Revision of the Genus *Leptodontium* (Musci) in the New World

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Abstract. Nineteen species of *Leptodontium* are recognized for the New World. The genus is divided into four sections, including two new species. Critical characters of taxonomic importance, such as stem and costal anatomy, and laminal papillae morphology, are described in detail. The species are mainly found in mountainous areas, on various substrates. Several species are disjunct from the New World to Africa, while two species are essentially pan-tropical in distribution.

*Leptodontium* (Pottiaceae) is a genus of mosses with wide distribution in the tropics and subtropics. Most of the species have been described from South America. At the beginning of the present study, there were 92 validly published species or valid combinations in the genus reported from the New World. *Leptodontium* in its American range was selected for revision on account of the need for careful evaluation of the numerous poorly defined species described for the area. Except as treated in certain regional floras, the genus has not previously been revised.

Heretofore, taxonomic treatments of species of *Leptodontium* have emphasized rather variable gross morphological characters, such as color and habit of the plants, and the size and shape of the leaves, resulting in problems with identification. Microscopic features of the stem, leaf areolation, papillae, and costal structure, which I consider critical to analysis of genetic relationships in the genus, have been seldom used or ignored.

**Historical Review**

The first species of the genus *Leptodontium* to be described was *L. flexifolium*, published in 1801 by Withering as a species of *Bryum*. Bridel, in 1826, published...
the two species then known under *Trichostomum*. The name *Leptodontium* was first published by Hampe (1847) as a genus to include the species *L. flexifolium* and *L. squarrosum*. However, Hampe's name is invalid as it was not accompanied by either a description or a diagnosis. Carl Müller (1849), in *Synopsis Muscorum Frondosorum*, considered *Leptodontium* a section of the genus *Trichostomum*. *Leptodontium* was first validly published as a generic name by S. O. Lindberg (1864), who proposed *L. squarrosum* as the type. Lorentz (1865) placed *Leptodontium* under *Didymodon* as a section. *Leptodontium* was recognized as a genus by Mitten (1869) in *Musci Austro-Americani*, but Jaeger and Sauerbeck (1870–80) referred the species of *Leptodontium* to *Didymodon*. A large number of new combinations was made in *Leptodontium* by Kindberg (1888–91) and Paris (1894–1900, 1903–06). Carl Müller (1901), in *Genera Muscorum Frondosorum*, retained *Leptodontium* as a section of *Trichostomum*. Brotherus (1902), in *Die natürlichen Pflanzenfamilien*, recognized the genus *Leptodontium*. A new subfamily, the *Leptodontioideae*, was proposed by Fleischer (1904–23) to include the genus, an arrangement followed by Chen (1941) in a treatment of Asian *Pottiaceae*. Brotherus (1924–25), in the second edition of *Die natürlichen Pflanzenfamilien*, did not recognize the *Leptodontioideae* as a valid segregate of the *Pottiaceae*, placing *Leptodontium* in the subfamily *Trichostomoideae*. The most recent index treatment of the genus *Leptodontium*, by the *Index Muscorum* (Wijk et al., 1964), recognizes 149 validly described species or valid combinations in *Leptodontium*, as well as numerous *nomina nuda*.

**Morphology**

Morphological structures of taxonomic importance in the genus *Leptodontium* are the cellular organization of the stem, the leaf areolation, papillae, costal structure, the propagula and associated asexual reproductive structures, the annulus, peristome, and spores. Hilpert (1933) found the central strand sometimes absent in species of *Pottiaceae* in which it is normally present. There seems to be no variation in expression of this character in *Leptodontium*, as the central strand is never present. In certain related genera, the central strand is absent (*Streptotrichum*) or apparently always present (*Rhexophyllum* and most species of *Bryoerythrophyllum*).

The stem of *Leptodontium* consists of a cortex of several layers of thick-walled cells surrounding a central cylinder of thin-walled cells (Fig. 80). A single epidermal layer of enlarged thin-walled cells (Fig. 72) is present in many species of *Leptodontium*, as it also is in species of related genera. The cells of this outermost layer are inflated near the stem apex but are collapsed in mature parts. The stem thus has a "fluted" appearance when viewed in cross section. Bastit (1891) asserted that the presence of enlarged thin-walled epidermal stem cells in *Polytrichum juniperinum* is a variable character, its expression dependent on the submergence of the growing stem in water, and cited the presence of the "épiderme aquatique" in such hygrophilic genera as *Sphagnum* and *Fontinalis*. In *P. juniperinum*, however, a single layer of epidermal cells is differentiated, though not inflated, in aerial stems, while in *Leptodontium* such is never the case. The presence or absence of an inflated stem epidermis has been used recently as a major taxonomic character in *Plagiothecium* and related genera (Ireland, 1969; Iwatsuki, 1970).

The leaves of *Leptodontium* are usually recurved to squarrose-recurved, having a sheathing base composed of elongate cells. Genera with similar leaves are *Streptotrichum*, *Rhexophyllum*, and *Bryoerythrophyllum*. The lamina is never bistratose, as
it often is in the genus *Rhophyllum*. The costa in cross section (Fig. 89) is composed of two stereid bands with a median row of guide cells. An epidermal layer of papillose cells similar to those of the lamina is absent in the costa of *Leptodontium* though present in *Rhophyllum* and species of *Bryoerythrophylax*. Short rudimentary leaves (Fig. 19–20) are present in one species of *Leptodontium*, occurring on the stem between the leaves and often seeming to arise in the same mass of rhizoids as do the propagula. These phylloid may be quite contorted and are usually stalked and costate.

The leaf cells of many species of *Leptodontium* bulge outward on both surfaces of the lamina (Fig. 138) and are oval to rounded-hexagonal in cross section, much as in species of *Hyophila* or *Triquetrella*. Other species have laminal cells with flattened surfaces and rounded-rectangular lumens (Fig. 77, 126).

All species of *Leptodontium* have papillose upper laminal cells. In plants with thin cell walls, the papillae may be hollow; in plants of the same species with thickened cell walls, the papillae are solid, more massive, and tend to be crowded or fused. Two
kinds of upper laminal papillae may be distinguished: cup- to c-shaped (lunate) and simple to multifid. Cup- to c-shaped papillae, as seen in the light microscope (Fig. 1, 30, 39) are circular or semicircular ridges on the cell walls, sometimes with one or more prominences on the rim. These grade into simple to bi- to trifid papillae on the basal cells of the leaves. The cup- to c-shaped type of papilla occurs one to several over each lumen. In specimens with thick-walled laminal cells, cup- to c-shaped papillae appear as rather flattened bi- to trifid papillae. Only certain species of *Leptodontium* in sect. *Verecunda* typically have cup- to c-shaped papillae, though these are widely represented in the Pottiaceae in such genera as *Barbula*, *Tortella*, *Pottia*, and *Tortula*.

Simple to multifid papillae may be either rounded (Fig. 2, 89), flattened (Fig. 4, 119), or columnar (Fig. 84). Simple, rounded papillae with only a slight tendency to branch are found in only one of the four sections of the genus (Fig. 2, 77). Rounded, simple to bi- to trifid papillae, very crowded, occurring 2–6 over each lumen (Fig. 3, 39, 97, 103) are found in various sections in species with flattened cell surfaces. Highly flattened, scarcely branching papillae (Fig. 4, 119) are found in two species of sect. *Coronopapillata*. Most papillae in the genus are scattered over the surface of the laminal cell, but simple to bi- to trifid spiculate papillae arranged in a crown-like ring over the center of the cell lumen are characteristic of most species of sect. *Coronopapillata*. The papillae are usually raised on the conical salient of the bulging cell walls (Fig. 6, 7, 138, 144, 149, 155). The apex of the salient may be greatly thickened, forming a columnar base for the crown-like ring of spiculate papillae. This results in a single coroniform structure over each cell lumen (Fig. 163). Very high, columnar, simple to bi- to trifid papillae (Fig. 84) are characteristic of *L. viticulosoides* var. *exasperatum*. These papillae are very similar to those found in *Triquetrella*.

Through the generosity of Dr. H. Robinson of the Smithsonian Institution, I have obtained scanning electron micrographs of the papilla structure in various species of *Leptodontium* (Fig. 11–18) which he has allowed me to publish here. The technique used in making the micrographs is published elsewhere (Robinson, 1971). Certain problems in interpretation due to mounting stresses are evident. Shrinkage of the specimen renders the surface wall of the cell lumen as a shallow pit, rather than the flattened or outwardly bulging surface seen in water or Hoyer’s Solution mounts with the light microscope. The papillae are seen to rise mainly from ridges formed from the protruding perpendicular wall of the lumens. Evidence is missing of the bulging salients seen in light microscopic studies of species of sect. *Coronopapillata*.

The upper laminal papillae of *L. flexifolium* (Fig. 11) are seen to be 2–3 branching between the base and the middle, with anastomoses prevalent between the rami as sinuose crests. These crests seem to be the basis for the observation of “cup- to c-shaped” papillae in light microscope studies. The laminal papillae of *L. viticulosoides* var. *panamense* (Fig. 12–13) and of *L. filicola* (Fig. 16) are much alike in both light and electron examinations. The papillae of *L. pungens* are thick, crowded, for the most part evenly spaced, 2–3 branching near the base and often secondarily branching above to form a massive crest. The papillae of *L. luteum* (Fig. 15) are granular, heterogeneous, but similar to those of *L. pungens* by the often massive apical crest. The papillae of *L. longicaule* (Fig. 17) and of var. *microruncinatum* (Fig. 18) are similar in electron representations. Those of *L. longicaule* are distinctly 2–3 branching above the base, while those of the variety are less delicate, mostly twice branching at the base. The scanning electron micrographs seem to support my interpretations of papilla morphology obtained through light microscopic studies of series of specimens.

The thickness of the upper laminal cell walls of *Leptodontium* is usually variable within each species. In sect. *Leptodontium* leaf cell walls are usually greatly thickened at the corners, giving the lumens an angular appearance (Fig. 78, 85, 91). This character, however, is sometimes indistinct or lacking and may be approached in thick-walled species of other sections. The degree of thickening of the lateral walls of the inner basal cells of the leaves of most species is highly variable. Plants of many species may have inner basal cells with thick, highly porous walls (Fig. 79, 86, 110). Porosity, however, is little apparent in plants of the same species with scarcely thickened walls.

Many species of *Leptodontium* reproduce asexually by propagula of various kinds. The propagula usually have short stalks, but long branching stalks, each branch ending in a propagulum, may be found in robust plants of some species, for instance, in the type of *L. pergemmascens* (= *L. flexifolium*). The propagula are deciduous at the juncture with their stalks. Obovoid propagula borne on the stem are present in many species. Two of these species, *L. filicola* and *L. planifolium*, are distinctive in having propagula produced in dense clusters among the upper leaves. Obovoid propagula are borne in a unique terminal gemma cup on the costa of leaves of *L. stellaticuspis* (Fig. 52). Claviform propagula are borne on the awn of the excurrent costa of *L.*
proliferum and on leafless branchlets of L. stoloniferum. Propagula borne on the apices of leaves often fall into the leaf axils and may appear to have originated there. Small, deciduous leaves on branchlets in the axils of leaves of L. viticulosoides var. flagellaceum are probably involved in asexual reproduction. Obovoid or claviform propagula are apparently never produced in two sections of the genus.

The annulus is irregularly deciduous, 2–3 rows of cells in height in sect. Verecunda (Fig. 8) and 4–6 rows of cells in height in the other sections (Fig. 9–10). The peristome of Leptodontium varies in color from light yellow (most species of sect. Verecunda) to deep red (species of sect. Coronopapillata). The teeth are separate or fused at the insertion (Fig. 8–10). A preperistome (Vorperistome) has been noted in Leptodontium by Brotherus (1924–25). It consists of short blunt teeth of usually one to four plates (Fig. 90, 171), often of a darker color than that of the peristome teeth. The preperistome is inserted with the peristome teeth near the base of the annulus. The divisions of the preperistome appear irregularly around the mouth of the capsule and adhere to the outer surface of the basal articulations of the teeth. The preperistome is only occasionally present in the species of Leptodontium in which it has been noted. It is best developed in certain specimens of L. viticulosoides (Fig. 90) from the Indian Himalayas. Other species in which a preperistome is sometimes present are L. flexifolium, L. stellatifolium, L. pungens, L. capituligerum (Fig. 171), L. araucarieti, and L. longicaule. Species of Encalypta (Encalyptaceae) and Leucophanes (Leucobryaceae) have similar preperistome development. Cavers (1911) reported that a “properistome” is often present in the Syrrhopodontaceae and Calymperaceae, and is sometimes present in the Seligeriaceae and Grimmiaeae. Philibert (1888) concluded that the Haplolepideous peristome is homologous to the inner row of teeth of Diplolepideous mosses. Developmental studies are needed to determine whether the preperistome in Leptodontium is homologous to a now lost outer peristome, or if it is simply the result of anomalous transverse divisions.

