform, sometimes brittle, often glossy, dark green to light yellow-green or occasionally glaucous above, brown below. Stems branching by many subperichaetial innovations, 1.0-4.0(-8.0) cm long, occasionally superficially papillose, in cross section rounded-triangular, oval or five-sided, central strand usually absent, occasionally indistinct or distinct and dark, cortical cells thin- to thick-walled, epidermis usually not differentiated, occasionally superficially thin-walled to entirely thin-walled and superficially collapsed, sometimes only differentiated in patches; axillary hairs of 6-9(-15)
uniserate cylindric cells, basal 1–2 cells brownish or rarely undifferentiated; red tomentum occasionally present. Leaves usually distant on stems, when dry appressed-incurved to spreading-incurved, sometimes somewhat twisted, secund or lax, when wet spreading, often strongly recurved at base to squarrose, ligulate to lanceolate or linear-lanceolate, 0.5–2.0 (–3.5) mm long, usually keeled, upper ventral surface with a broad, deep groove along costa, occasionally rather flat; leaf margins plane to broadly recurved along one or both margins in lower ½, entire or rarely serrulate above or below by projecting cell walls, rarely distantly denticulate above, rarely bistratose above; apex usually acute, seldom obtuse or rounded, an apicus of one translucent cell sometimes present; base scarcely differentiated in shape to oval, not sheathing, not or narrowly decurrent at margins. Costa subpercurrent by 1–2 cells, percurrent or more often short-excurrent in a broad mucro, this rarely elongate to 5–6 times its width at the lamina, usually "scalloped" marginally by projecting cell walls, ventral superficial cells usually long-rectangular and non-papillose, rarely short-rectangular to quadrate and papillose, dorsal cells short- to long-rectangular, usually papillose; in cross section semicircular to elliptical, ventrally weakly concave to bulging-convex, lamina inserted ventrally, ventral epidermis rarely present above ventral stereid band, consisting of 2–5 parenchymatous cells in one layer; ventral stereid band absent or weak to strong, guide cells 3–4 in one layer, dorsal stereid band weak to strong, dorsal epidermis usually absent, occasionally of one layer of weakly differentiated cells. Upper laminar cells usually highly heterogeneous, subquadrate or short-rectangular on margins grading to wider, short- to long-rectangular or rhomboid medially, but sometimes subquadrate and essentially homogeneous across lamina, (6–)8–12 (–14) μm wide, 1–3:1, walls often weakly thickened at corners to occasionally trigonous, sometimes porose and middle lamellae evident, sometimes thin-walled to evenly thickened; median cells superficially flat to convex, lumens usually rounded-angular to sharply angular. Upper laminar papillae rarely absent, usually low, simple to granular, not obscuring the lumens, centered over the lumens to apparently scattered, 1–3 (–5) per lumen, usually not crowded, sometimes large and obscuring the lumens, bifid, plate-like or granular, 3–5 per lumen, rarely multifid, 1 per lumen. Basal laminal cells usually differentiated as a group at base of costa, occasionally across leaf base or reaching higher along margins or both along margins and costa; basal marginal cells occasionally differentiated as 1–3 rows of narrowly rectangular, thin-walled cells extending into an often long, narrow decurrency; median basal cells hyaline to yellowish, weakly papillose above or smooth, occasionally bulging, short-rectangular to rhomboid, 9–15 μm wide, 2–4:1, walls thin to evenly thickened or irregularly thickened and porose. Leaves at base of branches long-triangular, weakly serrulate, weakly costate, laminal cells rhomboid. Dioicus. Perichaetial terminal, inner leaves weakly differentiated and weakly sheathing below to highly differentiated and strongly sheathing below, acuminate above, to 1.5 mm long. Perigonia terminal, gemmate. Seta (0.3–)0.4–0.8 (–1.0) cm long, brown to red-brown or yellow, twisted clockwise. Capsule stiyliform. Urn 0.7–1.2 (–1.5) mm long, oval to cylindrical, occasionally inclined and cernuous with an oblique mouth, neck short, brown to red- or yellow-brown; exothecial cells 20–40 μm wide, 2–4:1, thin- to thick-walled; stomata phaneropore, at base of urn, sparse; annulus weakly vesciculose, cells occasionally hexagonal and yellow-brown. Peristome absent. Spores (9–)10–13 (–15) μm in diameter, lightly papillose to low, spiculate-papillose, brown. Operculum rostrate, (0.4–) 0.5–0.8 (–1.7) mm long, oblique, cells in straight rows or occasionally somewhat twisted clockwise. Calyptra 1.2–1.5 mm long, cucullate, smooth.

