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The Tribe Pleuroweisieae (Pottiaceae, Musci) in Middle America¹

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Abstract. *Six species of Pleuroweisieae, Anoetangium 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. Intraspecific 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 Gyroweisida 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 *Anoetangium*, *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

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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 *Anoetangium aestivum*, *Molendoa sendtneriana*, *Hymenostylium recurvirostrum*, *Gymnostomum aeruginosum*, *G. angustifolium*, *Eucladium verticillatum*, *Gyroweisia reflexa* and *G. tenuis*, and one variety, *H. recurvirostrum* 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 genecotypic 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 *Anoetangium aestivum* and *Hymenostylium recurvirostrum* 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, *Anoetangium 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 *Anoetangium aestivum*. The north-south cline 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 *Anoetangium* (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 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 Pleuroweiseiae, including description of lamina insertion on the costa, differentiation of ventral costal epidermis and characteristics 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 Pleuroweiseiae 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 Pleuroweiseiae the stem is narrower and often fragile, the central strand is smaller or absent, the cortical cell walls are often less thickened, the differentiated epidermal 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 of differentiation of prosenchymatous cells smaller, except in *Molendoa* and *Anoectangium*, 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 circumscription of species, in the large-small stature gradient, and in minor geographic segregates 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 dimorphism 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 Pleuoweisieae. An acute, versus a blunt, apex has been long considered important in distinguishing such synonym pairs as *Anoetangium aestivum* 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 *Anoetangium aestivum* 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. *Anoetangium aestivum* never has a differentiated ventral stereid band. However, in most other species of Middle American Pleuoweisieae, 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 *Anoetangium* 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 Pleuroweiseiae, 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 Pleuroweiseiae, 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 Pleuroweiseiae 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

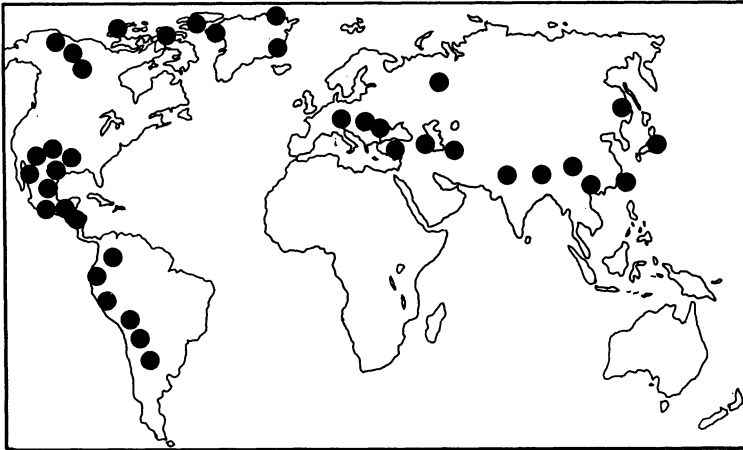


FIGURE 1. Known distribution of *Molendoa sendtneriana* (B.S.G.) Limpr.

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, *Anoetangium 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.

Anoetangium aestivum and *Hymenostylium recurvirostrum* 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 Pleuroweisieae is probably a heterogeneous assemblage. This treatment follows the interpretation 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 recurvirostrum* 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 *Husnotiella* (discussed in the section on excluded species), may apply to *Leptodontium viticulosoides* and *Hymenostylium recurvirostrum*, 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 differentiated, upper laminal cells different from those of stem leaves 2
1. Perichaetia borne terminally on elongate stems or branches; perichaetial leaves differentiated below middle, upper laminal cells similar to those of stem leaves 3
 2. Urn narrow-mouthed, smooth, not collapsed when dry; gametophytes not glaucous, 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, essentially homogeneous in size and shape except when thick-walled, laminal papillae (Fig. 15) usually multiple and centered over lumens *Anoetangium aestivum*
 2. Urn often wide-mouthed, often rugose and collapsed below when dry; gametophytes 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 triangular, rather heterogeneous in size and shape, laminal papillae (Fig. 25-26) usually broad and simple to granular or irregular, scattered over lumens *Molendoa sendtneriana*
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 *Eucladium verticillatum*
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 differentiated epidermal layer of cells ventral to the ventral stereid band, lamina inserted

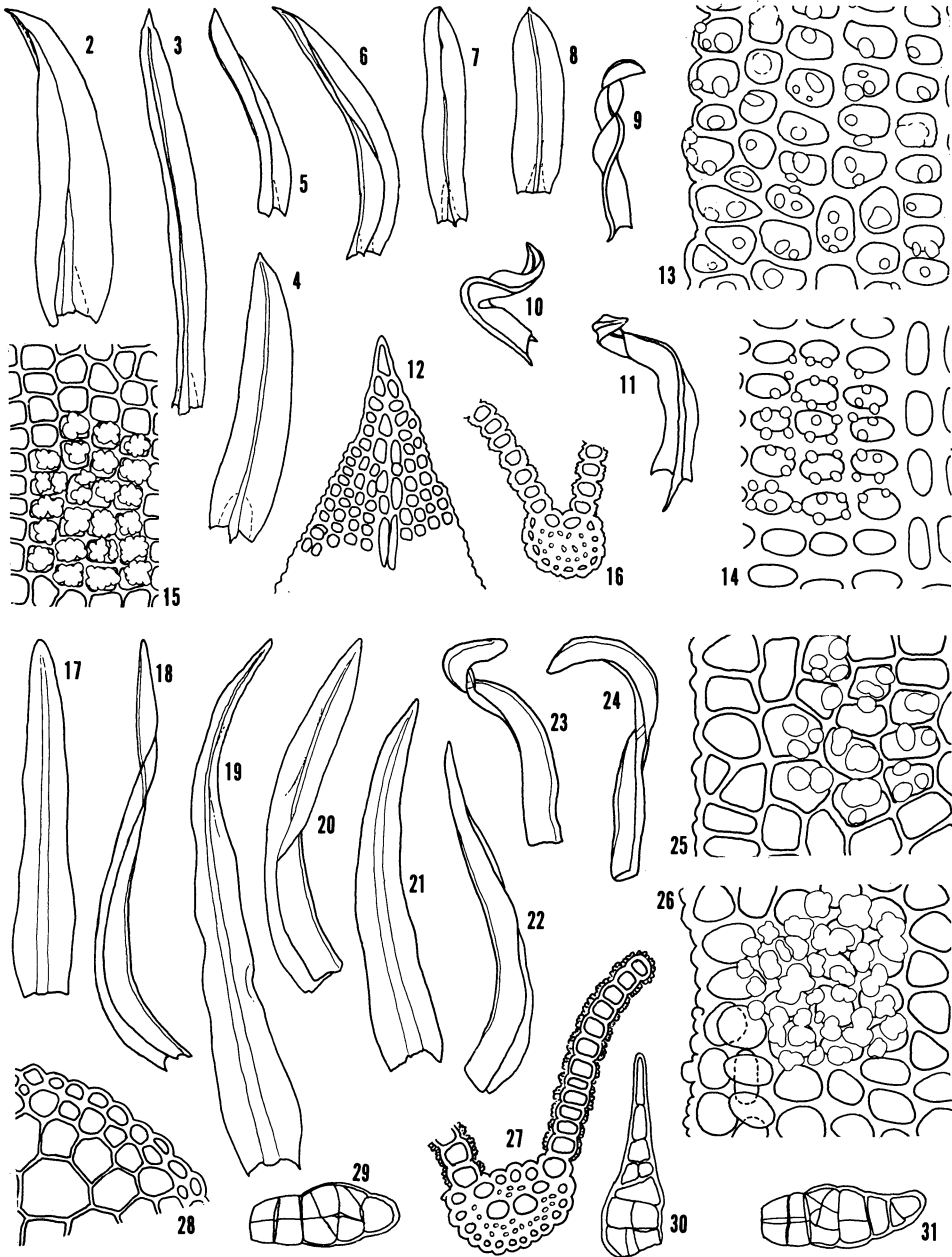
- ventrally, upper laminal cells usually highly heterogeneous, subquadrate marginally to apically, enlarged and rectangular medially, cell walls often thickened (occasionally trigonous) at the corners, laminal papillae usually simple and not crowded *Hymenostylium recurvirostrum*
4. Operculum deciduous; 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
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 *Anoectangium aestivum*
1. Lamina ventrally plane, concave or broadly grooved along costa, which is superficially 2–4 or more cells broad above 2
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
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 *Molendia 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