Fleischer (1904–23) noted that the spores of L. subdenticulatum (= L. viticulosoides var. viticulosoides) are heterogeneous. The spores of two varieties of L. viticulosoides do, in fact, fall into two size classes. The larger spores are 23–25μ in diameter, green, and nearly spherical, with the triradiate ridge scarcely distinguishable. The smaller spores are 17–23μ in diameter, yellowish to brownish, and lenticular to tetrahedral in shape, with a distinct triradiate ridge. The large and small spores occur in about equal numbers. A small number of spores of intermediate size is usually present, but these may be referred to one of the two kinds above on the basis of their shape and coloring. The spores, when mounted on a microscope slide, are usually dissociated from the tetrad. Chlorophyll fluoresces in the visible range when illuminated with ultraviolet light (Brody et al., 1965). Fresh spores of var. viticulosoides from African plants (Tanzania, Mt. Meru, Sharp et al. 7871 (DUKE)) were examined microscopically under ultraviolet light. The larger spores fluoresced red; the smaller exhibited no fluorescence and evidently lack chlorophyll, at least when mature. When the spores were cultured on inorganic media, the larger spores germinated, while the smaller failed to do so. Other mosses have heterogeneous spores, perhaps more commonly than now realized. I have seen specimens of the pseudautoicous Holomitrium crispulum Mart. from Cuba (Wright, Musc. Cuben. 41 (BUF)) and Brazil (Glaziou 9244 (BM)) which have this unequal development of the spores. Spores of two size classes have similarly been found in species of Macromitrium (Orthotrichaceae). This has been called an example of “heterospory” in the mosses (Ernst-Swarzenbach,
1939, 1942, 1943, 1944). The term “heterospory” in this case is inappropriate, as the two kinds of spores come from the same sporangium and evidently the same tetrad (Vitt, 1968). This is not strictly comparable to the situation in truly heterosporous plants such as Isoetes, Lycopodium, or Selaginella. The genus Macromitrium contains both monoicous and dioicous species. Some dioicous species are pseudautoicous. Fleischer (1904–23, 1920) suggested a correlation between heterothallism and the presence of large and small spores in the pseudautoicous species. Ernst-Swarzenbach (1939) and Ramsay (1966) surveyed the genus Macromitrium and found that the monoicous species have spores of one size class and the dioicous species have spores of two size classes. The culturing experiments of Ernst-Swarzenbach (1939) indicate that, for certain dioicous species of Macromitrium, the smaller spores form dwarf male plants, while the larger spores form full-sized female plants. In Ramsay’s (1966) cytological investigation of Macromitrium, she maintained that spores of monoicous species contain both an X and a Y sex chromosome, while spores of the dioicous species contain either an X or a Y chromosome, and are thus respectively female or male in potential. There seems to be no parallel in the relationship of “heterospory” and sexual differentiation of the spores of Leptodontium viticulosoides, which is autoicous or seldom dioicous, and in the dioicous species of Macromitrium. The absence of chlorophyll in the smaller spores of L. viticulosoides indicates that these may have simply aborted.

The cytology of the genus Leptodontium has not been studied, but Dr. L. E. Anderson (pers. comm.) found that L. viticulosoides var. viticulosoides (Tanzania, Mt. Meru, Anderson 20997 (DUKE)) has n=13. No evidence of sex chromosomes was seen.

Most microscopic observation of the species of Leptodontium were made from specimens mounted in Hoyer’s Solution (Anderson, 1954). Water mounts are often unsatisfactory for viewing species of Pottiaceae, as the laminal papillae may obscure the outlines of the leaf cells. Hoyer’s Solution is a better medium because the different index of refraction and the lysis of cell contents renders the areolation more distinct. The fine structure of the cell walls, however, seems to degrade in certain older preparations.

**Geographic Distribution and Maps**

Sufficient work has been accomplished in the field of bryogeography to show that bryophytes have geographic distributional patterns similar to those of higher plants (Sharp, 1939; Fulford, 1951; Anderson, 1963). Herzog (1926) reviewed the geographic distributions of the genera of mosses and noted that the disjunctive patterns among austral land masses are similar to those of certain families of seed plants. The long-distance disjunctions of certain austral families and genera of flowering plants (Good, 1964) and of certain genera of mosses (Herzog, 1926) and liverworts (Fulford, 1951, 1963) are such that floras of the southern parts of the world seem unusually closely related. An explanation of the floristic ties among the southern continental masses that has recently received attention by bryogeographers is Wegener’s (1924) theory of continental drift, which postulates that southern continents and islands were contiguous in the Upper Carboniferous and that major separation between South America and Africa did not occur until the Eocene. Evidence from recent studies in paleontology, geomagnetism, and geology seem to support the theory in its essentials (e.g., Jardine & McKenzie, 1972).

Among vascular plants, some austral families with notable continental disjunctions
which may have been formed or accentuated by continental drift are the Gunneraceae, Proteaceae, and Restionaceae (Good, 1964). Croizat (1947) suggested that most angiosperm families are phylogenetically bound to the southern hemisphere. Camp (1947) discussed the possibility of a southern origin for the Angiosperms. He cited the South American–African disjunctions of such genera as Mayaca (Mayacaceae), Vellozia (Velloziaceae), and Visinia and Symphonia (Hypericaceae), among others, as part of austral patterns of plant distribution supporting the notion that there existed, previous to the Tertiary, a southern flora with relatively free exchange of elements among the southern land masses. Fossil evidence of vascular plants for the existence of a widely distributed southern pre-Tertiary flora was reviewed by Chaney (1947).

Herzog (1926, 1932) suggested that evidence for the validity of the theory of continental drift provided by the continental disjunctions of certain mainly austral families of vascular plants is paralleled in the distribution of such moss genera as Pilotrichella, Squarridiurn, Lindigia, Jaegerinopsis, Braunia, and Dimerodontium. In the Hepaticae, certain species of the recently monographed genera Isotachis (Hatcher, 1960–61), Lepicolea (Scott, 1960), and Clasmatocolea (Grolle, 1956), among others, are common to South America and southern Africa. Fulford (1951, 1963) has summarized what is known of the continental disjunctions of genera and species of austral liverworts. She suggested that dispersal between South America and Africa may have taken place previous to the Cretaceous as there is no evidence of land connections since that time.

Studies of Asian and North American bryophytes by Iwatsuki (1958) and Sharp (1966) have shown that many “vicarious” species pairs actually represent disjunctions between populations of the same species. Anderson (1963) suggested that analysis of the degree of variation between continentally disjunct populations of species of mosses would probably show, in the majority of cases, little evidence of evolutionary change. The consensus of nearly all who work with the bryophytes is that the group is ancient and, for the most part, is evolving rather slowly.

Few recent revisions have been made of genera of South American mosses with representation in the Old World. Crosby’s (1969) revision of Pilotrichum, Reese’s (1961) revision of the genus Calymperes in the Americas, and Zanten’s (1959) revision of the family Trachypodaceae treat genera whose South American distribution is mainly limited to the northernmost regions. One species of the family Trachypodaceae is disjunct between South America and Africa. Malta’s (1926) monograph of the large genus Zygodon (Orthotrichaceae) indicates that there is little relationship between South American and African species of the genus. Only two species are common to the two continents and these are widespread in other parts of the world. Malta, however, may have recognized many “vicarious” species pairs. Matteri’s (1968) revision of Philonotis in southern Argentina recognizes 10 species of which one has a wide southern distribution, occurring in southern South America, southern Africa, and the Australia-New Zealand region. A review of the distribution of species of South American Hookeriaceae by Welch (1969) cites one wide-ranging species in the Americas, Oceania, and Asia, and 8 species in both southern South America and the Australia-New Zealand region, with one species of the last found also in Oceania, Madagascar, Mauritius and Réunion. These east-west distributions, according to Welch, may be due to continental drift.

The genus Leptodontium is widely distributed in the New World, having been collected as far north as Virginia in the United States and as far south as Patagonia.
Bartram (1949) suggested that Guatemala is the center of distribution of the genus, but the genus is actually most broadly represented in the Andes of Colombia, Ecuador, Peru, and Bolivia. Two widely spread American species occur throughout the tropics and subtropics of the Old World. Several American species are also found on high mountain ranges in central and southern Africa or are part of an austral element with disjunctions to southern Africa and certain southern islands. Several species have very narrow ranges or are endemic to areas of South America. A few species in the genus are found only outside of the New World. In general, the geographic distributions of the species are not related in such a way as to support taxonomic speculations on interspecific relationships, nor do the sections of the genus have distinctive distributions. The implication is that the genus is old, and most patterns of dispersal were established long ago. The geographic distributions of most species of the genus may be those of relict species whose ranges were once much wider. The genus *Leptodontium*
consists of rather disparate taxonomic elements. Few of the species have immediate close relatives. It is possible that many species or groups of intermediate relationships have died out.

*Leptodontium flexifolium* and *L. viticulosoides* are found throughout the New and Old World tropics and subtropics (Fig. 21–22). Populations of both species are present in temperate regions, including disjunctions from Mexico northwards to the Southern Appalachian Mountains. There, the two species are restricted to the Spruce-Fir zone, mostly above 5,500 ft. in elevation. The Southern Appalachian region is a center of disjunction for many tropically related bryophytes (Billings & Anderson, 1966). *Leptodontium viticulosoides* has southerly extensions from its tropical range into Argentina and South Africa, while *L. flexifolium* is often collected in northern Europe.

Several species of *Leptodontium* are less widely distributed but have long-distance range disjunctions. *Leptodontium capituligerum*, *L. longicaule*, *L. luteum*, *L. pungens* (Fig. 23), and *L. wallisii* are disjunct from the New World to central and southern Africa. *Leptodontium longicaule* (Fig. 24) has an austral distribution, including the Andes from Ecuador to Chile, South Africa, and the islands of Juan Fernandez, Tristan da Cunha, Gough, Réunion, and Crozet. *Leptodontium interruptum* (Mitt. ex Hook.) Broth., not known from the Americas, is another austral taxon with disjunctive distribution, having been reported from Australia, New Zealand, and Amsterdam Island (Sainsbury, 1955). Such austral distributions are evidence of the affinities of the moss floras of regions associated with the hypothetical “Gondwanaland.”

Long-distance transmission of viable spores of bryophytes by birds or wind seems commonly negligible, as the spores are released close to the soil, in still air, and are relatively thin-walled and easily desiccated. On the other hand, spores of some mosses have survived the dry environment of herbarium packets for as long as 16 years (Meyer, 1941). Schuster (1969) recently pointed out that the islands along the mid-Atlantic ridge, such as Tristan da Cunha, are only one million to 20 million years old and were probably populated by established species on the continents. It is probable that many austral distributions and disjunctions, including those of species of *Leptodontium*, are due to the dissemination of spores by various carriers.

Herzog (1926) reviewed the distribution of the genera of mosses on a world-wide basis. He pointed out that the South American-African disjunctions of mosses were on a basically different taxonomic level than were those observed for higher plants. The moss genera seemed disjunct at about the same frequency as were the families of the higher plants. My research in *Leptodontium* indicates that the relationship between representatives of the genus in Africa and South America is actually rather close at the specific level. Only two of the ten African species of *Leptodontium* are not also found in South America. There appears to be little evidence of evolutionary drift between continentally disjunctive populations of the same species. If the disjunctions are not recent, this observation would support the notion that evolution is slower in the bryophytes than that supposed for the higher plants. In the absence of fossil evidence, however, the point remains speculative.

Species of *Leptodontium* with Central American and Andean distribution are *L. brachyphyllum*, *L. filicola*, and *L. syntrichioides*. These species probably invaded Central America following its emergence from the sea at the end of the Pliocene. Bartram (1949), commenting on the representation of both North and South American species in the moss flora of Guatemala, suggested that the mountain chains of Central America provide a pathway for the exchange of floral elements of both hemispheres.
Several species of *Leptodontium* have narrow ranges or are known from only one or two collections. *Leptodontium stellatifolium* has been collected only in the Serra de Itatiaia of the southern Brazilian Highlands. Of the Andean species, *L. stoloniferum* is known only from Colombia, *L. stellaticuspis* from Ecuador, *L. apiculatum* and *L. subintegri folium* from Peru, *L. planifolium* and *L. proliferum* from Colombia and Bolivia, and *L. erythroneuron* from Colombia, Ecuador, and Peru. Except in the instance of *L. planifolium*, each of these species has no close relatives and is probably a senescent, rather than recent, species. The Andes Mountains are believed to have risen at the end of the Cretaceous, and the varied topography and rather stable climatic zonation seem ideal for the continued existence of relict species.

Five species of the genus *Leptodontium* are known from the southern Brazilian region. These are *L. araucarieti*, *L. filicola*, *L. viticulosoides*, and *L. stellatifolium*. Only the last species is endemic. Herzog (1926) listed six endemic genera of mosses for the area. The widely distributed hepatic genus *Isotachis*, monographed by Hatcher (1960–61), has a number of species disjunct between southern Brazil and the Andes, and one species disjunct between southern Brazil and the Caribbean region. Hatcher suggested that floristic exchange occurred between southern Brazil and the Bolivian Andes at some time in the past. The southern Brazilian region is an important floristic center for endemism and disjunction in the higher plants (Good, 1964).

Though not directly the concern of this treatment, an important range extension for *L. gemmascens* (Mitt.) Braithw. should be noted. Previously known only from Great Britain, the species was collected on Marion Island in the southern Indian Ocean by Huntley, and distributed as *L. proliferum* (Huntley 795, 2015, 2016, 2047 (NY)). A number of mosses are known to have bipolar distributions, among them *Sphagnum magellanicum* Brid., *Distichium capillaceum* (Sw.) B.S.G., and *Tortula papillosa* Wils. ex Spruce. Fulford (1951, 1963) listed hepatics with bipolar distribution. It is possible that sect. Verecunda, to which *L. gemmascens* belongs, was once very widely distributed, and the older segregates of the group now consist of disjunct or endemic populations. Colonization of at least some disjunctive stations by long distance dispersal cannot be ruled out, especially in view of the variety of structural modifications for asexual reproduction in sect. Verecunda.

The species of *Leptodontium* have wider distribution and less endemism than previous floristic work has indicated. This genus of mosses is evidently subject to the same forces of dispersal as have determined the distributions of recently revised and monographed genera of austral bryophytes.

**HABITATS**

The species of the genus *Leptodontium* are most often found at middle and high altitudes in mountainous regions of the tropics and subtropics. Herzog's Bolivian collections of the genus were frequently made in "Nebelwälder," the so-called "moosy forests." These are mountainous regions of high annual rainfall with misty forests rich in epiphytic mosses. Species of *Leptodontium* are often collected on tropical volcanos, where some are early colonizers of ash and lava. The genus is also characteristic of paramos, high treeless plateaus in the Andes, with windy, cold, and damp weather most of the year. Eyre (1963) stated that elevations of 6,000–10,000 feet are the regions of maximum precipitation and cloudiness on tropical mountains. Collections of *Leptodontium* are most often made between these altitudes in the tropics. Disjunctive populations of two species grow in the often misty Spruce-Fir forests on certain summits.
of the Southern Appalachian Mountains. Rainfall from 80–100 inches yearly is commonly recorded in many areas of the Southern Appalachians (Billings & Anderson, 1966). In Africa, species of the genus have been collected on isolated mountains, or “Inselberge,” in Central Africa—Cameroon Mountain in the west, and Kilimanjaro, Elgon, Ruwenzori, Kenya, and others in the east. These mountains have vegetational zones and climates similar to those of New World mountains, where many of the same species of *Leptodontium* may be found at similar altitudes.