Habitat. Rocks, boulder, rock wall, bluff, cliff, banks, shale, limestone, dolomite, serpentine, concrete, rarely trees; in seepage, along streams and rivers, near waterfalls; often in shade; 500–3700 m elevation.

Distribution. North, Central and South America, Europe, Asia, Africa and Australasia. In addition to the Middle American distribution of the types and representative specimens, this species is also reported from Mexico: Coahuila (Manuel, 1972).

Only one new synonym is added to the already extensive American synonymy compiled largely by Crum (1951) for Mexico, and by Andrews (1943), Crum and Bartram (1958) and Crum and Steere (1957) for the West Indies.

The variant with papillose stems that has long been known under the name Gymnostomum recurvirostrum var. scabrum (Grout, 1938–39) is apparently more common in the United States and Canada than in Middle America. The leaf apex of H. 1977] ZANDER: PLEUROWEISIEAE IN MIDDLE AMERICA 255
*H. recurvirostrum* occasionally may be apiculate by a translucent cell as in *Gymnostomum aeruginosum*. The leaf margins are seldom serrulate below as in *Eucladium verticillatum*. In cross section, the appearance of the costa is extremely variable. The most common expression, in specimens with both stereid bands present, is the absence of both ventral and dorsal epidermal layers of parenchymatous cells. However, occasionally one or both ventral and dorsal epidermal layers are differentiated or both may be variably present or not in the same collection. In collections with only the dorsal stereid band present, a single layer of parenchymatous cells is usually present ventral to the guide cells, though occasionally absent, and the dorsal epidermal layer may be present or absent or variable in differentiation in the same collection. The upper laminal cells may be medially elongate-enlarged in some leaves and little differentiated in other leaves of the same plant. Occasionally all leaves may have median cells little differentiated in shape, though sometimes isodiametrically enlarged to twice the size of the marginal cells. Occasionally the marginal cells may be longitudinally elongate, or variously longitudinally or transversely elongate, 2:1, in patches of cell pairs somewhat as is the case with *Anoectangium aestivum* in the West Indies. The upper laminal papillae are typically low, simple, not obscuring the lumens. Many variations exist, however, reflecting combination of clinal papillae attributes such as coalescence: simple to irregularly granular in shape, to distinctly bi-, tri- or multifid; thickness: low, to broad and flat, to isodiametric and massive; and, position: centered to scattered over the lumens, this somewhat correlated with laminal cell wall thickness and degree of superficial bulging. Examples of relatively uncommon expressions of papillae character states include: scattered irregular granules; 1–3 granules centered over each cell lumen; much thickened, simple to granular papillae obscuring the lumens; thickened granules to massive multifid papillae, usually 1 per lumen; bifid papillae, about 3–4 centered over each lumen; and, large, irregular, low, flat, plate-like papillae, obscuring the lumens. The basal laminal cells are seldom weakly inflated, but not to the extent of those of *Eucladium verticillatum*.

The urn may be ovoid and as short as 0.7 mm grading to cylindrical and as long as 1.2–1.5 mm, and occasionally is curved, with an oblique mouth. This phenomenon was noted by Crum (1957) in *Bryoerythrophyllum campylocarpum* (C.Muell.) Crum, and was discussed by Pursell (1976) for the *Fissidens bryoides* complex. Variation in capsule morphology in *H. recurvirostrum* in Europe and Asia was described by Dixon (1927).