1. *Anoectangium aestivum* (Hedw.) Mitt., Jour. Linn. Soc. Bot. 12: 175. 1869.



FIGURES 2-31. *Anoctangium aestivum* (Hedw.) Mitt. and *Molendoa sendtneriana* (B.S.G.) Limpr. — 2-16. *A. aestivum*. — 2-8. Moist leaves, $\times 30$. — 9-11. Dry leaves, $\times 30$. — 12. Leaf apex, $\times 300$. — 13-15. Leaf areolation, some papillae drawn in, $\times 750$. — 16. Cross section at mid-leaf, $\times 300$. — 17-31. *M. sendtneriana*. — 17-22. Moist leaves, $\times 30$. — 23-24. Dry leaves, $\times 30$. — 25-26. Upper leaf areolation, some papillae drawn in, $\times 750$. — 27. Costal cross section at mid-leaf, $\times 300$. — 28. Stem cross section, $\times 300$. —

Basionym: *Gymnostomum aestivum* Hedw., Spec. Musc. 32. 1801.

- Anoetangium compactum* Schwaegr., Spec. Musc. Suppl. 1(1): 36. 1811.
Gymnostomum euchloron Schwaegr., Spec. Musc. Suppl. 2(2): 83. 1827, syn. nov.
Gymnostomum guadalupense Spreng., Syst. Veg. 4(1): 145. 1827.
Gymnostomum lamprocarpum Mont., Ann. Sci. Nat. Bot. Ser. 2, 2(9): 49. 1838.
 Type(?): Dominican Republic, ex herb. *Montagne* anon., s.n. (MICH, NY).
Gymnostomum maschalocarpus Mont. in C.Muell., Linnaea 19: 200. 1846, nom. inval.
 (Art. 34, I.C.B.N., 1972).
Anoetangium aestivum (Hedw.) B.S.G., Bryol. Eur. 1: 37 (fasc. 29-30 Mon. 1). 1846,
 nom. inval. (Art. 33, I.C.B.N., 1972).
Zygodon compactus (Schwaegr.) C.Muell., Syn. Musc. 1: 683. 1849.
Zygodon pusillus C.Muell., Linnaea 19: 200. 1846, nom. illeg. (Art. 63, I.C.B.N., 1972).
Zygodon tenellus Mitt., Kew Jour. Bot. 3: 56. 1851. Type: Ecuador, Pichincha, Quito,
Jameson s.n. (MICH—isotype).
Anoetangium euchloron (Schwaegr.) Mitt., Jour. Linn. Soc. Bot. 12: 176. 1869,
 syn. nov.
Anoetangium caldium Mitt., Jour. Linn. Soc. Bot. 12: 176. 1869, syn. nov. Type:
 Ecuador, Pichincha, Quito, *Spruce* 238 (MICH—isotype).
Amphoridium peckii Sull. in Peck., Ann. Rep. Reg. Univ. New York Cab. Nat. Hist.
 22: 57. 1869. Type: U.S.A., New York, Catskill Mts., *Peck*, 1868 (BUF—isotype).
Anoetangium peckii (Sull. in Peck.) Sull. ex Aust., Musci Appal. n. 64. 1870.
Anoetangium apiculatum Schimp. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16: 160.
 1872, syn. nov. Type: Mexico, Veracruz, Orizaba, *Liebmann* s.n. (NY—isotype).
Anoetangium condensatum Schimp. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16:
 160. 1872. Type: Mexico, D.F., San Nicolás, *Bourgeau* 1352 (PC—lectotype); Vera-
 cruz, Cerro León, *Liebmann*, 1841 (MICH, NY—isosyntypes).
Anoetangium liebmannii Schimp. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16: 159.
 1872, syn. nov. Type: Mexico, Veracruz, Orizaba, *Liebmann* s.n. (PC—holotype,
 FH—isotype).
Anoetangium tenellum (Mitt.) Par., Ind. Bryol. 41. 1894.
Zygodon jamaicensis C.Muell., Bull. Herb. Boiss. 5: 558. 1897. Type: Jamaica,
 Contenti Road, *Harris* 10088 (FH—isosynotype).
Anoetangium jamaicense (C.Muell.) Par., Ind. Bryol. Suppl. 13. 1900.
Anoetangium gradatum Card., Rev. Bryol. 36: 107. 1909, syn. nov. Type: Mexico,
 Distrito Federal, Cañada, *Pringle* 10582 (PC—holotype, FH, NY, TENN—isotypes).
Anoetangium incrassatum Broth. in Børg., 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 uniseriate, 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 weakly 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

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29-31. Propagula, $\times 300$. Figures 2, 13 from GUATEMALA: *Standley* 84569; 3, 12 from MEXICO: *Liebmann* s.n.; 4, 16 from GUATEMALA: *Steyermark* 43399; 5 from GUATEMALA: *Standley* 84751; 6 from MEXICO: *Pringle* 10615; 7 from NICARAGUA: *Standley* 20340; 8 from JAMAICA: *Harris* 10088; 9-11 from MEXICO: *Crum* 1300; 14 from JAMAICA: *Orcutt*, 1928; 15 from MEXICO: *Sharp* 3739b; 17 from MEXICO: *Sharp* 1035; 18, 19 from GUATEMALA: *Sharp* 4782; 20-25, 27-28 from MEXICO: *LeSueur* E6a; 26 from MEXICO: *Crum* 281; 29-31 from U.S.A.: *Hermann* 23589.

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 sinuate; 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. Dioicous. 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; exothelial 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. Spores 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, roadcuts, 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*.

Anoetangium 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 southwestern 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 *Anoetangium* 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 *Hymenostylium 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 extraplanar 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 Mts., *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*.

Anoetangium 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*.