The habitats occupied by species of *Leptodontium* are various. Four of the 19 American species evidently grow on soil, rock, or trees. Ten species seem restricted to soil or rock, or both, and only one has been found solely in trees. One species has been collected solely from thatch, while another grows on both thatch and soil, and a third has been found on soil, rock, and thatch. The habitats of two species have not been recorded. Species of sect. *Crassicostata* have been collected only from soil and rock. Species which grow on thatch are only found in sect. *Verecunda*.

Little information is available on bryophytes associated in the natural habitat with *Leptodontium*. In the Southern Appalachians, *L. viticulosoides* var. *panamense* is found on trees in association with the hepatic *Herberta adunca* and the mosses *Paraleucobryum longifolium*, *Zygodon viridissimus*, *Uloca crispa*, *U. ludwigii*, *Neckera pinnata*, *Plagiothecium laetum*, *Brotherella recurvans*, and *Hypnum pallescens*. Herzog (1926) reported that species of *Leptodontium* are part of a *Macromitrium-Schlotheimia* Association in forests of the Bolivian cordilleras, and that *L. luteum* and *Williamsiella tricolor* (= *L. capituligerum*) are members of the *Bryum caulifolium-Ctenidium malacades* Association, one of the two moss associations of the Bolivian subalpine shrub zone.

**Generic Relationships**

Fleischer (1904–23) erected the subfamily Leptodontioideae to contain the genus *Leptodontium*. The subfamily has been recognized by Hilpert (1933) and Chen (1941) in major treatments of Pottiaceae. Various genera with leaf morphology similar to *Leptodontium*—leaves mostly lanceolate, recurved above a sheathing base filled with elongate cells—were referred to the subfamily by Herzog (1926). These genera are *Leptodontiopsis* Broth. in Mildbr., *Rhexophyllum* Herz., *Streptotrichum* Herz., *Triquetrella* C. Müll., and *Williamsiella* Britt. *Calytopogon* (Mitt.) Broth. was added to the subfamily by Chen (1941). Few of these genera seem to be closely related to the genus *Leptodontium*. *Leptodontiopsis*, according to Hilpert (1933), belongs in the Orthotrichaceae. Specimens I have seen of species belonging to this genus do have Orthotrichaceous habit and areolation, together with a rather undifferentiated costal structure, unlike that of *Leptodontium*. *Rhexophyllum* differs markedly from *Leptodontium* in the absence of a peristome, the irregularly bistratose lamina, and in the differentiated epidermal cells of the costa. *Streptotrichum* is probably very near *Leptodontium* in phylogenetic relationship as its gametophyte is very similar to that of *L. araucarieti*. The monotypic *Streptotrichum* differs, however, by the very long, spiculose peristome teeth arising from a short basal membrane. The peristome and laminal papillae of *Triquetrella* are similar to those of *Leptodontium*, but the genus differs by the small, ovate, acute leaves without differentiated basal cells. I consider the monotypic *Williamsiella* an expression of *L. capituligerum*. *Erythrophyllopsis* Broth. in Herz. is similar to *Leptodontium* in leaf shape, but is distinguished by the bistratose lamina, the differentiated ventral (adaxial) epidermis of the costa, and lacks
high-sheathing perichaetial leaves. Until detailed studies are made at the generic level, there seems little point in the recognition of this group of species as a subfamily apart from the Trichostomoideae.

Bryoerythrophyllum Chen, when fertile, is distinguished from Leptodontium by the undifferentiated perichaetial leaves. Sterile collections may be confused because of the similar leaf shapes. But, unlike Leptodontium, the stem of most species of Bryoerythrophyllum has a central strand of smaller cells, and many species possess a differentiated ventral epidermis of enlarged chlorophyllose cells on the costa. The only American species of Bryoerythrophyllum without a central strand may be distinguished by the ventral epidermal layer on the costa.

Gametophytic plants of Morinia ehrenbergiana (C. Müll.) Thér. are quite like those of certain species of Bryoerythrophyllum, but differ by the bistratose margin of the lamina.

For the convenience of students of the tropical bryoflora, I give below a key to American genera of Trichostomoideae similar in morphology to sections of Leptodontium with lanceolate leaves. The grouping of these genera here does not imply any close phylogenetic relationship, but may be of aid in identifying sterile collections.

**KEY TO NEW WORLD GENERA SIMILAR TO LEPTODONTIUM**

1. Lamina irregularly or completely bistratose
   2
2. Lamina entirely unistratose
   4
3. Lamina irregularly bistratose; peristome absent
   3
4. Perichaetial leaves not differentiated; stem with central strand, or costa with epidermis of cells similar to those of the lamina, or, more usually, both
   4
5. Perichaetial leaves differentiated, high-sheathing; stem without central strand, costa without a differentiated epidermal layer

**Phyletic Keys to Sections and Species of Leptodontium in the New World**

1. Small or filiform plants, stems usually 1–3 cm long; leaves ligulate to oblong-lanceolate, usually 1–3.5 mm long (Fig. 25–28, 44, 50, 57, 68); annulus 2–3 cell rows in height (Fig. 8) ........................................................................................................ sect. VERECUNDA (A)
2. Stems without epidermis of enlarged thin-walled, usually collapsed cells (not fluted in cross section, Fig. 80); laminal cells usually with angled lumens and irregularly thickened walls (Fig. 78); laminal papillae usually low, simple to 1–2-branching, but sometimes high, columnar (Fig. 84) ............................................................... sect. LEPTODONTIUM (One species in New World, 9. L. viticulosoides.)
3. Costa thick, in cross section semicircular, the ventral stereid band usually of more than 1 layer of cells (Fig. 97, 103, 108, 113); laminal papillae rounded, simple or branching, crowded (Fig. 3, 14, 97, 104, 108); propagula apparently never produced ................................................................................ sect. CRASSICOSTATA (B)
3. Costa not thickened, reniform in cross section, the ventral stereid band usually of one layer of cells (Fig. 119, 126, 138, 149, 162); laminal papillae usually spiculate, often in a crown-like ring over the center of each lumen, not crowded (Fig. 144); propagula often present on the stem

(A) SECT. VERECUNDA

1. Stem fluted in cross section (Fig. 72) .......................................................... 2
1. Stem not fluted in cross section (Fig. 80) .......................................................... 5
2. Upper laminal cells bulging, papillae grouped over the center of each lumen (Fig. 175); propagula abundant on the stem above ......................................................... 3
2. Upper laminal cells not or seldom bulging, papillae scattered over each lumen (Fig. 30, 39, 53, 70) .......................................................... 4

3. Leaves broadly acute (Fig. 57, 59); costa ceasing 6–15 cells below the apex, usually reniform in cross section (Fig. 58) .......................................................... 7. L. PLANIFOLIUM
3. Leaves narrowly acute (Fig. 172, 174); costa ending 2–3 cells below the apex, usually elliptical in cross section (Fig. 175) .......................................................... 8. L. FILICOLA

4. Plants arboreal; leaves distant, ovate-lanceolate, inner basal cells scarcely differentiated; propagula absent ...................................................................... 4. L. APICULATUM
4. Plants growing on soil or debris; leaves not distant, oblong, broadly acute, inner basal cells differentiated, hyaline, sharply demarcated; propagula (Fig. 67) borne on short leafless branchlets .......................................................... 5. L. STOLONIFERUM

5. Leaves bearing propagula on the excurrent costa; upper laminal papillae cup- to c-shaped (Fig. 1) .......................................................... 6
5. Leaves with subpercurrent costa, upper laminal papillae cup- to c-shaped or flattened, multifid; propagula borne on the stem .......................................................... 7

6. Leaves monomorphic; with obovoid propagula borne in an apical "gemma cup" (Fig. 52) .......................................................... 3. L. STELLATICUSPIS
6. Leaves dimorphic, with mostly claviform propagula borne on the awn of the excurrent costa of the upper leaves (Fig. 43–45) .......................................................... 2. L. PROLIFERUM

7. Leaves minutely crenulate (Fig. 40), costa and inner basal cells orange; peristome 400–450μ long .......................................................... 6. L. STELLATIFOLIUM
7. Leaves denticulate to dentate (Fig. 25–29, 31, 34–35), costa and basal cells uncolored or yellowish; peristome 200–240μ long .......................................................... 1. L. FLEXIFOLIUM

(B) SECT. CRASSICOSTATA

1. Leaves minutely crenulate, without teeth or sometimes denticulate near the apex (Fig. 111–112) .......................................................... 13. L. SUBINTEGRIFIGOLIUM
1. Leaves dentate above .......................................................... 2
2. Leaves weakly dentate above (Fig. 109), with straight, narrowly obtuse apex (Fig. 106–107), costa red throughout .......................................................... 12. L. ERYTHRONEURON
2. Leaves strongly dentate above, apex sharp, recurved, costa seldom red throughout .......................................................... 3

3. Leaf base usually sheathing ½ the leaf length (Fig. 100–102), submarginal cells of the sheathing base differentiated, wider than other laminal cells .......................................................... 11. L. WALLISII
3. Leaf base usually sheathing ¾–½ the leaf length (Fig. 93–94), submarginal cells of sheathing base similar to the upper leaf cells .......................................................... 10. L. PUNCTENS

(C) SECT. CORONOPAPILLATA

1. Leaves with hyaline fenestrations formed by sharply demarcated (Fig. 170) inner basal cells, sometimes iridescent .......................................................... 19. L. CAPITULIGERUM
1. Leaves without sharply demarcated hyaline fenestrations .......................................................... 2
2. Leaves short, 2.5–3.5 mm long, erect-appressed when dry, ovate-lanceolate with a low sheathing base (Fig. 130–131) .......................................................... 18. L. BRACHYPHYLLUM
2. Leaves longer, usually 3–5 mm, mostly spreading, twisted when dry, ovate-lanceolate to long-lanceolate, with a high oval sheathing base (Fig. 136, 143, 148) .......................................................... 3

3. Leaves dentate to the base or nearly so, often erose on the lower margins (Fig. 116–117, 121), upper laminal papillae usually flattened, seldom spiculate, never coroniform (Fig. 4, 15, 119) .......................................................... 14. L. LUTEUM
3. Leaves dentate only in the upper half, upper laminal papillae usually spiculate, sometimes coroniform ........................................ 4 4. Upper laminal cells 9–11 μ in diameter, papillae usually appearing scattered over each cell lumen (Fig. 126) 15. L. ARAUCARIETI 4. Upper laminal cells 11–17 μ in diameter, papillae usually coroniform, grouped in a ring over each cell lumen, on salients of the bulging cell walls (Fig. 114, 149) .... 5 5. Stems fluted in cross section (Fig. 72) ........................................ 16. L. LONGICAULE 5. Stems not fluted in cross section (Fig. 80) ................................. 17. L. SYNTRICHIOIDES

**ARTIFICIAL KEY TO THE NEW WORLD SPECIES AND VARIETIES OF LEPTODONTIUM**

1. Stem fluted in cross section, i.e., with an epidermis of thin-walled cells, usually collapsed (Fig. 72) ........................................ 2 1. Stem not fluted in cross section, lacking a differentiated epidermis of thin-walled cells (Fig. 80) ........................................ 15 2. Leaf margins without teeth or occasionally denticate near the apex (Fig. 111–112), minutely crenulate by projecting cell walls and papillae (Fig. 114); Andes of Peru ............................ 13. L. SUBINTEGRIFOLIUM 2. Leaf margins denticate in upper ¼–½, seldom crenulate between the teeth .......... 3 3. Leaves short, 1.75–2.00 mm long, apiculate by a long cell (Fig. 68–69), basal cells scarcely differentiated; Andes of Peru .............................. 4. L. APICULATUM 3. Leaves longer than 2 mm, not apiculate by a long cell, basal cells well differentiated ... 4 4. Inner basal cells forming sharply demarcated hyaline fenestrations (Fig. 63, 160, 170) ........................................ 5 4. Inner basal cells not sharply demarcated ........................................ 6 5. Leaves when dry erect, flexuose to contorted, lanceolate to ovate-lanceolate, with an acute apex (Fig. 159–161); upper laminal papillae often coroniform (Fig. 162–163); propagula when present obovoid (Fig. 166), borne on the stem above; Mexico, Central America, Andes, southeastern Brazil, Uruguay, Africa 19. L. CAPITULLIGERUM 5. Leaves when dry recurved at the base, incurved above, oblong to ovate-lanceolate, with a broadly acute apex (Fig. 62–63); upper laminal papillae cup- to c-shaped or simple to bi- or trifid, scattered over each cell lumen (Fig. 1, 64); propagula claviform (Fig. 67), borne on leafless branchlets; Andes of Colombia .............. 5. L. STOLONIFERUM 6. Leaves denticate to near the insertion (Fig. 116–117, 121); Andes, Africa ........................................ 14. L. LUTEUM 6. Leaves dentate only in the upper half ........................................ 7 7. Costal cross section near upper part of sheathing leaf base semicircular, with 2–3 ventral layers of stereid cells (Fig. 97, 103, 108, 113) ........................................ 8 7. Costal cross section near upper part of sheathing leaf base reniform or elliptical, with 1–2 ventral layers of stereid cells (Fig. 138, 169, 175) ................... 10 8. Leaves strongly denticate above (Fig. 95, 102), with a sharp, recurved apex (Fig. 94, 96, 101); costa seldom red throughout ........................................ 9 8. Leaves weakly denticate above (Fig. 109), apex narrowly obtuse, not recurved (Fig. 106–107); costa red throughout; Andes ........................................ 12. L. ERYTHRONEURON 9. Leaf base usually sheathing ½ the leaf length (Fig. 100–102); submarginal cells of sheathing base differentiated, in several rows, short-rectangular, 11–13 × 25–35 μ, wider than either the upper laminal cells or the inner basal cells; Central America, Andes, Africa ........................................ 11. L. WALLISII 9. Leaf base usually sheathing ½–¾ the leaf length (Fig. 93–94); submarginal cells of sheathing base similar to the upper leaf cells, not wider than the inner basal cells; Mexico, Central America, Andes, Juan Fernandez, southeastern Brazil, Africa ............... 10. L. PUNCENS 10. Upper leaves incurved to falcate-incurved when dry; propagula usually numerous and obvious, forming clusters on the stem between the upper leaves .............. 11 10. Upper leaves erect to spreading-recurved when dry; propagula, when present, scattered over the stem, not numerous or in obvious clusters ..................... 12 11. Leaves with broadly acute apex (Fig. 59); costa subpercurrent by 6–15 cells, reniform in cross section (Fig. 58); Andes of Colombia and Bolivia ......... 7. L. PLANIFOLIUM 11. Leaves with a narrowly acute apex (Fig. 174); costa subpercurrent by 2–3 cells, usually
elliptical in cross section (Fig. 175); Central America, Andes, southeastern Brazil .......