West Indian populations of *H. recurvirostrum* show a great variety of character state combinations and in aggregate differ significantly from continental collections in the greater frequency of unusual combinations of character states. About half of the West Indian collections examined possessed to varying degree one or more, but not all, of the following character states that are rare in mainland populations: plants large, stems with central strand, leaves long, margins plane and decurrent by narrow cells, median upper laminal cells only weakly differentiated from those of the margin, cell walls with corners highly thickened and bulging, costa stoutly excurrent, ventral stereid band present, and leaves rather broad above, the number of cells from costa to margin at midleaf comparatively large. These characters are extremely variable in expression and combination. Table 1 presents a comparison of character state combinations in selected collections including many types of synonyms of *H. recurvirostrum* from the West Indies and the American mainland. No satisfactory circumscription of a West Indian taxonomic entity can be made that would allow the practical identification of
Table 1. Comparison of some character state combinations in *Hymenostylium recurvirostrum* (Hedw.). Dix. 1 = Stem central strand present; 2 = stem epidermis present; 3 = leaf length (to-) mm; 4 = most leaves plane; 5 = leaf margins decurrent; 6 = median upper laminal cells longitudinally elongate 2:1 or more; 7 = upper laminal cell walls porose or corners thickened; 8 = laminal papillae mostly small, simple, occasionally bifid; 9 = ventral stereid band present in costa; 10 = ventral epidermis present in costa; 11 = dorsal epidermis present in costa; 12 = number of cells from costa to margin at midleaf (to-).

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A majority of specimens much less follow the “75 percent convention” discussed by Mayr (1942). Recognition of all permutations of character state combinations would lead to a multiplicity of artificial taxa. Reducing the number of possible taxa by singling out a few characters as “important” must be arbitrary without biosystematic evaluation.

Andrews (1943) studied West Indian collections and came to similar conclusions favoring reduction of various species based on West Indian types. In this he has been followed by Crum and Bartram (1958) and Crum and Steere (1957). Crum (1951), in a study of the Mexican moss flora, considered the synonyms *Gymnostomum orizabanum*, *G. uvidum* and *G. recurvirostrum* var. *scabrum* to be growth forms of *H. recurvirostrum*.

Local geographic expression of extremes in morphological variability, such as occurs in the West Indies, is apparently present elsewhere. Andrews (1943) states that *H. recurvirostrum* achieves its greatest variation in the mountains of Asia, represented, for example, by the synonyms *H. xanthocarpum* (Hook.) Brid. and *H. aurantiacum* Mitt. (Dixon, 1927). The facies “*H. aurantiacum*,” recognized by Chen (1941) and Saito (1975) for eastern Asia (as a species of *Gymnostomum*) is approached or essentially duplicated in significant characters by West Indian specimens. The features distinguishing *G. chenii* Saito (Saito, 1973) of the Himalayan region are likewise
matched (e.g. DOMINICAN REPUBLIC: Ekman 13844, JAMAICA: Harris 10094), except
that some leaves may always be found with evident, though much reduced simple
papillae. I have not seen sufficient material of Asian species of Gymnostomum and
Hymenostylium to make a satisfactory taxonomic judgement; however, the studies of
Andrews (1943) and Dixon (1927) together with the descriptions and excellent
illustrations of Chen (1941) and Saito (1973, 1975) of the above Asian species indicate
that a duplication of combinational variants in the West Indies probably occurs in
eastern Asia.

A collection of H. recurvirostrum from Mexico (Sharp 1592, TENN—as Barbula
lurida) is similar to Scopelophila cataractae (Mitt.) Broth. in the ligulate leaf shape
and pellucid, thin-walled laminal cells. However, it differs by the presence of a
distinct, though weak, ventral stereid band in the costa, ventral superficial costal
cells composed of elongate cells, and presence of laminal papillae, small, 1–3 centered
over each lumen.

Amphidium mougeotii (B.S.G.) Schimp. (e.g. U.S.A.: Tennessee, Tellico R. gorge,
Sharp & Nakanishi 3265—MEX—as H. recurvirostrum) is similar to most specimens
of H. recurvirostrum in general appearance and in the cross section of the costa.
It shows absence of a differentiated epidermal layer ventral to the ventral stereid band,
but may be distinguished by the tiny, crowded, verrucose upper laminal papillae,
numerous and scattered over the cell lumens.

Gymnostomum angustifolium Saito, found in eastern Asia, Alaska, and in the south-
eastern United States in the Southern Appalachians and south into Florida, may be
distinguished from H. recurvirostrum by the crowded leaves, strongly incurved when
dry, leaf margin seldom recurved below, leaf base little differentiated to short-ovate,
basal cells usually short-rectangular and little differentiated, upper laminal cell walls
evenly thickened, and laminal papillae rather massive, 1–2(–3) per lumen, often
multifid.