Partial list of specimens examined.—NORTH AMERICA. CANADA. BRITISH COLUMBIA: Queen Charlotte Islands, Moresby Island, *Schofield* 15418 (DUKE). U.S.A. ARIZONA: Santa Cruz Co., Patagonia Mts., Flux Canyon, *Bartram* 971 (DUKE, FH). NORTH CAROLINA: Jackson Co., E fork Tuckasegee, above Bonas Defeat, *Anderson* 10597 (DUKE). TENNESSEE: Sevier Co., Mt. LeConte, Roaring Fork, *Sharp*, 1934 (DUKE). WASHINGTON: Whatcom Co., Mt. Baker area, below Austin Pass, *Schofield* 40054 (DUKE). MEXICO. CHIAPAS: N of Mapastepec, *Sharp* 4616 (MEXU, MICH, TENN). CHIHUAHUA: Majalca, *Harvey* 1470 (MICH). DISTRITO FEDERAL: Desierto de los Leones, *Sharp* 25 (MEXU, MICH). DURANGO: Palos Colorados, W of Durango, *Sharp* 1789 (MEXU, MICH). GUERRERO: Taxco, *Frye & Frye* 2753 (MICH). HIDALGO: Apulco, *Sharp* 4148 (MEXU, MICH). JALISCO: above Etzatlán, *Pringle* 10615 (MEXU, PC, TENN); Guadalajara, Sierra de San Esteban, *Pringle* 10564; Los Arboles, Arroyo de La Resolana, *Crum* 1300 (FH, MEXU, MICH, NY, TENN); SW side of La Cumbre, on La Resolana Rd., *Crum*

1236 (MEXU, MICH). MÉXICO: Río Frío, *Sharp* 280 (TENN). MICHOACÁN: Morelia, Loma del Zapote, *Arsène* 7508 (FH); Zacapú, Cerro de Tecolote, *Sharp* 3739*b* (MEXU, TENN). MORELOS: Cuernavaca, *Pringle* 543 (FH, MEXU, NY, PC), 10659 (FH, MEXU, MICH). PUEBLA: Huauchinango, *Sharp* 3056 (TENN); Santa Rita, near Cañada Ipomalín, *Sharp* 3643 (FH, MICH, NY). SAN LUIS POTOSÍ: Charcas, *Lundell* 62 (FH, MICH). SONORA: W of Hermosillo, banks of Río de Sonora, *Richards & Drouet* 613 (FH). TLAXCALA: falls of Río Zuahuapan, near Amaxac, *Sharp* 408 (MEXU, MICH). VERACRUZ: Rancho Viejo, *Purpus* 15769 (FH). YUCATÁN: Izamal, anon. (ex Crypt. Herb. Field Mus.), 342 (FH).

CENTRAL AMERICA. GUATEMALA. EL PROGRESO: Finca Piamonte, *Steyermark* 43399 (FH). QUEZALTENANGO: Río Samalá, *Standley* 84751 (FH, NY), 84569 (MICH, NY); San Marcos Rd., 22.5 km WNW of Quezaltenango, *Hermann* 26332 (BUF). SAN MARCOS: Tajumulco, *Sharp* 5461 (DUKE, FH, MICH, NY); between San Sebastián and San Marcos, *Steyermark* 35701 (FH). EL SALVADOR: Laguna Ninfas, *Brinson* 1001 (DUKE, MICH). HONDURAS: Comayagua, *Standley & Chacón* 5727*a* (FH). NICARAGUA: Estelí, Cerro de las Animas, *Standley* 20340 (MICH). COSTA RICA: Cartago, Cerro de La Muerte, *King C-1179* (BUF). PANAMA: Chiriquí, Boquete, *Svihla* 2713 (NY).

WEST INDIES. CUBA: Pico Cuba, *Acuña*, 1936 (FH, PC). JAMAICA: St. Thomas, Cuna Cuna, *Britton* 958 (MICH); Abbey Green, *Orcutt*, 1928 (DUKE, MICH). HAITI: Massif de la Selle, *Furcy, Ekman* 1918 (FH, MICH, NY, PC). PUERTO RICO: Río de Maricao, *Steere* 5676 (FH, MICH). ST. CHRISTOPHER (St. Kitts): Bethesda, *Breutel*, 1841 (NY). GUADELOUPE: Sarnes, Bois des Bains, *Duss* 1034 (NY). MARTINIQUE: Grand Rivière, *Maurice*, 1967 (MICH). ST. VINCENT: 3 km W of South Rivers, *Andrle*, 1973 (BUF).

SOUTH AMERICA. VENEZUELA. ARAGUA: H. Pittier Nat. Pk., *Sharp* 4369 (BUF). ECUADOR. PICHINCHA: Quito, *Jameson* 112 (MICH). ARGENTINA. MISIONES: Parque Nacional Iguazu, *Grassi* 124 (FH).

EUROPE. NORWAY. HORDALAND: Ethe, *Hegewald* 3604 (BUF). GT. BRITAIN. SCOTLAND: Glen of Athol, *Mitten*, 1860 (MICH). SPAIN. MADEIRA: Ribeiro Frío, *Holmen & Rasmussen* 198 (DUKE).

2. *Molendoa sendtneriana* (B.S.G.) Limpr., Laubm. Deutsch. 1: 250.

1886.

FIG. 17-31

Basionym: *Anoectangium sendtnerianum* B.S.G., Bry. Eur. 1: 91 (fasc. 33-36 Mon. 7). 1846.

Zygodon sendtnerianus (B.S.G.), C.Muell., Syn. Musc. 1: 686. 1849.

Anoectangium peruvianum Sull., United States Expl. Exped., C. Wilkes, U.S.N., Botany, Musci 3. 1860, syn. nov. Type: "Andes of Peru," *U. S. Expl. Exped.*, 1838-1842 (MICH—isotype).

Anoectangium lechlerianum Mitt., Jour. Linn. Soc. Bot. 12: 177. 1869. Type: Peru, Puno, Macusani, *Lechler* 2720 (MICH—isotype).

Anoectangium glaucescens Schimp. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16: 160. 1872, syn. nov. Type: Mexico, Veracruz, Córdoba, *Mueller*, 1834 (PC—holotype, MICH, NY—isotypes).

Gymnostomum incurvans Schimp. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16: 159. 1872, syn. nov. Type: Mexico, Veracruz, Cerro de Borrego, *Mueller* s.n. (NY—isotype).

Zygodon excelsus C.Muell., Linnaea 42: 369. 1879, syn. nov. Type: Argentina, Salta, Nevado de Castillo, *Lorentz*, 1873 (BP, herb. no. 88396, 89195, 89196, 89197, 89198—isosyntypes).

Molendoa tenuinervis Limpr., Laubm. Deutsch. 1: 250. 1886, syn. nov. Type: Austria, Tirol, Windischmatrei, *Breidler*, 1871 (BP, herb. no. 33638—holotype).

Anoectangium excelsum (C.Muell.) Par., Ind. Bryol. 38. 1894, syn. nov.

Anoectangium tenuinerve (Limpr.) Par., Ind. Bryol. 41. 1894, syn. nov.

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

Molendoa excelsa (C.Muell.) Par., Ind. Bryol. 38. 1894, syn. nov.

Gymnostomum laeve Bryhn., Rep. Sec. Norw. Arct. Exp. Fram 2(11): 53. 1907.