12. Upper laminal cells 9–11 µ in diameter, papillae in surface view usually appearing scattered over each cell lumen (Fig. 5), cells not or little bulging ——— 8. L. filicola

12. Upper laminal cells 11–17 µ in diameter, papillae in surface view usually centrally grouped in a crown-like ring over each lumen and raised by the salient of the bulging cell wall (Fig. 6–7), or sometimes thickened and fused into a lens-shaped irregular cap (Fig. 7, 149) ————————————————————————————————————————————————————————————————————————— 14

13. Leaves spreading-recurved when dry, lanceolate to ovate-lanceolate with a high sheathing base (Fig. 124–125); Andes, southeastern Brazil ——— 15. L. Araucarietii

13. Leaves usually erect-appressed when dry, ovate-lanceolate with a short sheathing base (Fig. 130–131); Mexico, Central America, Andes ————————————————————————————————————————————————————————————————————————— 18. L. brachyphyllum

14. Leaves ovate-lanceolate to lanceolate (Fig. 136–137), margins recurved in lower ½–¾, upper laminal papillae distinctly branching, covering little of each lumen (Fig. 6, 138); Andes, Africa, Réunion ————————————————————————————————————————————————————————————————————————— 16a. L. Longicaule var. Longicaule

14. Leaves long-lanceolate (Fig. 147–148), margins recurved in lower ½–¾, upper laminal papillae usually low, indistinctly branching and covering most of each lumen, sometimes fused into a lens-shaped cap (Fig. 7, 149); Andes, Juan Fernandez, Tristan da Cunha, Gough, South Africa, Réunion, Crozet ————————————————————————————————————————————————————————————————————————— 16b. L. Longicaule var. Microtruncinatum

15. Robust plants, in loose mats, stems mostly 3–10 cm long; leaves ovate-lanceolate to long-lanceolate, mostly more than 3.25 mm long ————————————————————————————————————————————————————————————————————————— 16

15. Small plants, in a short turf, stems usually less than 3 cm long; leaves ligulate to oblong-lanceolate, mostly less than 3.25 mm long ————————————————————————————————————————————————————————————————————————— 20

16. Laminal cells bulging, papillae occurring singly or in a group over the center of each lumen ————————————————————————————————————————————————————————————————————————— 17

16. Laminal cells not bulging, papillae scattered over the lumens ————————————————————————————————————————————————————————————————————————— 18

17. Laminal cell walls greatly thickened at the angles, papillae high, columnar, simple to bi- or trifid (Fig. 84); Mexico, Central America, Andes of Ecuador ————————————————————————————————————————————————————————————————————————— 9c. L. viticulosoides var. Exasperatum

17. Laminal cell walls not greatly thickened at the angles, papillae low, spiculate, in a crown-like ring on the salient of the bulging cell walls (Fig. 6, 144); Central America, Andes ————————————————————————————————————————————————————————————————————————— 17. L. syntrichioides

18. Highly differentiated flagellate branchlets with small deciduous leaves (Fig. 81) present in some leaf axils; Mexico, Costa Rica ————————————————————————————————————————————————————————————————————————— 9d. L. viticulosoides var. Flagellaceum

18. Flagellate branchlets absent, or most or all of plant flagellate ————————————————————————————————————————————————————————————————————————— 19

19. Leaves often elongate to cirrhate (Fig. 75), the vaginate base mostly low and narrow (Fig. 73–76); dioicoous, seta usually 8–14 mm long, spores homogeneous; Southern Appalachians, West Indies, Mexico, Central America, Andes, southeastern Brazil ————————————————————————————————————————————————————————————————————————— 9b. L. viticulosoides var. Panamense

19. Leaves seldom cirrhate, the vaginate base mostly high and broad (Fig. 87–88); autoicoous (seldom dioicoous), seta usually 16–22 mm long, spores of two size classes and shapes; Mexico, Central America, Andes, Madagascar, Réunion, Himalayas, Formosa, southeastern Asia ————————————————————————————————————————————————————————————————————————— 9a. L. viticulosoides var. viticulosoides

20. Costa percurrent to excurrent; propagula usually present, borne on the leaf ————————————————————————————————————————————————————————————————————————— 21

20. Costa subpercurrent; propagula, if present, borne on the stem ————————————————————————————————————————————————————————————————————————— 22

21. Costa of upper leaves excurrent as an awn (Fig. 45), bearing a spherical to cylindrical cluster of numerous obovoid to claviform propagula (Fig. 49); Andes of Colombia and Bolivia ————————————————————————————————————————————————————————————————————————— 2. L. proliferum

21. Costa percurrent, ending in a “gemma cup” rimmed with hyaline teeth (Fig. 50–51), the cup bearing on the inner surface about 5 obovoid propagula (Fig. 52); Andes of Ecuador ————————————————————————————————————————————————————————————————————————— 3. L. stellatissimus

22. Leaf margins minutely crenulate by projecting cell walls and papillae (Fig. 40); costa and inner basal cells orange; southeastern Brazil ————————————————————————————————————————————————————————————————————————— 6. L. stellatifolium

22. Leaf margins denticulate to dentate above (Fig. 31), costa and inner basal cells unicolored or sometimes yellow at the insertion; southern Appalachians, Mexico, Central America, Andes, Europe, Africa, Himalayas, China, Formosa, Japan, southeastern Asia, Hawaii ————————————————————————————————————————————————————————————————————————— 1. L. flexifolium
Leptodontium (C. Müll.) Hampe ex Lindb.


Plants robust, in thick mats, or small, in a short turf, yellowish-green to reddish-brown above, yellowish-brown to reddish-brown below; stems 1–20 cm long, often with tomentum, with a central cylinder of thin-walled cells and a cortex of stereid cells, sometimes with a single epidermal layer of inflated thin-walled cells, these usually collapsed when mature giving the stem a fluted appearance in cross section; leaves erect to spreading, twisted to contorted when dry, spreading to squarrose-recurved when wet, lancingulate, oblong, or ovate- to long-lanceolate, carinate above, with a sheathing base, little or not decurrent to long and narrowly decurrent, margins recurved in the lower ¼–¾, dentate in the upper ½–¾ or seldom to the insertion, sometimes differentiated as a border of 1–5 rows of thicker-walled, less papillose cells; costa excurrent, percurrent, or ending 1–6(–15) cells below the leaf apex, in cross section reniform, elliptical or semicircular with 2–4 fully included guide cells, 1–2(–4) ventral and 1–3(–5) dorsal layers of stereid cells; upper laminal cells subquadrate, walls thin, evenly thickened or thickened only at the angles, sometimes bulging, in cross section rounded-rectangular to oval; papillae simple, multifid, columnar, or cup- to c-shaped; inner basal cells usually differentiated, larger than the upper laminal cells, rectangular, walls thin to evenly or laterally thickened, sometimes porose, thinly papillose with simple to multifid papillae. Rudimentary leaves, short, often stalked, sometimes present in the leaf axils.

Simple propagula of several cells, obovoid to claviform, often borne on short stalks on the stem, on the leaf apices, or on short leafless branchlets. Flagellate branchlets with deciduous leaves sometimes present.

Diocious or autoicous; perigonia lateral or terminal, paraphyses uniseriate filaments of several elongate cells, perichaetial leaves high-sheathing. Seta 3–30 mm long, usually twisted clockwise above. Urn cylindrical, mostly straight, usually about 0.5–0.8 × 2.0–3.5 mm, smooth or seldom rugose when dry, erect to horizontal; exothecial cells short-rectangular, with moderately thickened walls; stonata phaneroporous, restricted to the base of the urn; annulus of 2–7 rows of yellowish- or reddish-brown cells, irregularly deciduous. Peristome inserted near the base of the annulus, basal membrane absent or very low, teeth mostly cleft to the base, often variously anastomosing, divisions linear, yellowish-brown to reddish-orange, essentially smooth to deeply striate, rudimentary preperistome often present. Spores homogeneous or of two kinds, papillose. Operculum conic to conic-rostrate. Calyptra smooth, cucullate, 2.5–4.0 mm long.

I. Leptodontium sect. Verecunda Zander, sect. nov.

Fig. 1, 5, 8, 11, 16, 25–63, 68–69, 172–178

Type species: L. flexifolium (Dicks. ex With.) Hampe in Lindb.

Plants tenues, folia lingulata ad oblongo-lanceolata, propagula plerumque praesens, dioicae, perigonia terminalia, annulus e 2 stratis cellularum formatus.
Plants small, usually 1–3 cm long; stem fluted or not in cross section; leaves lingulate to oblong-lanceolate, costa reniform to semicircular in cross section, the ventral stereid band usually of 1 layer of cells, upper laminal cells sometimes bulging, with walls never greatly thickened at the angles, lumens in cross section rounded-rectangular or ovate to rounded-hexagonal, papillae cup- to c-shaped or flattened and mostly bi- or trifid, scattered or grouped over the center of each lumen; propagula often produced; dioicous, perigonia terminal; annulus 2–3 rows of cells in height, peristome teeth short, 140–240μ long, with 6–8 articulations, or long, 400–500μ with 7 articulations; spores 11–19μ in diameter.


Trichostomum flexifolium (Dicks. ex With.) Sm., Fl. Brit. 3: 1246. 1804.  
Didymodon flexifolius (Dicks. ex With.) Hook. f. & Tayl., Musc. Brit. 66, fig. 20. 1818.  
Desmatodon flexifolius (Dicks. ex With.) Hampe, Linnaea 13: 366. 1839.  
Trichostomum flexiscens Hampe, Linnaea 32: 128. 1863. Type: Colombia, Páramo Choachi, Lindig 2127 (BM—holotype; FH, NY, M—isotypes).  
Zygodon filiformis Lor., Moostudien 162. 1864. Type: Ecuador, Napo, Vulcane Imbabura, Wagner, 1859 (BM, FH, M—isotypes).  
Leptodontium flexifolium var. americanum (Grout) Grout, Moss Fl. N. Amer. 1: 171. 1938.

*Bryoerythrophyllum dentatum* (Mitt.) Chen, Hedwigia 80: 253, pl. 50, fig. 3-6. 1941.
*Bryoerythrophyllum pergemmaescens* (Broth.) Chen, Hedwigia 80: 261. 1941.
*Leptodontium filiformis* (Lor.) Steere, The Bryologist 51: 86. 1948.
Plants small, turf-forming, greenish- to yellowish-brown above, brown below, often entirely flagellate; stems 1–3(-5) cm long, not fluted in cross section, leaves erect-appressed, flexuose-twisted when dry, spreading-recurved when wet, lingulate, with a broadly acute, often mucronate apex, 0.3–0.75 x 1–3.5 mm, carinate above, with a scarcely sheathing base, little decurrent, margins recurved in the lower 1/2–1/3, dentate to denticulate in the upper 1/3, sometimes differentiated as 3–5 rows of thick-walled, less papillose cells; costa ending 3–8 cells below apex, dorsally papillose to near base, reinfert to semicircular in cross section, with 2–4 fully included guide cells, 1 ventral and 2–3 dorsal layers of stereid cells; upper laminal cells subquadrate, 11–15μ in diameter, lumens rounded-rectangular in cross section, walls evenly and moderately thickened, papilae low, cup- to c-shaped or flat, bi- to trifid, 4–7 over each lumen; inner basal cells differentiated in the lower part of the sheathing base, short rectangular, mostly 15–17 x 30–45μ, little papillose, walls evenly and moderately thickened.

Propagula obovoid, 45–55 x 70–130μ, with mostly 3 transverse septa, borne on short branching stalks on the stem.

Dioicous, perigonia and perichaetia terminal, perichaetial leaves 2–3(-4) mm long. Seta 10–15 mm long, yellowish-brown, twisted counter-clockwise above, clockwise below. Um cylindrical, 0.5–0.6 x 1.5–2.0 mm, erect, brown to yellowish-brown; exothecial cells short-rectangular, 30–56 x 50–75μ; annulus of 2–3 rows of cells. Divisions of peristome teeth linear, 15–20μ wide at the mouth of the capsule, 200–240μ long, yellowish-brown, lightly striate, with about 8 articulations, preperistome sometimes present, low. Spores 13–17μ in diameter, yellowish-brown, lightly papillose. Operculum conic-rostrate, 0.5–0.7 mm long. Calyptra about 3 mm long.

Habitat: soil, logs, trees, rock, thatched roofs.

Distribution: Southern Appalachians, Mexico, Central America, Andes, Europe, Africa, Himalayas, China, Formosa, Japan, Southeast Asia, Hawaii (Fig. 21). Found at high altitudes in the tropics and subtropics, usually above 2,000 m and as high as 4,600 m elevation. Occurs at lesser altitudes in Europe, and has been collected at less than 300 m in Great Britain.