Hymenostylium recurvirostrum has many of the gametophyte characters of
Leptodontium, including the usual absence of a central strand in the stem (always
absent in Leptodontium), the leaves lanceolate, carinate above, strongly recurved
when wet, often recurved lower margins and differentiated basal cells, usually
elongate superficial cells of the costa and ventral epidermis of the costa seldom
present over the ventral stereid band (never present in Leptodontium). It is par-
ticularly similar to L. viticulosoides (P.Beauv.) Wijk & Marg. in the extreme poly-
morphy, the terminal branching pattern, usual absence of a stem epidermis (never
present in L. viticulosoides), often thickened corners of the upper laminal cell walls,
the upper laminal cells often longitudinally elongate medially, especially in flagellate
plants and the simple laminal papillae. Some collections from the West Indies with serru-
late or denticulate upper leaf margins bear a striking resemblance to L. viticulosoides.
Leptodontium viticulosoides is distinguished by the robust plant size, usually dentate
leaves, broad, reniform costal cross section with usually 4 guide cells, convolute-sheathing
perichaetial leaves, long-cylindric, peristomate capsule with irregularly deciduous annulus,
spores often anisosporous and inflorescence often autoicous; it is found in mesic to
variably dry and wet habitats, but is not a hygrophyte as is H. recurvirostrum.

The specific epithet of H. recurvirostrum has been rendered by various authors
with the ending -re. Andrews (1943) pointed out that the basionym Gymnostomum
recurvirostrum Hedw. is partly based on a pre-1801 combination in Pottia with the
ending of the specific epithet -a, and therefore the correct neuter form is -um. Had
the pre-1801 specific epithet ended in -is, which is also linguistically possible according to Andrews, Hedwig (1801) would have used the neuter ending -re.


4. Gymnostomum aeruginosum Sm., Fl. Brit. 3: 1163. 1804. Fig. 47-60

Plants in loose or compact turf or cushions, light or dark green above, light to dark brown below. Stems often branching below, to 2.7 cm, rounded-triangular to five-sided in cross section, central strand usually present, cortical cells not differentiated or darker, thick-walled, with smaller lumens, epidermis occasionally differentiated, of thin- to thick-walled cells, often collapsed in mature portions of stem; axillary hairs of 3–10 uniseriate cylindrical cells, usually 1(–2) basal cells shorter, brownish, but these occasionally undifferentiated; red tomentum sometimes present. Leaves seldom crowded above, distant and smaller below, when dry incurved to strict, appressed to weakly spreading, when wet spreading-recurved, ligulate to oblong-lanceolate, (0.3–)0.5–0.8(–1.1) mm long, ventral surface flat to broadly convex across leaf or occasionally weakly keeled; margins plane or occasionally recurved below, entire or sometimes denticulate below, often bistratose above; apex rounded or broadly acute, sometimes apiculate by a papilllose translucent cell; base little widened to elliptical, little sheathing and not recurrent except occasionally along the costa. Costa rarely strong, subpercurrent by 2–5 cells, seldom percurrent, ventral superficial cells often subquadrature above, papilllose and little different from the laminal cells or occasionally short- to long-rectangular, weakly papilllose to smooth; dorsal superficial cells usually elongate, seldom short-rectangular to quadrate above; cross section ovate to semicircular, ventrally flat to convex, lamina inserted laterally or to a 90° angle ventrally, ventral epidermis present above ventral stereid band, 2–3(–5) cells in one layer; ventral stereid band rarely strong, often lacking, guide cells 2(–6) in one layer, rarely 2–3 cells differentiated ventrally as an incomplete second layer, dorsal stereid band usually weak, rarely lacking or strong; dorsal epidermis occasionally differentiated. Upper laminar cells often in longitudinal rows that cross-cross at right angles between the end of the costa and the leaf apex, subquadrature, with usually thin walls, seldom thickened at corners, superficially flat to convex, often “wrinkled” in cross section by hollow papillae, lumens rounded-quadrate, (6–)7–10(–12) μm wide, 1:1, essentially homogeneous in size and shape, occasionally short-rectangular along the costa; papillae small, low, simple to bifid, seldom large and granular, apparently scattered, often crowded, with mostly 3–5 salients per lumen. Basal laminar cells weakly differentiated as a group across the leaf or reaching higher along the costa, yellowish to hyaline, smooth, little bulging, scarcely wider than the upper laminal cells, rectangular, mostly 2–4:1, thin- to thick-walled. Leaves at base of branches small, triangular to ovate, strongly denticulate to entire on the margins, weakly costate, laminar cells quadrate to rhomboid. Spherical to obovoid or spindle-shaped propagula rarely present, of 5–10 multiseriate cells, basal cells hyaline, borne on branching stalks in leaf axils. Dioicous. Perichaetia terminal, inner leaves ovate-lanceolate, differentiated and sheathing below, to 1.5 mm long. Perigonia terminal at ends of short branches, gemmate. Seta 0.3–0.6 cm, yellow to red-brown, twisted clockwise. Urn 0.5–0.8 mm, ovoid to elliptical, with a short neck, smooth when dry, yellow to red-brown; exothecial cells quadrate to rectangular, 25–40 μm wide, 1–3:1, thin-walled; stomata phaneropore at base of urn; annulus in 1(–)2–3(–4) rows, transversely rectangular or seldom nearly isodiametric, reddish or yellowish, weakly vesiculose. Peristome absent. Spores 9–12 μm in diameter, essentially smooth, brown. Operculum not seen. Calyptra about 1.2 mm long, cucullate, smooth.