Anoectangium liebmännii var. *viride* Card., Rev. Bryol. 36: 107. 1909, syn. nov. Type:

- Mexico, Nuevo León, Sierra Madre, near Monterrey, *Pringle 10455* (PC—syntype, FH, MEXU—isosyntypes), *10457* (FH—isosyntype).
- Anoetangium handelii* Schiffn., Ann. Naturhist. Hofmus. Wien 27: 490. 1913, syn. nov. Type: Turkey, western Kurdistan, Cataonia, *Handel-Mazetti 2024* (FH—holotype).
- Molendoa obtusifolia* Broth. & Par. ex Card., Rev. Bryol. 40: 36. 1913, syn. nov. Type: Mexico, Puebla, near Puebla, *Nicolas*, 1911 (BP—isosyntype); Veracruz, Jalapa, *Orcutt 5361* (FH, MICH—isosyntypes).
- Molendoa boliviana* Broth. in Herz., Biblioth. Bot. 87: 30. 1916, syn. nov. Type: Bolivia (Cochabamba, Cumbre de Liryuni, near Lake Laittu, *Herzog 2651* (BP, herb. no. 89249—isodeotype).
- Molendoa boliviana* var. *brevifolia* Herz., Biblioth. Bot. 87: 30. 1916, syn. nov. Type: Bolivia, Cochabamba, Chocayatal, *Herzog 3574* (BP—isodeotype).
- Molendoa herzogii* Broth. in Herz., Biblioth. Bot. 87: 30. 1916, syn. nov. Type: Bolivia, Cochabamba, above Comarapa, *Herzog 4226* (BP, herb. no. 89199—isodeotype).
- Anoetangium sendtnerianum* var. *tenuinerve* (Limpr.) Moenk., Laubm. Eur. 257. 1927, syn. nov.
- Molendoa obtusifolia* var. *incrassata* Thér., Smiths. Misc. Coll. 85(4): 4. 1931, syn. nov. Type: Mexico, Puebla, Hacienda Batán, *Arsène 5007* (PC—holotype, BP, FH—isodeotypes).
- Molendoa obtusifolia* var. *densissima* Thér., Rev. Bryol. Lichénol. 5: 94. 1933, syn. nov. Type: Mexico, México, Los Reyes, *Woronow 570* (PC—holotype).
- Anoetangium obtusifolium* (Broth. & Par. ex Card.) Grout, Moss Fl. N. Amer. 1(3): 150. 1938, syn. nov.
- Anoetangium incurvans* (Schimp. ex Besch.) Bartr., THE BRYOLOGIST 49: 111. 1946, syn. nov.
- Molendoa sendtneriana* var. *tenuinervis* (Limpr.) Pilous, Preslia 30: 167. 1958, syn. nov.

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-oblong, linear, ovate- 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 sinuate 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 evenly 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. Dioicous. Perichaetia 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, gemmate, 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 cylindrical, yellow-brown, often collapsed and rugose below when old, neck short; exothelial 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, travertine, 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 *Anoetangium 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 Pleuoweisieae 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. hornschurchianum*. 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 *Anoetangium aestivum* or *Hymenostylium recurvirostrum*. European specimens are commonly more robust than are 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 schliephackei* 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 (cf., Brotherus, 1924; Chen, 1941). This genus and species is recognized by such recent authors as Podpěra (1954) and Savicz-Ljubitzkaja and Smirnova (1970). However, Hilpert (1933) suggested that *P. schliephackei* 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* fo. *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 "andreaeid" 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 *Anoetangium* 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 sinuate 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* 13690—DUKE), the laminal papillae are similar to those of *M. sendtneriana*, being granular, weakly centered to scattered, though other collec-

tions from the same region intergrade to the typical expression. Certain sterile specimens 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 mucro 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 catenulate when dry, not apically broadly obtuse or rounded when small, not crowded or glaucous. The upper laminal cells in *D. rigidulus* are usually superficially bulging, 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, Gåsefjorden, *Simmons 3884* (DUKE). CANADA. NORTHWEST TERR.: Ellesmere Island, Disraeli Fiord, *Brassard 4095* (DUKE); Distr. of Mackenzie, Nahanni Nat. Pk., Virginia Falls, *Scotter 22257* (BUF, NY). U.S.A. ALASKA: Central Distr., Firth R. Basin, *Sharp MC58227* (DUKE). ARIZONA: Cochise Co., South Huachuca Canyon, *Haring 10307* (DUKE); Pima Co., Empire Mts., *Bartram 134* (DUKE). ARKANSAS: Boston Mts., near Ponca, along Buffalo R., *Anderson 12196* (DUKE). COLORADO: Boulder Co., Steamboat Mt., 3 km NW of Lyons, *Hermann 23589* (BUF), *23593* (BUF); Larimer Co., 5 km NNW of Masonville, *Hermann 24569* (BUF). TEXAS: Brewster Co., *Orcutt 7161* (DUKE); Tom Green Co., 8 km W of San Angelo, *Redfearn 27144* (DUKE). MEXICO. CHIAPAS: s. loc., *Diill 15* (MICH); Las Casas, *Sharp 3374* (MEXU, MICH, TENN); Chensivilmut, above Huixtan, *Sharp 1271* (TENN). *4718* (MEXU, MICH). COAHUILA: Santa Elena, *Johnston 8193-c* (FH); La Casita, *Crum 281* (MICH). DISTRITO FEDERAL: Mixcoac, *Arsène 9462* (FH); Desierto, *Reiche*, 1913 (H-BR). GUERRERO: Chilpancingo, *Sharp 1035* (MICH, TENN), *1088* (MICH). HIDALGO: Jacala, *Chase 7444* (FH). NUEVO LEÓN: Cañon Sta. Rosa, 8 km E of Iturbide, *McGregor & Rosario 17* (NY, TENN). OAXACA: Tamazulapan Mixe, *Sharp* et al. *2603* (TENN); Zempoatépetl, above Tamazulapan Mixe, *Sharp* et al. *4557* (TENN). Puebla: Huauchinango, along Río Necaxa, *Sharp 3146* (FH, MEXU, MICH). San Luis Potosí: Charcas, *Lundell 57* (FH, MICH); 16 km E of San Luis Potosí, *McGregor & Rosario 685* (TENN); W of Xilitla, *Sharp 5925* (MEXU, MICH, TENN). SONORA: 5 km S of Nacozari, *Richards* et al. *706* (FH, MICH), *709* (FH), *710* (FH, MICH, NY); 1.5 km N of Jécori, *Richards* et al. *719* (FH). TAMAULIPAS: 37 km SW of Victoria, *Bowers* et al. *4051* (TENN). VERACRUZ: "Negro country," *LeSueur E6a* (FH); Cerro de Borrego, *Sharp 1918* (MEXU), *1929* (MEXU, MICH, TENN); Altotongo, toward Atzalan, *Sharp 5572* (MICH, TENN); Tuxptango, *Sharp 1271* (TENN). ZACATECAS: Chalchihuites, *Martinez*, 1945 (MICH).