Bartram (1949) considered L. flexifolium in the Americas a distinct species, based on L. orcuttii. It presumably differed from European collections in the wider leaf border, the thinner-walled exothecial cells of the um, and the more deeply striate peristome teeth. These characters, however, are developed variously throughout the range of L. flexifolium. The type specimens of L. filesens and L. filiformis exemplify a flagellate form with nearly entire, mucronate leaves (Fig. 29). Leptodontium spongiosum (= L. flexifolium), described by Herzog (1926) from Bolivian collections, may represent non-propaguliferous plants of L. proliferum, a distinct species. The leaves (Fig. 27) of specimens identified as L. spongiosum, including Herzog 3181, 3593, and 4396, are similar to the lower sterile leaves of L. proliferum (Fig. 43–44), differing in the smaller size, to 2 mm long, and the costa usually ceasing 4–6 cells below the apex. The ovate leaves of L. spongiosum, however, intergrade in shape with those of specimens of L. flexifolium from other parts of the world, such as Meyer 746 (H) of the Congo, and certain Central American collections. I have found no character by which plants with all leaves resembling the lower sterile leaves of L. proliferum can be identified as non-propaguliferous plants of the same.

Specimens from various parts of the world show a tendency towards a much thickened, often spurred costa, e.g., the type of L. tenerascens of the Congo, the type
of L. warnstorffii of Java, the type of L. brevicaule of Hawaii (Fig. 34–35), and Grubb & Guymer B74 (BM) of Colombia.

The preperistome of L. flexifolium is only occasionally present. It is rudimentary, consisting of one or two small, dark yellow plates adhering to the basal articulations of each of most of the peristome teeth. Leptodontium styriacum (Jur. in Geh.) Limpr., of Central Europe, is close to L. flexifolium in general morphology, but differs in the apiculate leaves and the spindle-shaped propagula.


Mauna Kea, Berggren, 1874 (FH); Pua Akala, deciduous Acacia koa, bark, 6,400 ft., Hoe 11430 (CANNM). Huamula, base of Puu Huluhulu, lava, 6,610 ft., Neal & Hartt 682 (FH).


ZANDER: REVISION OF LEPTODONTIUM

(US); tree, 2,000–2,400 ft., Standley 34953 (FH, NY). Inter-American Highway, 97 km S of Cartago, Bowers 822-D (TENN); Bowers 835 (TENN). SAN JOSÉ: Potreros, between Guayabillos and Cabeza de Vaca, 2,150–2,350 m, Dodge & Thomas 4922 (FH, MICH, NY). Páramo of Chirripó, soil, 3,300–3,400 m, Bowers 849-1 (TENN); Bowers 849-B (TENN); 11,400 ft., Bowers 57-859B (US). Volcán Irazú, 3,300 m, Valerio 293 (DUKE, FH, US); S slope, upland pastures, 3,000 m, Holm & Itis 1177 (FH); Holm & Itis 1183 (TENN).

VENEZUELA. MÉRIDA: Laguna Mucubaji, above Los Apartaderos, below bluff, 3,625–3,655 m, Steyermark 57504 (FH). MIRANDA: Pico de Naiguata, above Los Chorros, 2,200–2,765 m, Steyermark 62955 (FH).

COLOMBIA. Guadalupe, bog, 2,900 m, Lindig, 1863 (NY, S-PA). BOYACA: 5 km E of Farm Ritacuba, edge of peat, 4,300 m, Grubb & Guymer B74 (BM). Valle de las Playas, on and between boulders, Grubb & Guymer 170 (BM, FH); boulders, 4,100 m, Grubb & Guymer 170a (BM, FH). CUNDINAMARCA: Páramo Choauchi, 3,600 m, Lindig 2127 (BM, FH, NY, M, MICH). MAGDALENA: Sierra Nevada de Santa Marta, Hoya del Río Donachui, SE slopes, Cancurúia, roofs of Indian huts, 2,400 m, Cuatrecasas & Castaneda 24787 (US).

ECUADOR. EMBABURA: Vulcane Imbabura, trachyt und trachytischem Tuffe, 9,000–12,000 ft., Wagner, 1859 (BM, FH, M). PICHINCHA: Pichincha, near summit, soil, 14,700 ft., Bell 309 (BM, FH). San Juan, Quito, thatch, 11,500 ft., Bell 729 (BM, FH); 12,000 ft., Bell 317 (BM, FH).

PERU. ANCASH: Yerupajagruppe, Ostrand, 4,500 m, Kinzl 4f (JE).

BOLIVIA. Im oberen Chocayatal, 4,000 m, Herzog 3593 (JE). Choquecota chico, Hochtal, verlandeten Seboden, 4,500 m, Herzog 3181 (M); Herzog 4396 (FH, JE, M, S-PA). Yanakaka-Berge, Hochregion, 4,000 m, Herzog 3744 (FH, JE). LA PAZ: Rio Saujana, Waldgrenze, Felsblocken, 4,400 m, Herzog 3229 (H, JE, M, S-PA).


AUSTRIA. Styria, collector's name unreadable, s.n. (NY).

CAMEROON. Kamerunberg, Grassland, 2,800 m, Hintz 56a (H). Cameroons Mt., Mann, s.n. (NY).

CONGO. Ninango, Lava des Kraterkegels, 3,300 m, Mildbraed 2009 (H). KIVU: Vulkan Karisimbi, 3,100 m, Prope Yezured 746 (H); Rand des Südrakters auf moorigem Boden, 3,400 m, Mildbraed 2063 (H); N slope, soil, 3,760 m, Derscheid 2514 (FH, US).

KENYA. Mons ad limitis vegetationis, Kolb, 1898 (H). SIKKIM. Himalaya, Hooker 267 (NY); Nangkli, Hooker 114 (NY).


FORMOSA. TAIWAN: Mt. Niitaka, near summit, Noguchi 6834 (US).

JAPAN. HONSHU: Kikko, Kamiji 107, 130 (FH). SUMATOMA. Mt. Singgalang, near Bukittinggi, Diplucosia-shrublet, 2,700 m, Meijer 6183 (CANM).

JAVA. Ardiendo, bei Lalidjawa, an Tjemarra, 2,700 m, Fleischer s.n. (FH); am Waliran, 2,800 m, Fleischer s.n. (FH). Ardiembourgberge, am Waliran, 2,800 m, Fleischer, 1901 (FH).
2. Leptodontium proliferum Herz., Biblioth. Bot. 87: 33, fig. 8. 1916. Fig. 43-49

Type: Bolivia, Cochabamba, Tunariseen, Herzog 3429 (JE—lectotype; BM, CANM, H, NY, M, s-PA—isolectotypes).

Plants small, turf-forming, greenish- to yellowish-brown; stems 1–2 cm long, not fluted in cross section, without tomentum; leaves erect-appressed when dry, spreading-recurred when wet, dimorphic but intergrading, upper leaves oblong-lanceolate, mostly entire, costa excurrent in a short awn, lower leaves oblong to ovate-lanceolate, dentilcate in the upper \( \frac{1}{4} - \frac{1}{2} \), costa percurrent to subpercurrent, \( 0.8-1.0 \times 2.0-3.5 \) mm, carinate above, with a scarcely sheathing base, not decurrent, margins recurved in the lower \( \frac{1}{2} \), often differentiated as 2–4 rows of thick-walled, less papillose cells; costa reniform to semicircular in cross section, mostly thin-walled, papillae low, cup- to c-shaped 4–6 over each lumen; inner basal cells of lower leaves and most laminal cells of upper leaves rectangular, mostly 15–20 \( \times \) 25–35 \( \mu \), thin-walled.

Propagula obovoid to claviform, 30–40 \( \times \) 85–110 \( \mu \), with mostly 3 transverse septa, borne in spherical to cylindrical clusters on sterigmata-like projections on the excurrent costa of the youngest of the upper leaves.

Dioicus, perigonia and perichaetia terminal, perichaetial leaves to 4 mm long.

Habitat: decaying organic material.

Distribution: Andes of Colombia and Bolivia. Known only from three collections, at 4,400 and 4,500 m elevation.

Certain sterile collections from Bolivia, which are here referred to \( L. \) flexifolium, have monomorphic, nearly ovate leaves (Fig. 27) similar to the lower leaves of \( L. \) proliferum (Fig. 43-44). These specimens, which include the type of \( L. \) spongiosum (= \( L. \) flexifolium), and Herzog 3181 (JE, M) and 3593 (JE), may be non-propaguliferous forms of \( L. \) proliferum. Collections of \( L. \) flexifolium from various regions, such as Meyer 746 (H) from the Congo, and certain Central American collections, seem to intergrade with the non-propaguliferous Bolivian collections.

\( L. \) proliferum is similar to \( L. \) flexifolium in the leaves which bear propagula on the excurrent costa, but here is considered a distinct species as the leaves are not dimorphic—all have an excurrent costa—and the propagula are obovoid, never claviform. \( L. \) proliferum has been considered endemic to Great Britain, but a robust form was recently collected on Marion Island, in the southwestern Indian Ocean (Huntley 795 (BM, NY); 2015 (BM, NY, US); 2016 (NY, US); 2047 (NY)), and distributed as \( L. \) proliferum.

COLOMBIA. CALDAS-TOLIMA: Nevado del Ruiz, páramo, 4,400 m, Barclay & Juajibioy 6334 (CANM).


**Type:** Ecuador, Pichincha, Bell 728 (BM—holotype; FH—isotype).

Plants small, in a low turf, greenish- to yellowish-brown; **stems** 1-2 cm long, *not fluted in cross section*, without tomentum; leaves erect-appressed, flexuose when dry, spreading-recurred when wet, oblong-lanceolate, 0.6-0.8 × 1.3-1.8 mm, carinate above, with a scarcely sheathing base, not decurrent, margins recurved in the lower ½—¾, distantly dentate in the upper ½; **costa percurrent**, dorsally not papillose, **ending in a “gemma cup” rimmed with hyaline teeth**, semicircular to circular in cross section, with 2-4 fully included guide cells, 1 ventral and 2 dorsal layers of stereid cells; upper laminal cells subquadrate, 9-11μ in diameter, lumens rounded-rectangular in cross section, walls slightly and evenly thickened, **propagula cup- to c-shaped**, 2-4 over each lumen; inner basal cells short-rectangular, 11-13 × 15-25μ, not papillose, walls moderately thickened.

**Propagula obovoid, 25-35 × 45-65μ**, with mostly 2 transverse septa, **about 5 in number, borne on the inside surface of each “gemma cup.”**

Apparently dioicous, perichaetia terminal, perigonia and sporophyte not seen.

**Habitat:** thatched roofs, soil.

**Distribution:** Andes of Ecuador. Paramos, reported from 3,500 and 4,400 m elevation, only two collections known.

In the two collections I have seen of this unique species, only one leaf was found with propagula (Fig. 52) that had not yet fallen from the “gemma cup.” Several mosses, such as *Tortula pagorum* (Milde) De Not., produce propagula which are held in cup-like rosettes formed by enclosing leaves, and, in *Tetraphis pellucida* Hedw., this “gemma cup” is elevated above the plant by a leafless stalk formed by the stem. But as far as I know, *L. stellaticuspis* is the only moss with such a propagula-bearing cup formed terminally on the leaf.

**ECUADOR.** San Juan, páramo, thatch of cottage, 11,500 ft., Bell 728 (BM, FH). **PICHINCHA:** Pichincha, páramo, turf, 14,500 ft., Bell 365 (BM, FH).

4. **Leptodontium apiculatum** Zander, sp. nov. 

**Type:** Peru, Lima, heights above Atacongo, Stork, Horton & Vargas 9278 (us—holotype; FH—isotype), distributed as *L. laxifolium* Broth.

Plantae tenues, laxe caespitosae, 1-3 cm altae; caules striati; folia dissita, sicca flexuosa, madida recurvo-patula, oblongo-lanceolata, 1.75-2 mm longa, valde apiculata, carinata, e basi vix vaginata, anguste decurrentia, marginibus superne dentatis, costa subpercurrentis, cellulis superne subquadratis ad anguste-rectangularis, 11-13 × 11-15μ, papillae lunate, cellulæ basis vix differentes. Caetera desunt.

Plants slender, in thin, loose mats, greenish-brown; **stems** 1-3 cm long, *fluted in cross section*, without tomentum; **leaves distant**, erect, flexuose when dry, spreading-recurred when wet, **oblong-lanceolate with a narrowly acute apex apiculate by a long cell**, 0.8-0.5 × 1.75-2.00 mm, carinate above, with a scarcely sheathing base, long and narrowly decurrent, margins plane or reflexed below, dentate in the upper ¾-¼; costa ceasing 4-5 cells below apex, not or scarcely papillose dorsally, semicircular to reniform in cross section, with 2-4 fully included guide cells, 1 ventral and 2 dorsal layers of stereid cells; upper laminal cells subquadrate to short-rectangular, 11-13 × 11-15μ, lumens rounded-quadrate in cross section, walls moderately and evenly thick-
ened, papillae low, bi- to trifid, 4-7 over each lumen; inner basal cells scarcely differentiated, restricted to a few rows near the insertion, rectangular, mostly 13–17 X 30–45 μ, scarcely papillose.

Sterile.

Habitat: trees.

Distribution: Andes of Peru. Known only from two collections, made at unknown elevations in mountainous regions.

This species is distinctive in the section for its arboreal habitat and distant, oblong-lanceolate leaves. The plants are filiform and are probably easily overlooked in the field.

PERU. LIMA: Lima, heights above Atacongo, epiphyte, branches of Acnistus, Lucuma, etc., Stork et al. 9278 (FH, US).

LA LIBERTAD: Trujillo, inter Lichenes, Standaerh, 1904 (H).

5. **Leptodontium stoloniferum** Zander, sp. nov. FIG. 62–67

Type: Colombia, Cundinamarca, Páramo Choachi, Lindig 2127 (M—holotype, separated from isotype of *L. filescens*).