Habitat. Calcareous boulder, travertine, limestone, volcanic rock, trailside bank, soil, cave wall; damp, moist areas; 1700–2900 m elevation.

Distribution. North, Central and South America, Europe, Asia and Africa. In addition to the Middle American distribution of types and representative specimens, this species is also reported, as synonyms, from MEXICO: Coahuila (Bartram, 1949b) and San Luis Potosi (Crum, 1951). The collection (CUBA: Wright 8) reported by Sullivant (1862) is Hymenostylium recurvirostrum.

Axillary hair variations include collections with 3–6 uniseriate, hyaline cells, or the basal 1(–2) cells differentiated, with thicker, brownish walls and the hairs mostly 3 to mostly 8 cells in length. Robust specimens and “phenocopies” of Molendoa sendtneriana have at least some leaves recurved on the lower margins. The lower leaf margins are occasionally denticulate, but not serrulate as in Eucladium verticillatum. No Middle American specimens were found with two costal stereid bands, though this is common in strongly costate collections from the United States. The upper laminal cell walls are rarely thickened at the corners as in Hymenostylium recurvirostr-
trum. The annulus of the capsule in some European specimens is rather high, of 3–4 rows of weakly vesiculose cells, but not revolvable and highly vesiculose as in species of Gyroweisia.

I am unable to distinguish small, sterile forms of G. aeruginosum, by any combination of characters, from gametophytic plants of Gyroweisia tenuis (Hedw.) Schimp., which is known in the New World only from Michigan in the United States (Steere, 1939). Collections of Gymnostomum aeruginosum with sporophytes were seen from several states of Mexico and in Guatemala, and all sterile material is referred to this species. If, however, undoubted Gyroweisia tenuis is ever found in Middle America, a reevaluation of geographic distribution will be necessary based only on plants with sporophytes.

Small forms of Gymnostomum aeruginosum and of Molendoa sendtneriana are very similar, especially those with ligulate leaves and large granular papillae. For example, the collection U.S.A.: Hermann 22392 has terminal perichaetia but gametophytes almost identical with those of fertile M. sendtneriana from the same region. Conversely, collection U.S.A.: Anderson 12061 has perichaetium borne on short lateral branches but perigonia terminal on elongate branches, and gametophytes within the typical range of variation of G. aeruginosum. Both collections are placed with G. aeruginosum, the former considered a phenocopy phenomenon and the latter a rare aberration. However, the possibilities of intergeneric hybridization or of occasional lack of fertile and sterile branch dimorphism in M. sendtneriana must not be discounted. This problem might be resolved through intensive fieldwork and experimental study, especially of the sympatric Colorado populations.