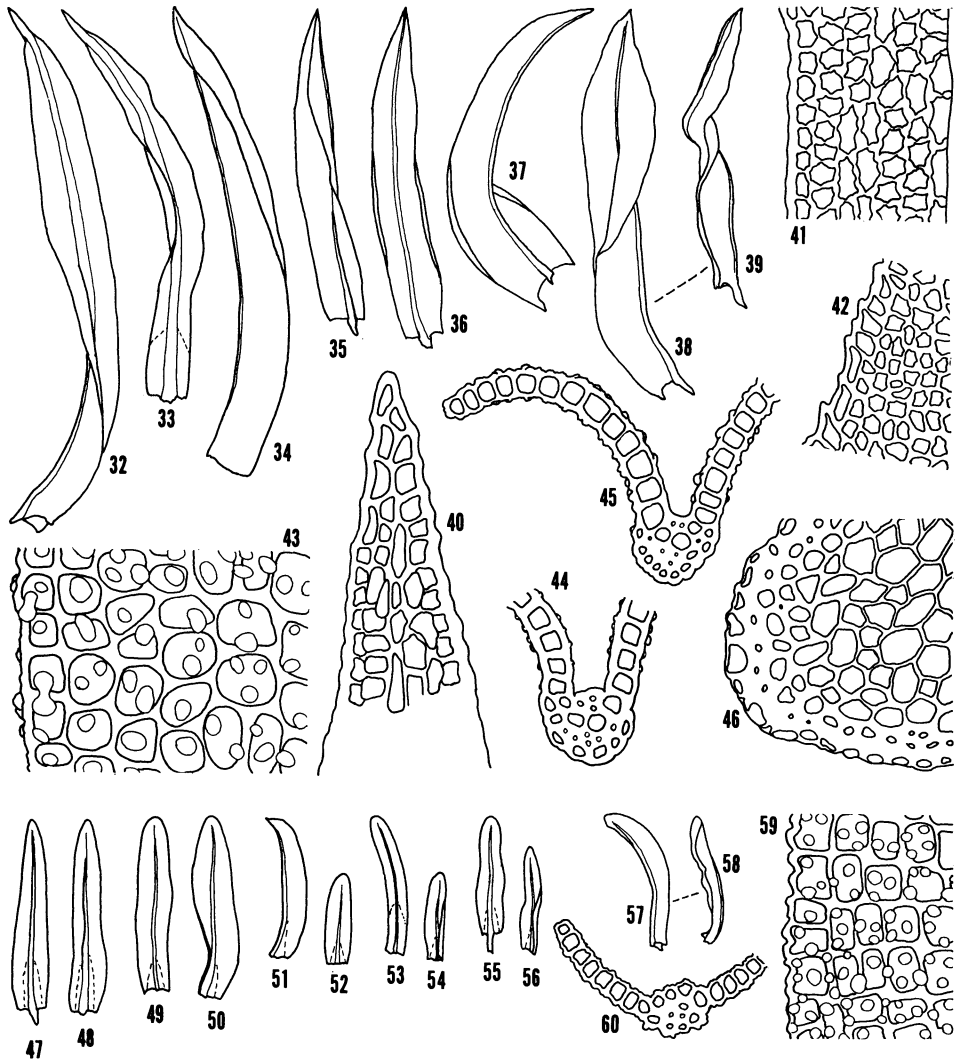
CENTRAL AMERICA. GUATEMALA. BAJA VERAPAZ: Jicaro, *Sharp 2805* (MEXU, TENN). HUEHUETENANGO: pass above Todos Santos, *Sharp 4782* (FH, MEXU, MICH); Zaculeu, *Standley 82781* (FH, NY); Chémal, *Standley 81672a* (FH). ZACAPA: San Lorenzo, *Steyermark 43169* (FH).

SOUTH AMERICA. COLOMBIA. META: Páramo de Sumapaz, *Cleef 7915* (BUF). ARGENTINA. CÓRDOBA: Ongamurá, *Hosseus 219* (FH).

EURASIA. GERMANY. Bavaria, Garmisch-Partenkirchen, *Arnold 12* (BP—herb. no. 33641). AUSTRIA-SWITZERLAND. Rhaetic Alps, anon. (ex herb. Schimper), s.n. (BUF). CZECHOSLOVAKIA. Tatra, *Degen*, 1912 (BF); Liptoský, *Pilous 252* (BF); Magas Patra, *Györfy*, 1909 (BP—herb. no. 33637). ROUMANIA. Carpathian Mts., Mt. Bucsecs, *Vajda*, 1962 (BP—herb. no. 65931). U.S.S.R. Turkmen S.S.R., Ashkhabad, *Radde*, 1886 (BP—herb. no. 33639).

3. *Hymenostylium recurvirostrum* (Hedw.) Dix., Rev. Bryol. Lichénol. 6: 96. 1934. FIG. 32-46
- Basionym: *Gymnostomum recurvirostrum* Hedw., Spec. Musc. 33. 1801.
- Gymnostomum curvirostrum* Hedw. ex Brid., Jour. Bot. (Gott.) 1800(2): 273. 1801, nom. illeg. (Art. 63, I.C.B.N., 1972).
- Weissia curvirostris* C.Muell., Syn. Musc. 658. 1849, hom. illeg. non Lam. & Cand., 1805.
- Hymenostylium curvirostrum* Mitt., Jour. Linn. Soc. Bot. Suppl. 1: 32. 1859, nom. illeg. (Art. 63, I.C.B.N., 1972).
- Weissia stillicidiorum* Mitt., Jour. Linn. Soc. Bot. 12: 134. 1869. Type: Ecuador, Andes Quitensis, Pastaca River, *Spruce* 227 (MICH—isolectotype); Cuba, *Wright* 8 (NY—syntype, BUF—isosyntype).
- Gymnostomum stillicidiorum* (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1869-1870: 282. 1870 (Ad. 1: 42).
- Gymnostomum orizabanum* Schimp. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16: 159. 1872. Type: Mexico, Veracruz, Orizaba, *Müller* s.n. (NY—isodeotype).
- Gymnostomum rupestre* var. *latifolium* Zett., K. Sv. Vet. Akad. Handl. 13(13): 11. 1876.
- Barbula curvirostris* Lindb., Musci Scand. 22. 1879, nom. illeg. (Art. 63, I.C.B.N., 1972).
- Barbula curvirostris* f. *α scabra* Lindb. Musci Scand. 22. 1879.
- Pottia glauca* C.Muell., Bull. Herb. Boiss. 5: 555. 1897. Type: Jamaica, Contenti Rd., *Harris* 10083 (MICH, NY—isodeotypes).
- Pottia nanangia* C.Muell., Bull. Herb. Boiss. 5: 556. 1897. Type: Jamaica, Contenti Rd., *Harris* 10094 (MICH, NY—isodeotypes).
- Trichostomum crustaceum* C.Muell., Hedwigia 37: 235. 1898. Type: Puerto Rico, Utuado, *Sintenis* 125 (MICH, NY—isodeotypes).
- Zygodon eggersii* C.Muell., Hedwigia 37: 235. 1898. Type: Dominican Republic, Isabel de la Torre, *Eggers* 2819 (MICH—isodeotype).
- Hymenostylium pseudo-rupestre* C.Muell., Gen. Musc. Frond. 396. 1900.
- Hymenostylium crustaceum* (C.Muell.) Broth., Nat. Pfl. 1(3): 389. 1902.
- Hymenostylium eggersii* (C.Muell.) Broth., Nat. Pfl. 1(3): 389. 1902.
- Hymenostylium glaucum* (C.Muell.) Broth., Nat. Pfl. 1(3): 389. 1902.
- Hymenostylium nanangium* (C.Muell.) Broth., Nat. Pfl. 1(3): 389. 1902.
- Hymenostylium stillicidiorum* (Mitt.) Broth., Nat. Pfl. 1(3): 389. 1902.
- Weissia recurvirostris* (Hedw.) Dix., Jour. Bot. 40: 377. 1902, hom. illeg. non Hedw., 1801.
- Hymenostylium longopulvinatum* Dusén, Ark. Bot. 6(8): 7. 1906.
- Gymnostomum widum* Card., Rev. Bryol. 36: 70. 1909. Type: Mexico, Morelos, Cuernavaca, *Pringle* 10433 (PC—lectotype, FH, NY—isolectotypes); 10533 (PC—syntype, FH, NY—isosyntypes).
- Eucladium curvirostre* C.Jens., Danm. Moss. 2: 315. 1923, nom. illeg. (Art. 63, I.C.B.N., 1972).
- Leptodontium angustinerve* Thér., Smithsonian Misc. Coll. 85(4): 10. 1931, syn. nov. Type: Mexico, Puebla, Esperanza, *Arsène* 4741 (US—isolectotype); 4743 (FH—isosyntype).
- Hymenostylium glaucum* var. *cylindricum* Bartr., Jour. Washington Acad. Sci. 26: 8. 1936. Type: Jamaica, Farm Hill Works, *Orcutt* 5461 (FH—holotype, PC—isodeotype).
- Gymnostomum recurvirostrum* var. *scabrum* (Lindb.) Grout, Moss Fl. N. Amer. 1(3): 160. 1938.
- Gymnostomum recurvirostrum* var. *latifolium* (Zett.) Flow. ex Crum. THE BRYOLOGIST 72: 243. 1969.