Plantae tenues, laxe caespitosae, 1.0–3.0 cm altae; caules striati; folia sicca inferne recurva, superne incurva, madida recurvo-patula, oblonga ad ovato-lanceolata, e basi vaginata, 3.0–3.5 mm longa, marginibus supere denticulatis vel dentatis, costa subpercurrens, cellulis superne subquadratis, 13–15 μ, papillae simplices vel ramosae, cellulis e basi rectangularibus, fenestrae hyalinae formanibus. Propagula clavata, ramulis curtis portata. Caetera desunt.

Plants small to medium-sized, intermixed with other mosses in a mat, greenish-brown to yellowish-brown; stems 1.0–3.0 cm long, fluted in cross section, without tomentum; leaves when dry recurved at the sheathing base, incurred above, when wet spreading recurved, oblong to ovate-lanceolate with a broadly acute apex, 1.0–1.2 x 3.0–3.5 mm, margins recurved in lower half, denticulate to dentate in upper ¼–½; costa ending 2–3 cells below apex, smooth or nearly so dorsally, reniform to semi-circular in cross section, with 4 fully included guide cells, 1 ventral and 2–3 dorsal layers of stereid cells; upper laminal cells subquadrate, 13–15 μ, in diameter, lumens rounded-rectangular in cross section, walls evenly thickened to moderately thickened at the corners, papillae cup- to c-shaped or simple to bi- or trifid, 4–6 over each lumen, inner basal cells rectangular, 15–18 x 65–85 μ, scarcely papillose, thin-walled, forming sharply demarcated hyaline fenestrations.

Propagula claviform, 30–35 x 110–175 μ, with mostly 4–6 transverse septa, borne on leafless branchlets to 2 mm long emerging between the upper leaves.

Evidently dioicous; perichaetia terminal, perigonia and sporophyte not seen.

Habitat: thatched roofs.

Distribution: Andes of Colombia. Known from specimens probably comprising a single collection, 3,600 m elevation.

This species was discovered intermixed with an isotype collection of *L. filescens* (= *L. flexifolium*). It is referred to sect. Verecunda by its small size, the oblong leaves, and the presence of morphological modifications for asexual reproduction, but differs from other members of the section by the sharply demarcated hyaline fenestrations formed by the enlarged, thin-walled inner basal cells, and by the short, leafless, propaguliferous branchlets emerging between the upper leaves.

COLOMBIA. No exact locality given, tectis, 3,600 m, no collector cited, Herb. Hampe, 1881 (BM).

CUNDINAMARCA: Páramo Choachi, tectis, 3,600 m, Lindig 2127 (M—separated from isotype of *L. filescens*).


Plants small, turf-forming, brown above, reddish- to yellowish-brown below; stems 2–3 cm long, not fluted in cross section, without tomentum; leaves erect-incurved, flexuose when dry, spreading-recurved when wet, crowded, lingulate, with an acute to obtuse and mucronate apex, 0.3–0.5 × 1.2–1.5 mm, little carinate above, with a scarcely sheathing base, not decurrent, margins reflexed in the lower ½, minutely crenulate in the upper ½ by projecting cell walls and papillae; costa orange, ending 4–6 cells below apex, dorsally papillose, flattened-elliptical in cross section, with 2–4 fully included guide cells, 1–2 ventral and 1 dorsal layer of stereid cells; upper laminal cells subquadrate, 9–11μ in diameter, lumens rounded-rectangular to rounded-hexagonal, walls moderately and evenly thickened, bulging, papillae flattened, simple to bi- or trifid, 2–8 over each lumen; inner basal cells orange, rectangular, mostly 9–11 × 40–50μ, scarcely papillose, walls evenly thickened.

Propagula large, obovoid, mostly 35–45 × 75–90μ, with 2–4 transverse septa, borne on the stem.

Dioicous, perigonia and perichaetial leaves 2.0–2.5 mm long. Seta 8–10 mm long, yellowish-brown, twisted clockwise above. Urn cylindrical, 0.2–0.4 × 1.25–1.50 mm; exothecial cells short-rectangular, mostly 20–25 × 20–40μ; annulus of 2–4 rows of reddish-brown cells. Divisions of peristome teeth linear, 15–20μ wide at the mouth of the capsule, 400–450μ long, light yellowish-brown, indistinctly striated, with 5–7 articulations, preperistome sometimes present, short. Spores 17–19μ in diameter, brown, lightly papillose. Operculum conic, about 0.4 mm long. Calyptra about 2.5 mm long.

Habitat: rock.

Distribution: southeastern Brazil. Reported from elevations between 2,100 and 2,931 m.

The distinguishing characters of this endemic species are the crowded, lingulate leaves with costa and inner basal cells orange, and the minutely crenulate but never dentate leaf margins. **Leptodontium anoectangiaceum** is reduced to synonymy on the basis of its original description which refers to these features, as I have not been able to locate the type.

**BRAZIL.** Rio DE JANEIRO: Glaziou 7064 (BM). Itatiaia, 2,931 m, Massart 622 (H); 2,500 m, Glaziou 5205 (BM, S-PA); 2,500 m, Schiffner 750 (BM, H, M); in saxis, 2,200 m, Dusén, 1902 (FH, H, NY, M); rupibus, 2,200 m, Dusén, 1902 (S-PA); auf Felsen, 2,100 m, Ule 1824, 1827 (H). Planalto, Rizziti 1168 (FH).
7. *Leptodontium planifolium* Herz., Biblioth. Bot. 87: 37. 1916. Fig. 56-61

Type: Bolivia, Río Saujana, Herzog 3225 (JE—holotype; S-PA—isotype).

Plants small, in thick mats, greenish- to yellowish-brown; stems 2–4 cm long, *fluted in cross section*, without tomentum; leaves incurved, *flexuose-twisted when dry*, spreading-recurved when wet, *oblong-lanceolate with a broadly obtuse apex*, 0.4–1.0 × 1.5–3.5 mm, carinate above, with a slightly sheathing base, short and narrowly decurrent, margins recurved in lower half, dentate in upper ½; *costa ending 6–15 cells below apex*, dorsally papillose, *reniform in cross section*, with 3–4 fully included guide cells, 1 ventral and two dorsal layers of stereid cells; upper leaf cells subquadrate, lumens rounded-hexagonal in cross section, 8–13μ in diameter, walls evenly and moderately thickened, bulging, *papillae multifid*, centrally grouped over each lumen; inner basal cells mostly short-rectangular, 9–13 × 25–35μ, scarcely papillose, walls moderately thickened.

*Propagula numerous*, spherical to ovoid, 40–45 × 40–50μ, with mostly 2 transverse septa, *borne on short stalks in dense clusters on the stem between the upper leaves*.

Sterile.

Habitat: not given.

Distribution: Andes of Colombia and Bolivia. Known from only two collections, at high elevations.

This species is very close to *L. filicola* and may be an extreme form of that species. I have seen no intergrades, however. Collections of *L. filicola* have narrowly acute leaf apices, with the costa usually ending about 2–5 cells below the apex, while plants of *L. planifolium* have a more obtuse leaf apex, with the costa ending 6–15 cells below the apex (Fig. 59).

**COLOMBIA.** Páramo de Chisaca, SE of Bogotá, in mats, 11,000–12,000 ft., Schultes 20210 (CANM).

**BOLIVIA.** LA PAZ: Waldgrenze des Río Saujana, 3,400 m, Herzog 3225 (JE, S-PA).

8. *Leptodontium filicola* Herz., Biblioth. Bot. 87: 34, pl. 9, fig. 2. 1916.

Fig. 5, 16, 172–178

Type: Bolivia, Santa Cruz, Herzog 4512 (JE—holotype).


Plants small, in dense mats, greenish- to yellowish-brown; stems mostly 2–3 cm long, *fluted in cross section*, without tomentum; leaves *incurved to falcate-incurved when wet*, *oblong-lanceolate, with an acute to narrowly obtuse apex*, mostly 0.75–1 × 2.5–3 mm, carinate above, with a slightly sheathing base, little decurrent, margins recurved in lower ½–¾, dentate in upper ½, *costa ending 2–3 cells below apex*, dorsally papillose above, *usually elliptical in cross section*, but sometimes reniform, with 4 fully included guide cells, 2 ventral and 2 dorsal layers of stereid cells; upper laminal cells subquadrate, 9–11μ in diameter, lumens rounded-hexagonal in cross section, walls evenly and moderately thickened, bulging; *papillae simple to bifid*, centrally grouped over each lumen; inner basal cells short-rectangular, mostly 10–12 × 20–35μ, scarcely papillose, walls evenly and moderately thickened.

Propagula numerous, obovoid, 30–35 × 35–55(−175) μ, with usually 2(−6) transverse septa, borne on short stalks in dense clusters on the stem between the upper leaves.

Dioicus, perigonia and perichaetia terminal, perichaetial leaves 4–5 mm long. Setae up to 4 per perichaetium, 14–17 mm long, yellowish-brown, twisted counter-
clockwise above, clockwise below. Urn cylindrical, 0.3–0.4 × 1.5–2.0 mm, erect, brown; exothecial cells rectangular, 30–45 × 65–100 μm; annulus of about 2 rows of yellowish-brown cells. Divisions of peristome teeth linear, 9–11 μm wide at the mouth of the capsule, 400–500 μm long, reddish-orange, obliquely striate, with about 7 articulations. Spores 11–13 μm in diameter, yellowish-brown, lightly papillose. Operculum conico-rostrate, about 1 mm long. Calyptra 2.5–3.0 mm long.

Habitat: soil, logs, trees, rock.

Distribution: Central America, Andes, southern Brazil. Found in mountainous regions, infrequently collected, 1,800–3,650 m elevation.

The strongly incurved leaves clustered around dense masses of propagula borne on the upper stem is characteristic of both this species and L. planifolium. The latter, however, is distinguished by the broadly acute leaf apices with the costa ceasing 6–15 cells below the apex (Fig. 59). In some collections, such as Schwabe 210 (M), and in the holotype of L. filicola, the lamina of some leaves is little developed near the apex, resuting in an awn-like projection of the costa. Only a single collection, Rizziui 1048 (FH) from Brazil, was found with sporophytes having well developed peristome teeth. Other fruiting collections have short, incurved peristome teeth, colorless and nearly smooth.

COSTA RICA. Above Los Lotes, N of El Copey, Finca la Cima, 2,100–2,400 m, Standley 42777 (FH). ALAJUELA: Volcán Poas, Valerio 284 (FH); 2,500 m, Valerio 285a (FH). CARTAGO: Volcán de Turrialba, S slope, 2,000–2,400 m, Standley 35160a (FH).


PERU. Mito, trees, 9,000 ft., Bryan 397a (FH).

BOLIVIA. SANTA CRUZ: Florida de San Mateo, 2,000 m, Herzog 3638 (H). Zwischen San Mateo und Sunchal, Baumfarn, 1,800 m, Herzog 4512 (JE).

CHILE. Aconcagua: Zapallar Tigre, Schwabe 210 (JE, M).


II. LEPTODONTIUM sect. LEPTODONTIUM

Plants robust, usually 3–10 cm long; stem not fluted in cross section; leaves ovate-lanceolate to long-lanceolate or cirrhate, costa reniform in cross section, the ventral stereid band of usually 1 layer of cells, upper laminal cells with walls usually greatly thickened at the angles, lumens in cross section rounded-rectangular to oval, papillae rounded to columnar, simple to bi- or trifid, not crowded, scattered to centrally located over each lumen; simple propagula absent; dioicous or autoicous, perigonia terminal or lateral; annulus 4–6 rows of cells in height; peristome teeth 120–400 μm long, with 8–12 articulations; spores 17–45 μm in diameter, sometimes heterogeneous.


KEY TO THE VARIETIES OF L. VITICULOSOIDES

1. Numerous flagellate branchlets, with small deciduous leaves, present in some leaf axils; Mexico, Central America............................................................................................................ 9d. var. FLAGELLACEUM
2. Laminal papillae high, columnar; Mexico, Central America, Ecuador...................................................................................................................... 9c. var. EXASPERATUM

1. Flagellate branchlets absent, or entire plant more or less flagellate.................................................................................................................... 2
2. Laminal papillae low, mostly hemispherical 3
3. Spores heterogeneous; New and Old Worlds ............................................ 9a. var. viticulosoides
3. Spores homogeneous; New World ........................................... 9b. var. PANAMENSE

9a. **Leptodontium viticulosoides** var. viticulosoides

*Neckera viticulosoides* P. Beauv., Prodr. 78. 1805. Type: Réunion, Bory-St.-Vincent, s.n. (not seen).

*Encalypta squarrosa* Brid., Muscologiae recentiorum . . . Suppl. 1: 93. 1806. (= *Neckera viticulosoides* P. Beauv. fide Chen, 1941.)

*Didymodon squarrosus* Hook., Musc. Exot. 2: pl. 150, fig. 1–8. 1819. Type: Nepal, Gardner, s.n. (BM—holotype).


*Trichostomum subdenticulatum* C. Müll., Synop. Musc. 2: 626. 1851. Type: Java, Blume, s.n. (FH—isotype).


ZANDER: REVISION OF LEPTODONTIUM

Holomitrium maclennanii Dix., Smithsonian Misc. Collect. 72(3): 2, pl. 1, fig. 2. 1920.
Type: Uganda, Mt. Elgon, Dummer 3445 (us—holotype).
Type: Brazil, Sao Paulo, Campos do Jordao, Hoehne, 1923 (JE—holotype; S-P—iso-lectotype).