I am unable to distinguish Gymnostomum aeruginosum and G. calcareum in New or Old World collections using any of the characters or combinations of characters given by recent authors. I support Crum and Anderson's (1956) referral of all eastern North American material of the latter name to G. aeruginosum, including certain Southern Appalachian specimens previously identified as Anoectangium euchloron (= A. aetricum) (Sharp, 1938), but would go further in referring G. calcareum to the synonymy of G. aeruginosum. Observed variation in a series of specimens is on a gradient correlated with plant stature as in other polymorphic species of Pleuroweisieae.

Propaguliferous forms of Gymnostomum aeruginosum are rare, Portugal: Sérgio 1319; Greece: Pierrot 88, Zander 4078; U.S.A.: Zander 4485, and a few propagula were found in a collection from Mexico (sonora: Richards et al. 709) but not attached to the plants. The holotype of Gyroweisia luisieri, described from propaguliferous material without sporophytes, is matched in gametophyte characteristics in a propaguliferous specimen from Greece with sporophytes (Zander 4078). Most propaguliferous collections of G. aeruginosum are curiously similar to those of M. sendtneriana in the small stature and short, elliptical to ovate leaves, but may be distinguished from the latter when lacking perichaetium by the somewhat smaller, essentially homogeneous upper laminal cells, the simple (to bifid) crowded papillae, and the costa occasionally distinctly broadened and thicker in the upper half of the leaf. Some European collections of Gyroweisia tenuis have been reported (Malta, 1931) to be propaguliferous.


WEST INDIES. HAITI: Morne des Commissaires, Mackaness 64 (MICH), 271 (MICH).


Plants in a loose turf, light to dark green above, brown to red-brown below. Stems seldom branching, to 2.5 cm, in cross section round to rounded-triangular or five-sided, central strand distinct, cortical cells substereid, epidermis occasionally differentiated as a single layer of small, thin-walled, usually collapsed cells; axillary hairs of 13–16 long-cylindrical, hyaline cells, or basal 1–2 cells brownish; red tomentum usually present below. Leaves not crowded, mostly about equal in size, when dry spreading-incurved from the base and obscurely catenulate, weakly twisted and sub-tubulose above, when wet spreading, oblong- to linear-lanceolate, 1.7–3.0 mm long, deeply concave to keeled, with broad ventral groove along costa, margins plane, coarsely and distantly dentate in upper 1/2–1/3, teeth ending in a large, translucent, weakly papillose or smooth cell; apex acute, apiculate by a translucent, papillose cell; base scarcely differentiated in shape to short-ovate, not sheathing, not decurrent. Costa percurrent to shortly excurrent, ventral superficial cells above quadrate or at up to a 90° angle, with 3–4 ventral epidermal cells in one layer, a distinct ventral stereid band, 4–5 guide cells, a strong dorsal stereid band, and a dorsal epidermal layer usually differentiated. Upper laminal cells subquadrate to hexagonal, 6–7–10 µm wide, walls evenly thickened, essentially homogeneous, occasionally longitudinally elongate along the costa; papillae usually large, massive, multiple, occasionally bifid, covered over the lumens, mostly 4–6 salients per lumen. Basal laminal cells weakly differentiated as a small group reaching higher along the costa, yellowish, smooth, scarcely wider than upper laminal cells, short-rectangular, mostly 2–4:1, thick-walled. Leaves at base of branches small, deltoid, weakly serrulate, weakly costate, apiculate, laminal cells rhomboidal. Dioicus. Perichaetial leaves, leaves little different from stem leaves, weakly sheathing at base. Perigonia lateral on stem, bud-like. Sporophyte not seen.

Habitat. Cliff, ledge, bluffs; in shade; moist areas.
Distribution. Mexico, Costa Rica, Guatemala and Panama.