Plants in turfs or cushions, often 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)



FIGURES 32-60. *Hymenostylium recurvirostrum* (Hedw.) Dix. and *Gymnostomum aeruginosum* Sm. — 32-46. *H. recurvirostrum*. — 32-38. Moist leaves, $\times 30$. — 39. Dry leaf, same as 38, $\times 30$. — 40. Leaf apex, $\times 300$. — 41-42. Upper leaf areolation, $\times 300$. — 43. Same, $\times 750$. — 44-45. Costal cross sections at mid-leaf, $\times 300$. — 46. Stem cross section, $\times 300$. — 47-60. *G. aeruginosum*. — 47-57. Moist leaves, $\times 30$. — 58. Dry leaf, same as 57, $\times 30$. — 59. Upper leaf areolation, $\times 750$. — 60. Costal cross section at mid-leaf, $\times 300$. Figure 32 from JAMAICA: Harris 10094; 33, 41 from CUBA: Wright 8; 34-35, 44 from DOMINICAN REP.: Norris et al. B6405; 36-37, 40, 43, 45-46 from MEXICO: Arsène 4743; 38-39 from GUATEMALA: Sharp 2532; 42 from HAITI: Mackness 7; 47-48 from GUATEMALA: Sharp 2494; 49-50 from U.S.A.: Bartram 919; 51-52 from U.S.A.: Richards et al. 709; 53-54, 59-60 from MEXICO: Sharp 543; 55-56 from MEXICO: Sharp 3398; 57-58 from MEXICO: White 373.

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 $\frac{2}{3}$, 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 apiculus 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 semi-circular 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 laminal 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 laminal 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. Dioicous. Perichaetia 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 systylious. 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 vesiculose, 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.*

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, small, 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-).

	1	2	3	4	5	6	7	8	9	10	11	12
West Indian collections												
HAITI: <i>Bartlett 17818</i>	++	-	2.0	+	+	-	+	+	-	-	-	16
DOM. REP.: <i>Eggers 2819</i>	+	-	1.6	+	-	±	+	+	+	+	+	15
DOM. REP.: <i>Norris et al. B6405</i>	+	-	1.8	+	±	±	+	+	+	+	-	16
DOM. REP.: <i>Ekman 13844</i>	-	++	2.0	-	++	+	-	+	+	-	+	16
CUBA: <i>Wright 8</i>	-	±	2.0	-	+	+	++	+	-	±	+	8
JAMAICA: <i>Harris 10094</i>	-	-	3.5	-	++	-	++	+	+	+	+	15
JAMAICA: <i>Orcutt 5461</i>	-	-	2.0	±	-	±	+	+	+	-	±	15
JAMAICA: <i>Harris 10083</i>	-	-	1.3	+	±	±	+	+	+	-	-	19
HAITI: <i>Makaness 7</i>	-	-	2.0	±	-	-	+	+	±	+	+	21
Continental collections												
GUATEMALA: <i>Sharp 4853</i>	+	-	1.1	-	-	-	-	-	-	+	+	8
MEXICO: <i>Reese 5507</i>	±	±	1.2	±	-	-	-	+	-	+	+	10
MEXICO: <i>Pringle 10433</i>	-	+	1.4	-	+	+	+	+	+	-	-	11
MEXICO: <i>Stanford 1809</i>	-	++	0.9	-	±	-	-	-	-	+	±	10
GUATEMALA: <i>Steyermark 50282a</i>	-	+	0.9	+	-	-	+	-	-	-	+	12
MEXICO: <i>Arsène 4800</i>	-	±	1.5	-	+	+	+	-	+	-	+	11
MEXICO: <i>Lundell 68</i>	-	-	2.0	-	-	-	-	±	+	-	±	11
GUATEMALA: <i>Sharp 2532</i>	-	-	2.0	-	-	+	-	±	+	-	-	19
MEXICO: <i>Vera Santos 3114</i>	-	-	1.1	-	+	+	+	-	-	+	-	9
ECUADOR: <i>Spruce 227</i>	-	-	1.8	-	-	+	++	+	-	-	+	12

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*—MEXU—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 southeastern 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 particularly similar to *L. viticulosoides* (P.Beauv.) Wijk & Marg. in the extreme polymorphy, 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 serrulate 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 anisoporous 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*.

Partial list of specimens examined.—NORTH AMERICA. CANADA. BRITISH COLUMBIA: Schofield 25112 (DUKE). U.S.A. ALASKA: Adak Island, Smith 4114 (BUF). COLORADO: San Miguel Co., 5 km S of Telluride, Hermann 24427 (BUF). IOWA: Winneshiek Co., Decorah, Shimek, 1919 (MICH). MICHIGAN: Alger Co., Pictured Rocks, near Munising, Hermann 16091 (DUKE). NEW YORK: Niagara Co., gorge of Niagara R., Zander 4252a (BUF). NORTH CAROLINA: McDowell Co., Linville Caverns, Anderson & Jones 9577 (DUKE). TEXAS: Hays Co., Devil's Backbone, Flowers & Dietert MGF897 (DUKE). VERMONT: Lamoille Co., Smuggler's Notch, Groat, 1912 (DUKE). BERMUDA: Church Cave, Britton 1086 (NY). MEXICO. CHIAPAS: Huixtan, Sharp 4731 (MEXU, MICH). GUERRERO: 20 km W of Chilpancingo, Sharp 1053 (MICH, NY), 1088 (MEXU); 30 km W of Chilpancingo, Sharp 1153a (MEXU). HIDALGO: San Nicolás, Sharp 4080c (MICH); Sharp 1592 (TENN). MORELOS: Cuernavaca, Frye & Frye 2750 (DUKE, MICH, NY). PUEBLA: Esperanza, Arsène 4800 (FH, NY). SAN LUIS POTOSÍ: Charcas, Lundell 68 (FH, MICH), 69 (MICH). TAMAULIPAS: 32 km NE of Victoria, Reese 5507 (MEXU); Ocampo, Stanford 1809 (DUKE, MICH, TENN). VERACRUZ: Las Vigas, Arsène 18914 (FH); Sierra Madre Occidental, Vera Santos 3126 (FH, MICH, NY).

CENTRAL AMERICA. GUATEMALA. ALTA VERAPAZ: N of Cobán, Sharp 2991 (FH). EL QUICHÉ: Nebaj, Sharp 2405 (FH, MEXU), 2532 (MEXU). HUEHUETENANGO: Jacaltenango, Sharp 4830 (MEXU); San Miguel Acataro, Sharp 4853 (FH, MICH, NY); above San Juan, Sharp 5010 (FH, MEXU); crossing of Río San Juan, E of San Rafael Pétzal, Standley 82880 (FH, NY); Sierra de los Cuchumatanes, Steyermark 50000a (FH, MICH, NY); 50152 (FH, NY), 50282a (FH).