Plants slender to large, in tufts or loose mats, greenish- to yellowish-brown above, brown below; stems 2–20 cm long, not fluted in cross section, often with a thick tomentum, reddish-brown below to white above; leaves erect to spreading, flexuose-twisted to contorted when dry, squarrose-recurved when wet, ovate- to long-lanceolate with an acute apex, 0.8–1.2 × 3.25–3.5 mm, carinate above, with an ovate sheathing base, little decurrent, margins recurved in the lower ¼–½, dentate in the upper ¼–½; costa ending 3–5 cells below apex, dorsally papillose in the upper ½, reniform in cross section, with 4 fully included guide cells, 1–2 ventral and 1–2 dorsal layers of stereid cells; upper leaf cells subquadrate, 11–15 μm in diameter, lumens rounded-angular in cross section, walls thickened only at the corners, or seldom little thickened, papillae low, simple to bifid, scattered over each lumen; inner basal cells rectangular to long-rectangular, 11–13 × 65–75 μm, scarcely papillose, walls occasionally laterally thickened, porose to non-porose.

Autoicous, or seldom dioicous, male plants smaller than the female, perigonia lateral or terminal, perichaetia terminal, perichaetal leaves (4–)7–10 mm long. Seta (9–)16–22(–25) mm long, yellowish-brown; exothecial cells short-rectangular, 20–30 × 50–65 μm; annulus of 4–6 rows of reddish-brown cells. Divisions of the peristome teeth linear, 15–20 μm wide at the mouth of the capsule, 250–400 μm long, reddish- to yellowish-brown, lightly striated, with mostly 10–12 articulations, rudimentary preperistome occasionally present, to 140 μm long. Spores heterogeneous, of two size classes, 17–20 μm and 23–25 μm or more in diameter, the larger nearly spherical, translucent, and the smaller lenticular to tetrahedral in shape, light brown, both lightly papillose. Operculum conic-rostrate, 1.2–1.5 mm long. Calyptra about 6 mm long.
Habitat: soil, trees, logs, rock.
Distribution: Mexico, Central America, Andes, southern Brazil, Africa, Madagascar, Réunion, Himalayas, Formosa, Southeast Asia (Fig. 22). Widely distributed in the Americas. Found in mountainous regions, often in páramos, mostly 1,500–3,000 m elevation, but as high as 4,000 m (Ecuador) and as low as 100 m (Brazil).
Leptodontium viticulosoides var. viticulosoides produces spores of two kinds. The smaller brown spores are lenticular to tetrahedral, occasionally adhering to the larger, spherical green spores as small “caps.” Estimated visually, the larger and smaller spores are about equally represented in numbers in a sample from a capsule. Certain collections of the var. exasperatum have similarly heterogeneous spores, but the plants are distinguished by the high, columnar laminal papillae.
A preperistome is sometimes present, and may be highly developed, adhering to the lower articulations and reaching to more than half the length of the peristome teeth.

Most sexual specimens of var. viticulosoides are autoicous; however, certain collections are dioicous. The male plants of the latter are often flagellate, smaller than the female, with perigonia lateral or terminal. Dioicous specimens have been collected in Mexico: Crum 531, 601 (TENN); in Bolivia: Cochabamba, Herzog 3461 (M), Herzog,
TABLE 1. Comparison of the distinguishing gametophytic characters of *Leptodontium viticulosoides* var. *viticulosoides* and var. *panamense*.

<table>
<thead>
<tr>
<th>var. <em>viticulosoides</em></th>
<th>var. <em>panamense</em></th>
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<tbody>
<tr>
<td>Stems often tomentose</td>
<td>Stems seldom tomentose</td>
</tr>
<tr>
<td>Leaves often long but seldom cirrhate (Fig. 87–88)</td>
<td>Leaves often cirrhate (Fig. 75)</td>
</tr>
<tr>
<td>Leaves seldom long decurrent</td>
<td>Leaves often long and narrowly decurrent</td>
</tr>
<tr>
<td>Sheathing base usually high and broad (Fig. 87–88)</td>
<td>Sheathing base usually short and narrow (Fig. 73–76)</td>
</tr>
<tr>
<td>Teeth above usually sharp and little papillose, the cells usually elongate (Fig. 91)</td>
<td>Teeth above usually blunt and papillose, the cells not elongate (Fig. 78)</td>
</tr>
<tr>
<td>Upper leaf cells mostly 11–15μ in diameter</td>
<td>Upper leaf cells mostly 9–11μ in diameter</td>
</tr>
<tr>
<td>Differentiated inner basal cells usually not papillose below, reaching high in the sheathing base</td>
<td>Differentiated inner basal cells usually papillose to near insertion, mostly restricted to the bottom of the sheathing base</td>
</tr>
</tbody>
</table>

1907 (s-PA); and, in Argentina: Catamarca, Lorentz, 1890 (s-PA). Some collections are evidently both autoicous and dioicous, *e.g.*, Brazil: Rio Grande do Sul, Sehnem 125 (TENN). The entirely perigonial plants in such mats may have arisen from the same protonema as the autoicous plants. Old World collections seem entirely autoicous, differing from New World collections otherwise only in a tendency to shorter capsules, not or little curved.

*Leptodontium viticulosoides* var. *viticulosoides* is not as variable as is the very similar var. *panamense*, seldom having cirrhate leaves or appearing flagellate. The most common expressions of var. *viticulosoides* are plants with large leaves, long setae, to 20–22 mm, and long capsules, to 3–4 mm. Forms with short, broad leaves, for example the types of *L. quennoae*, *L. radicosum*, and *L. turgidum*, have been collected in many parts of the world. Most collections from India and Nepal, including the type of *L. squarrosum*, are depauperate.

Fleischer (1904–23) illustrated "Brutknollen" on the tomentum of *L. subdentculatum* (= *L. viticulosoides*) from Java, but I was unable to locate these propagula in any collection of the species.

As sporophytes are infrequently found in herbarium collections, much of the data on the geographic distribution of the species are based on sterile specimens, identified to variety by rather variable gametophytic characters (see Table 1). It is probable that biosystematic studies of *L. viticulosoides* in many parts of the tropics are necessary before a more satisfactory bryogeographical evaluation of varietal distribution can be made.

**MEXICO.** Jalisco: La Ferrería, above Manantlán, rotted log, 7,200 ft., Crum 885 (NY); rock, 8,000 ft., Crum 1001 (TENN). El Cuartón, above Manantlán, rock, 9,000 ft., Crum 1194 (TENN). La Cumbre, 10 mi. SW of Autilán, abundant on oaks at 5,100 ft., Crum 601 (TENN); oak, 5,300 ft., Crum 512a (CANM, DUKE, NY, TENN); oak, 5,100 ft., Crum 574 (TENN). MEXICO: Nevada de Toluca, volcano, 12,000 ft., Patrick 279 (FH). SINALOA: Los Gusanos, Ortega 6906 (FH). GUATEMALA. Without precise locality, Sarg 9 (H).

**ECUADOR.** Andes Quitensis, Spruce 20 (NY), Spruce 30 (BM). Ostkordillera, 3,000 m, epiphyte, Rimbach, s.n. (M, s-PA); Rimbach 1, 6 (FH, JE). AZUAY: Cuenca, ad arbore, 2,800 m, Rimbach, 1890 (M). CHIMBORAZO: El Altar, páramo region, 4,000 m, Meyer 5447 (JE),


ARGENTINA. CATAMARCA: Quefion, Lorentz, 1890 (S-PA). Prope Tambo, Lorentz, 1873 (H, NY, S-PA). SALTA: Camino de Salta a Jujuy, Garolera-Romero 8054 (FH). Cuesta prope Orán, Lorentz, s.n. (NY), Lorentz, 1873 (S-PA). TUCUMAN: Sierra de Aronguia, Bäumen in der "Aliso" Waldzone, 1,600 m, Kühn, 1920 (JE).

BRAZIL. Brasilis australis, Weir, s.n. (NY, S-PA). BAHIA: Sincora, Martius 10 (M). RIO DE JANEIRO: Serra de Itatiaia, Dusen 406 (S-PA), 2,200 m, Dusen, 1902 (FH, M, S-PA); 1,400-2,000 m, Schiffner 453 (Schiffner, Musc. Brasil. 61) (BM, S-PA); Waldchen, Zweigen, 2,000 m, Ule 1785 (H); paludosis partis superioris montis, ad Araucariae brasilienae truncos, 2,500 m, Schiffner 771 (BM, H, W), Schiffner 1868 (BM, W). RIO GRANDE DO SUL: Montenegro, super rupes in sole, 450 m, Sehnem 2919 (FH); Porto Alegre, rock, 100 m, Sehnem 297 (FH, NY); rupem, 700 m, Sehnem 125 (TENN). SANTA CATARINA: Passo do Socorro, pau vivo, 700 m, Reitz & Klein 15621 (US). Sao Joaquim, pedra, 1,300 m, Reitz & Klein 16016, 16018 (US). Serra Geral, Ule 56 (BM, NY). SAO PAULO: Campos do Jordao, Serra da Mantiqueira, auf Podocarpus lambertii, 1,700 m, Koehne 668 (JE, S-PA).

CAMEROON: Cameroon Mt., Mann, 1862 (NY). In montibus Camerunensibus supra Buea pagum die 20 m, 2,650 m, Dusën, 1891 (H).

CONGO. EASTERN: Mt. Elgon, heath zone, epiphyte, 12,000 ft., Dummer 3445 (US).


RHODESIA. Chimaninani Mts., Melsetter Dist., forest floor, 5,000 ft., Mitchell 242 (US).


RHODESIA. Chimanimani Mts., Melsetter Dist., forest floor, 5,000 ft., Mitchell 242 (US).


REUNION. Without precise locality, Rodriguez, 1889 (H, NY), 1891 (FH). Mafate, Rodriguez, s.n. (H); ad terram, 800 m, Rodriguez, s.n. (Renaud, Musc. Madag.-Madag. 16) (FH); ad terram, sub humidam, 800 m, Rodriguez, s.n. (Renaud, Musc. Madag.-Madag. 112) (FH).

NEPAL. Without precise locality, Gardner, s.n. (BM); Wallich, s.n. (NY), 1820 (BM).

ASSAM. Khasia Mts., Hooker & Thomson, s.n. (NY); 4,000 ft., Hooker fil. & Thomson 123 (FH, NY, s-PA). Khasia Hills, Hooker, s.n. (NY).

FORMOSA. Prov. TAIANAN: Mt. Kodama, tree trunk, 2,200 m, Noguchi, 1932 (TENN).


9b. *Leptodontium viticulosoides* var. *panamense* (Lor.) Zander, comb. nov.

*Fig. 2, 12–13, 73–80*


_Leptodontium sulphureum var. panamense_ Lor., Moostudien 161. 1864. Type: Panama, _Chiriqui, Wagner, 1856_ (FH, M, NY— isotypes).  


_Trichostomum sartorii_ C. Müll., _Linnaea_ 38: 637. 1874. Type: Mexico, _Mirador, Sartorius, s.n._ (FH, NY— isotypes).  


Amphoridium sullivantii (C. Müll.) Lesq. & James, Man. Mosses N. Amer. 159. 1884.


Desmatodon sartorii (C. Müll.) Par., Ind. Bryol. 319. 1894.


Leptodontium serrae (C. Müll.) Par., Ind. Bryol. Suppl. 225. 1900.


Leptodontium excelsum (Sull.) Britt., The Bryologist 11: 66. 1908.


Leptodontium helicoides Card., Rev. Bryol. 36: 75. 1909. Type: Mexico, Michoacan, Borelia, Jesus del Monte, Solorzano 12 (H—isotype); Solorzano, s.n. (JE—isotype).


Leptodontium ulocalyx var. cirrhifolium (Mitt.) Bartr., Fieldiana, Bot. 25: 122. 1949.

Diffsers from the typical variety by the dioicous inflorescence with terminal or sometimes axillary and clustered perigonia, the seta usually 5–14 mm long, and the spores homogeneous, 25–30μ in diameter.

Habitat: trees, soil, rock.

Distribution: Southern Appalachians, West Indies, Mexico, Central America, Andes, southern Brazil. Evidently common, growing in diverse ecological situations; collected in cloud forests, high altitude swamps, dry ridges, and on volcanos, usually 1,000–3,000 m elevation, but as high as 4,400 m (Ecuador) and as low as 300–600 m (Mexico).

Plants with cirrhate leaves to 12 mm long (Fig. 75), such as the types of L. cirrhifolium and L. subcirrhifolium, have been frequently collected in various localities in South America, and probably represent an ecological form as they intergrade with more commonly encountered plants with leaves 3.5–4.5 mm long. Certain other forms which have rather small, evenly thickened upper laminal cells, indistinctly papillose, and a short seta, are known from Mexican collections as L. brevisetum or Holomitrium serratum, both names here included in the synonymy of var. panamense. Several collections from Mexico and Central America, such as Sharp M59172E (us) and Standley 62708 (us), have flagellate branches, with small, narrow leaves (Fig. 73), comparing well with forms found at high elevations in the Southern Appalachian Mountains. A characteristic longitudinal elongation of some of the upper laminal cells of Appalachian specimens seems to distinguish this disjunctive population. Robust plants of var. panamense, with ovate-lanceolate leaves (Fig. 74), such as the type of L. helicoides of Mexico, generally have perichaetial leaves that are relatively short, 6–7 mm long, while plants with flagellate branches and narrower leaves have longer perichaetial leaves, to 12 mm long. These too are probably ecological forms. The var. panamense and var. viticulosoides are vegetatively very similar and are difficult to distinguish when not fruiting. A comparison of the rather subtle gametophytic characters which are correlated with the sporophytic differences between the two varieties is given in Table 1.
(FH); alpine meadow, 3,300 m, Standley 81117 (FH). Mountains SW of Malacatancito, tree, 1,800–2,400 m, Standley 626299 (FH). Jalapa: Volcán Junay, cloud forest near top, 1,300–2,500 m, Steyermark 32461 (FH, S-PA, US), Potero Carrillo, 13 mi. NE of Jalapa, Quetzaltenango: Boxatin, wet log, 2,400 m, Standley 83741 (FH, NY, TENN). Volcán Santa María, 3,000–4,200 m, Steyermark 34122 (FH, NY). Volcán Zunil, moist slopes around spring, 2,500–3,000 m, Steyermark 34914a (FH).