There was little variation between the five collections examined. The basal cells of the axillary hairs of Norris 20436 are of clear, little thickened walls, while the first and sometimes also the second basal cells of Valerio 86 and Crosby 3964 are differentiated, brownish, with slightly thicker walls than the distal cells. The collection Sharp 2399 is fertile, the perichaetal leaves having the structure of those typical of Gymnostomum, not of Leptodontium in which the species was originally placed by Bartram (1929). This species is closely related to G. angustifolium Saito, which is found in Japan, Alaska (Baranof Island, Worley & Hamilton 9201—DUKE—as Anoectantium aestivum), and the eastern United States in North Carolina, Tennessee, Arkansas, and Florida, but has not yet been found in Middle America though this seems likely. Gymnostomum angustifolium is similar to G. valerianum in most characteristics, but the leaves differ when dry. They are less obviously catenulate, with entire or occasionally sinuose upper margins, the upper lamina commonly ventrally concave, rarely keeled, the upper laminal cells larger, more pellucid, less obscured by the papillae, which are somewhat thicker and occasionally scattered over the lumens.

**Basionym:** Weissia verticillata Brid., Jour. Bot. (Gott.) 1800(2): 283. 1801.

**Bryum verticillatum** (Brid.) Brid., Muse. Rec. 2(3): 40. 1803, hom. illeg. non Dicks. ex With., 1801.


**Coscinodon verticillatus** (Brid.) Brid., Bryol. Univ. 1: 374. 1826.

**Mollia verticillata** (Brid.) Lindb., Musci Scand. 21. 1879.


Plants in turfs and cushions, virid- to light-green above, light- to yellowish-brown below. Stems branching irregularly, 0.5–2.0 cm, in cross section elliptical, central strand absent, cortical cells wide-lumened, thin- or thick-walled, epidermis present, of large, thin-walled, bulging cells, usually difficult to distinguish from cortical cells when these are thin-walled; axillary hairs numerous, of 5–10 uniseriate, clear, long-cylindrical cells; occasionally weakly radiculose below. Leaves not crowded, usually larger above, 1.7–2.0(–2.2) mm long, when dry erect-spreading, incurved, when wet spreading-recurved, oblong-lanceolate to narrowly lanceolate or linear, broadly concave ventrally, margins plane, entire above and serrulate below or occasionally entire throughout; apex narrowly acute to subulate; base scarcely differentiated to ovate, not sheathing. Costa strong, decurrent at base, often 40–50 μm wide at base, shortly excurrent in a broad, thick mucro; ventral superficial cells quadrate, short-rectangular or elongate; dorsal superficial cells elongate; cross section semicircular or elliptical, ventrally weakly concave to bulging-convex; with lamina inserted laterally, with a single layer of 5–6 ventral epidermal cells, a weak to strong ventral stolid band, guide cells 4–7 in one layer with occasionally 1–2 guide cells in a second layer ventrally, a usually strong dorsal stolid band, and a single layer of dorsal epidermal cells usually differentiated. Upper laminal cells subquadrate, with clear, pellucid walls, weakly to evenly thickened, seldom weakly thickened at the corners, superfluously flat to weakly convex, lumens rounded-quadrate to oval, 8–10 μm wide, 1:1, but occasionally mediately elongate to 15 μm, smaller along the laminal margins, papillae indistinct and low, simple, mostly 2–5 per lumen and scattered, occasionally multifid, scattered to centered. Basal laminal cells highly differentiated as a group across leaf base, hyaline, smooth, mediately bulging-rectangular, mostly 12–15(–24) μm wide, mostly 4–5:1, thin-walled. Leaves at base of branches smaller, little differentiated, or very small, ovate to long-triangular, serrulate, weakly costate at base to strongly costate, laminal cells rhomboidal to rectangular. Dioicous. Perichaetia terminal, inner leaves ovate-lanceolate, to 2.5 mm long. Perigonia not seen. Sporophyte not seen.

Habitat. Calcareous rock, wet areas in gorges and arroyos.

Distribution. North and Central America, Europe, Asia and Africa. In addition to the Middle American distribution of the representative specimens, this species has also been reported from MEXICO: Baja California N. (Crum & Steere, 1958).

The minute serrulation along the lower leaf margins of **Eucladium verticillatum** is considered diagnostic by recent and past authors. However, in a few collections, especially those from Bermuda, this character is weak or disconcertingly absent. Such variation, together with the occasional weak serrulation or crenulation sometimes present along the lower margins of **Gymnostomum aeruginosum** and **Molendoa sendtneriana**, necessitate the study of other significant characters for accurate determination. In **E. verticillatum**, the median upper laminal cells are often distinctly
larger than the marginal cells, and occasionally longitudinally elongate, a modification paralleled in *Hymenostylium recurvirostrum*.