WEST INDIES. CUBA: Havana, Campo Florido, Ekman 19016 (FH, NY). JAMAICA: New Haven Gap, Nichols 98 (MICH, NY); Trelawny Parish, Hermann 22932 (DUKE, MICH, NY, PC); trail from Morcos Gap to Vinegar Hill, Maxon & Killip 1316 (FH, NY); Stoney Valley River, Orcutt 5908 (FH); Chestervale, Patterson 1 (NY, TENN); Maris Bank, Jäderholm, 1922 (FH, NY). HAITI: Massif des Matheux, Ekman 5501 (MICH); Morne Jeffard, Bartlett 17818 (MICH); Morne des Commissaires, Holdridge 1299 (FH, MICH), Mackaness 7 (FH, MICH). DOMINICAN REP.: Sierra de Neiba, near Haitian border, Norris et al. B6405 (MICH); de la Vega, Valle Nuevo, Ekman 13844 (FH, MICH, NY). PUERTO RICO: Mt. Britton, Steere 7085 (MICH).

SOUTH AMERICA. TRINIDAD: Quare Dam, Simmonds 357 (MICH). BRAZIL. SANTA CATARINA: Sierra da Pedra, Reitz C242 (FH).

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

Gymnostomum rupestre Schleich. ex Schwaegr., Spec. Musc. Suppl. 1(1): 31. 1811.
Gymnostomum calcareum Nees, Hornsch. & Sturm, Bry. Germ. 1: 53. 1823, syn. nov.
Weissia calcarea (Nees, Hornsch. & Sturm) C.Muell., Syn. Musc. 1: 659. 1849, syn. nov.
Weissia rupestris (Schwaegr.) C.Muell., Syn. Musc. 1: 657. 1849, hom. illeg. non Hedw., 1801.

Hymenostylium calcareum (Nees, Hornsch. & Sturm) Mitt., Jour. Linn. Soc. Bot. Suppl. 1: 33. 1859, syn. nov.

Trichostomum aeruginosum (Sm.) Lindb., Oefv. K. Vet. Ak. Foerh. 21: 229. 1864.

Trichostomum calcareum (Nees, Hornsch. & Sturm) Lindb., Oefv. K. Vet. Ak. Foerh. 21: 229. 1864, syn. nov.

Trichostomum rupestre (Schleich. ex Schwaegr.) Mild., Bryol. Silesiaca 106. 1869.

Mollia aeruginosa (Sm.) Lindb., Musci Scandinavici 106. 1879.

Mollia calcarea (Nees, Hornsch. & Sturm) Lindb. in Braithw., Brit. Moss Fl. 1: 239. 1885, syn. nov.

Gyroweisia pusilla Broth., Nat. Pfl. 1(3): 389. 1902.

Eucladium aeruginosum (Sm.) C.Jens., Danm. Moss. 2: 313. 1923.

Anoetangium arizonicum Bartr., Moss Fl. N. Amer. 1(3): 192. 1938, syn. nov. Type: U.S.A., Arizona, Santa Cruz Co., Whitehouse Canyon, Bartram 919 (FH—holotype, DUKE—isotype).

Gyroweisia luisieri Sérgio, Bol. Soc. Cine. Nat. Portugal 14: 81. 1972, syn. nov. Type: Portugal, Estrada Porto—Viana, Ofir, Sérgio 1319 (LISU—holotype).

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 papillose translucent cell; base little widened to elliptical, little sheathing and not decurrent except occasionally along the costa. Costa rarely strong, subpercurrent by 2–5 cells, seldom percurrent, ventral superficial cells often subquadrate above, papillose and little different from the laminal cells or occasionally short- to long-rectangular, weakly papillose 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 laminal cells often in longitudinal rows that cross-cross at right angles between the end of the costa and the leaf apex, subquadrate, 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 laminal 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, laminal 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 Potosí (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 recurviro-*

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 perichaetia 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 *Anoetangium euchloron* (= *A. aestivum*) (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 4488, 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 perichaetia 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.

Partial list of specimens examined.—NORTH AMERICA. CANADA. BRITISH COLUMBIA: Yale, Fraser R., Schofield & Williams 23460 (DUKE). QUEBEC: Rimouski Co., Bic, Lepage 1841 (DUKE). U.S.A. ARIZONA: Santa Cruz Co., White House Canyon, Bartram 88 (DUKE).

ARKANSAS: Franklin Co., Cass, Spy Rock Hollow, *Anderson 12061* (DUKE). CALIFORNIA: Kern Co., above mouth of Kern R. Canyon, *MacFadden 21858* (DUKE); Santa Clara Co., Fall Cr., *Schofield & Thomas 26445* (DUKE). COLORADO: Ouray Co., San Juan Mts., *Hermann 23224* (DUKE). FLORIDA: Wakulla Co., *Shornherst*, 1939 (DUKE). IDAHO: Bonner Co., Lake Pend Oreille, *Leiberg* s.n. (DUKE). ILLINOIS: Peoria Co., Peoria, *McDonald 17* (DUKE). IOWA: Fayette Co., Echo Valley Pk., *Conrad 7-104* (DUKE). MAINE: Oxford Co., Snow Falls, *Parlin 13599* (DUKE). MICHIGAN: Keweenaw Co., Manganese R. gorge, *Richards 237* (DUKE). MONTANA: Flathead Co., Bowman L., *Hermann 18016* (DUKE); Glacier Co., Appekuny Falls, *Hermann 22392* (DUKE). NORTH CAROLINA: Macon Co., Dry Falls on Cullasaja R., 3 km NW of Highlands, *Sharp 3718* (DUKE, MICH), *Zander 4488* (BUF). NEW YORK: Tompkins Co., Enfield Glen, 10 km SW of Ithaca, *Zander 4267* (BUF). MEXICO. CHIAPAS: S of Las Casas, *Sharp 3398* (MICH, TENN). DISTRITO FEDERAL: Contreras, *Sharp 543* (TENN). MICHOACÁN: Morelia, *Amable 1595* (FH). PUEBLA: Santa Barbara, *Nicholas 124* (PC). SAN LUIS POTOSÍ: Charcas, *Lundell 46* (FH). SONORA: W of Moctezuma, *White 373* (MICH); 5 km S of Nacozari, *Richards et al. 709* p.p. (FH, NY). VERACRUZ: Altotonga, *Sharp 5570* (MICH).

CENTRAL AMERICA. GUATEMALA. EL QUICHÉ: Nebaj, *Sharp 2441* (FH), *2494* (FH). HUEHUETENANGO: Río Pucal, *Standley 65804* (FH).

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

SOUTH AMERICA. VENEZUELA. ARAGUA: H. Pittier Nat. Park, *Sharp 84* (BUF). CHILE. VALDIVIA: Coiral, *Dusén 281* (FH). VALPARAÍSO: Valparaíso, Grotte de Janumé, *Costes 1921* (FH).

EUROPE. FRANCE: ALPES-MARITIMES, Nice, anon. (ex herb. Schimper), s.n. (BUF). PORTUGAL: Lisboa, Sintra, *Hermann 16033½* (BUF). GREECE: Delphi, *Pierrot 88* (LISU); Kos, Mt. Dikeos, above Zia, *Zander 4078* (BUF).