**Partial list of specimens examined.**—**MEXICO.** COAHUILA: El Chorro, McVaugh, 1951 (MICH), Crum 233 (MICH); Buenos Aires, Crum 210 (MICH). SONORA: Moctezuma, Arroyo El Sano, White 321 (MICH); Cajón de la Higuera, 370 (MICH), 371 (MICH), 374 (MICH). BERMUDA. Paget Parish, Richards & Massey 2331 (MICH); Church Cave, Britton, 1905 (NY); Smuggler’s Cave, Castle Harbor, Britton, 1900 (NY); Paynter’s Vale, Britton 271 (NY).

**SPECIES NOT TREATED**


What may be the holotype (MEXICO: Veracruz, Orizaba, anon., s.n.—PC) has both “*Anoectangium breutelianum*” and “*Gymnostomum euchloron*” written on the packet, but is clearly *Hymenostylium recurvirostrum* by the terminal perichaetia and other characters. Paris (1903) refers this species to *A. euchloron*, but he may have seen other material.


The type of this taxon has not yet been located; it is not in the herbarium of H. G. Winter (z), though this is indicated in the original publication. Andrews (1922) saw type material but did not give a disposition. The original description, “... annulo persistente simplici ...”, does not indicate *Gyroweisia* as the appropriate genus, in spite of the transfer by Brotherus (1902), while the words “... in subulam breviusculam obtusatam integerrimam opacam carnosulam paulisper flexuosam attenuata ...” reminds one of *Luisierella barbula* (Schwaegr.) Steere.

**SPECIES EXCLUDED**

Several species with combinations in *Anoectangium* and *Gymnostomum*, based on Middle American types, have been excluded from the Pottiaceae by other authors, and are listed in the Index Muscorum (Wijk et al., 1959–69).

Two Middle American species previously recognized in *Gyroweisia* belong to a single new combination in *Husnotiella*.

*Husnotiella obtusifolia* (Broth.) Zander, comb. nov.


This species differs from other species of *Husnotiella* by the autoicous or rhizautoicous inflorescence, the operculum occasionally with twisted cells, the peristome teeth often red and well developed, to 240 μm long, the annulus usually highly vesiculose, revolvable and deciduous, the leaves often plane-margined, with thin-walled, enlarged basal cells and the costa often not or only weakly spurred. These
characters are not all present in combination in most specimens, and future study may necessitate synonymy with H. revoluta Card., which intergrades in many respects. The collection Arsène 666 has the gametophyte characters of H. revoluta and the sporophyte characters of H. obtusifolia. Husnotiella revoluta is known to occasionally possess a variable, rudimentary peristome and an annulus sometimes deciduous in parts (Brotherus, 1924; Cardot, 1909, 1913; Grout, 1938–39) and specimens I have seen are indeed variable in this regard. Steere (Steere & Chapman, 1946) has referred Trichostomum obtusifolium to the synonymy of Globulinella globifera (Hamp.) Steere in Steere & Chapman, though apparently without seeing the type.

In the past, Gyroweisia has been treated as a "wastebasket" genus. Of the South American species, G. benoistii Thér. is probably Globulinella sp., judging from the original description and illustration, and I agree with Andrews (1922) that G. boliviiana Williams and G. lindigii (Hamp.) Broth. are probably Didymodon tophaceus (Brid.) Lisa from isotype material of both in Andrews’ herbarium (cu) that I was able to examine through the courtesy of Dr. R. T. Clausen. Gyroweisia brevicaulis (Hamp. ex C.Muell.) Broth. of Java and New Caledonia is Luisierella barbula, judging from specimens in the Fleischer herbarium (FH). As noted previously, Gyroweisia luisiari Sérgio of Portugal is a propaguliferous variant of Gymnostomum aeruginosum, q.v.

Additional specimens examined.—MEXICO. HIDALGO: Mineral del Chico, Orcutt 6684 (FH). PUEBLA: Cerrro Guadalape, Arsène 666 (H-BR). TAMAULIPAS: 37 km SW of Victoria, scrub oak forest, 1100 m, Bowers et al. 4053 (TENN), Smith et al. 2778 (MEXU, TENN).

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