5. *Gymnostomum valerianum* (Bartr.) Zander, THE BRYOLOGIST 75: 277.

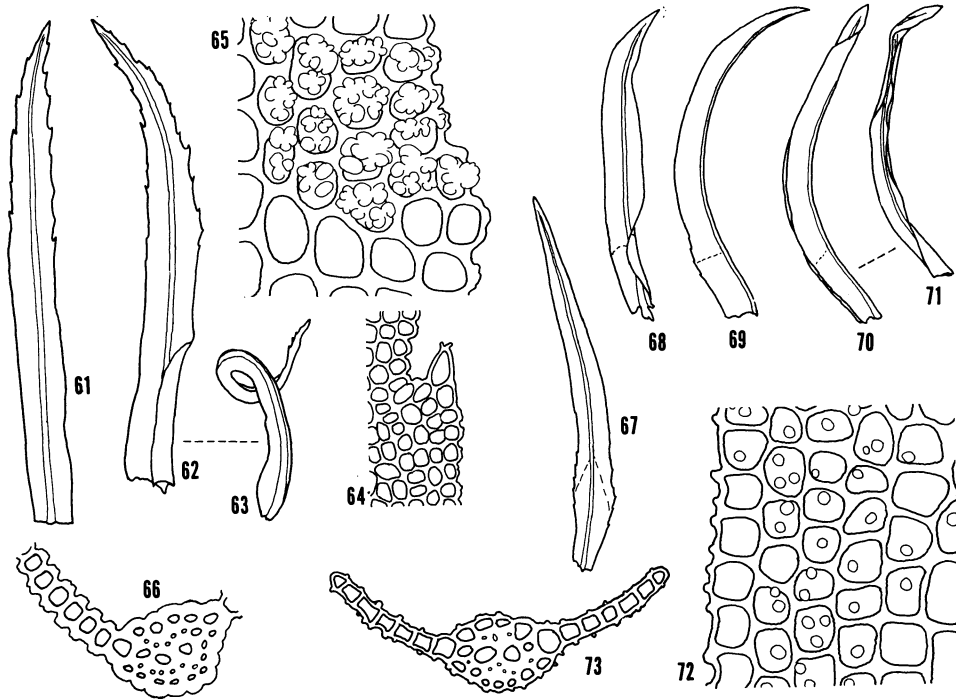
1972.

FIG. 61-66

Basionym: *Leptodontium valerianum* Bartr., Jour. Washington Acad. Sci. 19: 18.

1929. Type: Costa Rica, San José, Piedra Blanca, *Valerio 86* (FH—holotype; PC—isotype).

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 $\frac{1}{2}$ - $\frac{1}{3}$, 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 and little different from the laminal cells to short-rectangular or elongate, papillose; dorsal superficial cells elongate, papillose; in cross section ovate, ventrally bulging-convex, lamina inserted laterally 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 μ m wide, 1:1, walls evenly thickened, essentially homogeneous, occasionally longitudinally elongate along the costa; papillae usually large, massive, multiple, occasionally bifid, centered 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. Dioicous. Perichaetia terminal, leaves little different from stem leaves, weakly sheathing at base. Perigonia lateral on stem, bud-like. Sporophyte not seen.



FIGURES 61-73. *Gymnostomum valerianum* (Bartr.) Zander and *Eucladium verticillatum* (Brid.) B.S.G. — 61-66. *G. valerianum*. — 61-62. Moist leaves, $\times 30$. — 63. Dry leaf, same as 62, $\times 30$. — 64. Leaf margin, $\times 300$. — 65. Upper leaf areolation, $\times 750$. — 66. Costal cross section at mid-leaf, $\times 300$. — 67-73. *E. verticillatum*. — 67-70. Moist leaves, $\times 30$. — 71. Dry leaf, same as 70, $\times 30$. — 72. Upper leaf areolation, $\times 750$. — 73. Costal cross section at mid-leaf, $\times 300$. FIGURES 61-66 from MEXICO: Norris 20436; 67 from MEXICO: Crum 233; 68-71 from MEXICO: White 371; 72-73 from MEXICO: White 370.

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 *Anoec-tangium 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.

Additional specimens examined.—MEXICO. SINALOA: 10 km W of Las Palmitas, Norris et al. 20436 (MICH). GUATEMALA. EL QUICHÉ: Nebaj, Sharp 2399 (FH). SAN MARCOS: Volcán Tajumulco, Steyermark 35696a (FH). PANAMA. CHIRIQUÍ: S of Boquete, Crosby 3964 (DUKE).

6. *Eucladium verticillatum* (Brid.) B.S.G., Bryol. Eur. 1: 9. 1846 (fasc. 33–36 Mon. 3). FIG. 67–73

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

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

Grimmia verticillata (Brid.) Sm., Engl. Bot. 18: 1258. 1804.

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

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

Hymenostylium verticillatum (Brid.) Braithw., Brit. Moss Fl. 1: 242. 1885, nom. inval. (Art. 34, I.C.B.N., 1972).

Tortula verticillata (Brid.) Mitt., Rep. Sci. Res. Voyage Challenger Bot. 1(2): 89. 1885.

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 stereid band, guide cells 4–7 in one layer with occasionally 1–2 guide cells in a second layer ventrally, a usually strong dorsal stereid 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, superficially flat to weakly convex, lumens rounded-quadrate to oval, 8–10 μm wide, 1:1, but occasionally medially 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, medially 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 Sauce, *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

Anoetangium breutelianum B.S.G. ex Besch., Mém. Soc. Natl. Sci. Nat. Cherbourg 16: 160. 1872, nom. nov. for *Zygodon pusillus* C.Muell. and for *Gymnostomum euchloron* Schwaegr., nom. illeg. (Art. 57, I.C.B.N., 1972).

What may be the holotype (MEXICO: Veracruz, Orizaba, anon., s.n.—PC) has both "*Anoetangium 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.

Gyroweisia barbulatea (C.Muell.) Broth., Nat. Pfl. 1(3): 389. 1902.

Basionym: *Weissia barbulatea* C.Muell., Linnaea 38: 634. 1874.

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 obtusam integerrimam opacam carnosulam paulisper flexuosam attenuata . . ." reminds one of *Luisierella barbula* (Schwaegr.) Steere.

SPECIES EXCLUDED

Several species with combinations in *Anoetangium* 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.

Basionym: *Gyroweisia obtusifolia* Broth., Nat. Pfl. 1(3): 389. 1902. Type: Mexico, Veracruz, *Strebel* s.n. (BM—holotype).

Trichostomum obtusifolium Hamp., Bot. Zeit. 28: 49. 1870, non P. Beauv., 1805, nom. illeg. (Art. 64, I.C.B.N., 1972).

Gyroweisia papillosa Thér., Smithsonian Misc. Coll. 85(4): 6. 1931. Type: Mexico, Michoacán, Morelia, *Arsène* 4927 (PC—lectotype, FH—isotype); Loma Santa Maria, *Arsène* 7887 (PC—syntype).

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 μ m 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. boliviana* 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 luisieri* Sérgio of Portugal is a propaguliferous variant of *Gymnostomum aeruginosum*, q.v.

Additional specimens examined.—MEXICO. HIDALGO: Mineral del Chico, *Orcutt 6684* (FH). PUEBLA: Cerro Guadalupe, *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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