Getena area, N of Sija, soil, 9,500 ft., Sharp 2258 (FH); bark, 9,800 ft., Sharp 2293 (FH, TENN); limbs of Alder, 9,800 ft., Sharp 2269 (FH); limb of fir, 9,900 ft., Sharp 2291 (FH, TENN). Quetzaltenango: Boxatin, wet log, 2,400 m, Standley 83741 (FH, NY, TENN). Volcán Santa María, 3,000–4,200 m, Steyermark 34122 (FH, NY). Volcán Zunil, moist slopes around spring, 2,500–3,000 m, Steyermark 34914a (FH).

HHONDURAS. COMAYAGUA: El Achote, bog, 1,500 m, Standley 56102 (BM, FH, NY, S-PA, US). Morazán: Joya Grande, along road between El Zamorano and Suyapa, log, 1,500 m, Standley & Williams 1458 (BM, NY).

EL SALVADOR. SAN VICENTE: Volcán de San Vicente, log in forest, 1,200–1,500 m, Standley 89515 (FH, NY, US). Morazán: Joya Grande, along road between El Zamorano and Suyapa, log, 1,500 m, Standley & Williams 1458 (BM, NY).

NICARAGUA. CHINANDEGA: Volcán Viejo, 5,000 ft., Oersted, 1847 (BM, FH, H, JE, NY, S-PA). JINOTEGA: vicinity of Jinotega, rock in oak forest, 1,030–1,300 m, Standley 9570 (FH, NY).


HAITI. Massif de la Hotte Ma Blanche, S slope, rotten pine log, 1,500 m, Ekman H569 (NY, S-PA). Morne Vincent, ground, Holdridge 3167 (FH). Morne La Selle, near summit of Pic La Selle, 8,800 ft., Wetmore 3087 (CANM, FH).

DOMINICAN REPUBLIC. Valle Nuevo, sobre roca cubierta de detritus vegetales húmidos, 2,560 m, Jiménez M76 (FH). El Montazo, 1,900 m, Jiménez M57 (FH).

Río Quinimari, pié de la Peña de Pata de Judío, bark, 2,400 m, Steyermark & Dunsterville 100620 (US); debajo del Cerro Las Copas, epiphyte, 2,500–2,700 m, Steyermark & Dunsterville 100675 (US).


Magdalena: Hoya del Río Donachuí, Meollaca, rocky páramos, 3,400 m, Cuatrecasas & Casteneda 24641 (FH, TENN, US). SANTANDER: Road from Pamplona to Toledo, moist soil, 2,800–3,000 m, Killip & Smith 20709 (BH, FH, NY, US). VALLE: Hoya del Río Bugalagrande, Barragán, 3,000–3,080 m, Cuatrecasas 20170B (US).

ECUADOR. Without precise locality, Spruce, s.n. (Spruce, Musc. Amazon. And. 28) (BM, NY). AZUAY: Sevilla de Oro, Pallatanga, mountain forest, 3,400 m, Harling 2327a (S-PA). Vicinity of Portovelo, Rose 24040 (NY). CARCHI: Canton Talcan, trail from Pun to Chingual, covering stump, 2,936 m, Mexia 7619a (BM, FH, NY, S-PA, US). MORONA-SANTIAGO: Chimborazo, Jameson, s.n. (NY). GUAYAQUIL: Spruce 28c (BM, FH, NY, S-PA); NW slopes, bank, 8,500 ft., Bell 861 (BM), 862 (FH).

PICHINCHA: Andes Quitensis in monte Tunguragua, Spruce 25 (S-PA).

PERU. CUSCO: Valle de Marcapata, 4,000 ft., Herrera 1178a (NY).

BOLIVIA. Coranital, gefallenen Baumstücken, 2,600 m, Herzog 4045 (JE, M). Near Yungas, 4,000 ft., Rusby 3190 (NY). COCHABAMBA: Comarapa, Nebelwald, 2,600 m, Herzog 2932c (JE). Incacorral, Bergurwald, 2,200 m, Herzog, 1908 (JE). Tablas, Waldgrenze, 3,400 m, Herzog 2919 (M). Oberen Coranital, 2,600 m, Herzog 3371 (BM). LA PAZ: Near Paraiso, Apolo-San José trail, 4,500 ft., Williams 2129 (BM, NY).

BRAZIL. Without precise locality, Glaziou 17983 (H, NY). MINAS GERAIAS: Mt. Pedra-branca, acumine, arbores, Mosén 43 (FH, S-PA). Caldas, Mosén, 1873, 1874 (S-PA). Rio de JANEIRO: Without precise locality, Glaziou 3540 (BM, H, S-PA), 6369 (BM, NY). Itatiaia, Granitifels, Waura 400 (S-PA); Luederwaldt, 1913 (JE), 1,400–2,000 m, Schiffner 453 (M); 2,200 m, Dusén, 1903 (FH, S-PA); Felsen der Agullias-Negras, Ule 2069 (FH, M), rupestribus, 1,300–2,750 m, Schiffner 474 (FH); ad truncos Araucar. bras. 2,500 m, Schiffner 766 (Schiffner, Muse. Brasil. 60) (BM, S-PA); 2,750 m, Schiffner 1874 (BM, FH, S-PA); saxis, 2,200 m, Dusén, 1903 (FH, JE, NY, M). Organ Mts., Rizziti 1005 (US). Tijuca, Walde, Ule 2059 (FH). RIO GRANDE DO SUL: Sao Francisco do Paula, Taimbe, humo, 1,000 m, Sehnem 5334 (FH); Faxinal, arboreum, 1,200 m, Sehnem 5321 (FH). SANTA CATARINA: Serra Geral, Baumstämnen, Ule 846 (S-PA). Bom Jardim, Rio do Rastro, pedra, 1,400 m, Reitz & Klein 16076 (US). Bom Retiro, log and pasture, 1,650 m, Smith & Reitz 10366 (US); Campo dos Padres, epiphyte, 1,950 m, Reitz 2484 (FH, NY), 2487 (FH); epiphyte, 2,000 m, Reitz 2408 (FH), 2424 (FH, NY, US); terestre 2,200 m, Reitz 2537 (FH). São Joaquim, Urupema, podre, 1,200 m, Reitz & Klein 18894 (US). SÃO PAULO: Without precise locality, Puiggari, 1882 (M). Mt. Jaragua, 800–1,000 m, Schiffner 1253 (BM, M, S-PA); prope Taipas, terram, 1,500 m, Schiffner, s.n. (Krypt. Exs. Mus. Hist. Natur. Vindobon. 2591) (BM, CANM, FH, M, NY, S-PA, US). Mantiqueira, Podocarpus lamberti, 1,600 m, Koehne 645 (JE). Unuarama, Templo dos Druidas, arbores, 1,800 m, Kuhlmann 32526 (JE, S-PA).

9c. Leptodontium viticulosoides var. exasperatum (Card.) Zander, comb. nov.

FIG. 9, 82–86

Leptodontium exasperatum Card., Rev. Bryol. 36: 74. 1909. Type: Mexico, Vera Cruz, Orizaba, Müller, s.n. (NY—lectotype).

Differents from the typical variety by the large, often columnar laminal papillae, simple to bi- or trifid, 4–11 µ high, occurring 1(–3) on the bulging cell walls over the center of each lumen (Fig. 84), and spores sometimes homogeneous.

Habitat: soil, decaying logs, rock.
Distribution: Mexico, Central America, Ecuadorean Andes. Mountainous regions, from 1,400–3,200 m elevation.

The distinctive geographic range of this aptly named variety is evidence supporting its recognition as a taxon apart from the closely related vars. panamense and viticulosoides. There is, however, some variability in the height of the laminal papillae. Additionally, the spores may be homogeneous (e.g., Mexico, Jalisco, McVaugh 10341j (MICH)) as with var. panamense, or heterogeneous (e.g., Mexico, Jalisco, Crum 842 (TENN)) as with var. viticulosoides.

MEXICO. CHIAPAS: above Paval, N of Mapastepec, bank, 6,400 ft., Sharp 4460 (TENN).

Sierra N of Mapastepec, N slope, soil, 6,000 ft., Sharp 4591 (TENN).

CHIHUAHUA: Rayon Dist., Mojarachic, Knoebloch 10008 (FH).

Durango: El Salto, boulder, in canyon, 8,300 ft., Sharp 1838a (DUKE);
	near Salto, soil, 8,400 ft., Sharp 1818 (TENN);

boulder, 8,300, Sharp 1827 (TENN);

3 km W of El Salto, boulder, 8,800 ft., Sharp 1850 (TENN).

Durango-Sinaloa border, Durango-Magullen highway, rock in shade, 8,750 ft., Hevoly, Martin & Arms, 1960 (CANN).

GUERRERO: Asoleadero, 15 km W of Camotla, fir-pine forest, bark, decaying branch on ground, 2,650 m, Dieterle 3219 (CANN).

HIDALGO: Mineral del Chico, Orcutt 6732 (FH); Orcutt 6738 (FH).


Sierra Madre, W of Bolaños, Rose c (NY).

La Ferreria, above Manantlán, summit, oak and pine, 8,000 ft., Crum 1008 (TENN);

rotted log, 7,200 ft., Crum 885 (CANN, FH, TENN);

summit, rock, 8,000 ft., Crum 1016 (NY, S-PA, TENN).

MICHOACAN: Cerro Grande, where road joins main Toluca-Morelia highway, 2,700 m, Frye & Frye 2802 (DUKE).

Vicinity of Morelia, Cerro Azul, 2,300 m, Arsene 4549 (us);

Arsene 7939 (US).

OAXACA: Sierra Juárez, near Llama de las Flores, fallen tree trunk, 7,500 ft., Sharp 45 (TENN).


VERACRUZ: Orizaba, Müller, s.n. (NY).

GUATEMALA. AMATITLÁN: Volcán Pacaya, Kellerman, 1907 (DUKE).

HUEHUETENANGO: Madron, Vogel 8960b (DUKE, TENN, US).

Above Huehueteango, base of juniper, 10,500 ft., Sharp 4768 (FH, TENN).

Top of Cerro Chemalito, 3½ mi. W of Santa Eulalia, 3,100–3,150 m, Steyermark 49956 (FH, NY, S-PA).

QUETZALTENANGO: N of Sija, Getena area, soil, 9,500 ft., Sharp 2258 (TENN).

TÓNOCAPÁN: Road between Huehueteango and Sija, tree, 3,000–3,300 m, Standley 62664a (FH).

COSTA RICA. CARTAGO: Hotel La Georgina, 97 km S of Cartago, tree trunk, Bowers 824 (TENN).

ECUADOR. La Dormida, Round Camp, 11,805 ft., Whymper 1348 (BM).

PICHINCHA: Pichincha, Jameson, s.n. (BM).

Andes Quitensis, Cayambe, 10,000–11,000 ft., Spruce 30 (BM).

9d. Leptodontium viticulosoides var. flagellaceum (Bartr.) Zander, comb. nov. FIG. 81

Leptodontium sulphureum var. flagellaceum Bartr., Contr. U.S. Natl. Herb. 26: 75, fig. 15. 1928.

Type: Costa Rica, Heredia, Cerros de Zurqui, Standley & Valerio 50508 (us—holotype; FH, JE, NY—isotypes).

Diffs from the typical variety in the occasional presence in the leaf axils of numerous stolon-like flagellate branchlets up to 6 mm long, with oblong to rectangular deciduous leaves, to 0.75 mm long, costa usually ½–¾ the length, margins entire or sometimes deeply dentate above. Sterile.

Habitat: trees.

Distribution: Mexico and Costa Rica, known from few collections, at high altitudes.

The leaves of the flagellate branchlets (Fig. 81) are deciduous and probably figure in asexual reproduction. Specimens of var. panamense are sometimes attenuate, with flagellate branches, but show little of the dimorphism distinguishing plants of var. flagellaceum.
MEXICO. CHIAPAS: Road from San Cristobal del las Casas to Tenejapa, tree trunk, above 8,000 ft., Sharp M59137b (TENN). VERACRUZ: Near El Puerto above Acultzingo, bark of oak, 7,700 ft., Sharp 654 (TENN).

COSTA RICA. HEREDIA: Cerros de Zurqui, NE of San Isidro, tree, 2,000–2,400 m, Standley & Valerio 50508 (FH, JE, NY, US).

III. LEPTODONTIUM sect. Crassicostata Zander, sect. nov. Fig. 3, 14, 93–115

Type species: L. pungens (Mitt.) Kindb.

Plants robustae, folia oblongo- ad longo-lanceolata, costa crassis, propagula desunt, dioicae, perigonia terminalia.

Plants slender to robust, usually 2–10 cm long; stem fluted in cross section; leaves oblong- to long-lanceolate, costa semicircular in cross section, the ventral stereid band usually of more than 1 layer of cells, upper laminal cell walls not bulging, never greatly thickened at the angles, lumens in cross section rounded-rectangular, papillae usually rounded, simple to bi- or trifid, crowded, scattered over each lumen, or sometimes grouped over the center; propagula absent; dioicous, perigonia terminal; annulus 4–6 rows of cells in height; peristome teeth usually 300–450μ long, with 10–15 articulations; spores 17–30μ in diameter.


Leptodontium braunioides C. Müll., Linnaea 42: 325. 1879. Type: Argentina, Tucumán, montibus inter Siambon et Tafi, Lorenz, 1873 (NY, s-PA—isoletespes).


Trichostomum pungens (Mitt.) Par., Ind. Bryol. 1329. 1898.


Leptodontium acutifolium var. grimmiioides (Britt.) Herz., Biblioth. Bot. 87: 35. 1916.


Plants in dense mats, greenish-yellow to reddish-brown above, reddish-brown below; stems 2–5 cm long, fluted in cross section, without tomentum; leaves erect, little contorted or twisted when dry, spreading-recurved when wet, ovate-lanceolate to lanceolate, with a narrowly acute apex often filled with scarcely papillose rhomboidal cells, 1.0–1.3 × 3–4 mm, carinate above, with a sheathing base, not decurrent, margins recurved in the lower ½–¾ of the leaf, dentate in the upper ½–⅔, the marginal row of cells above scarcely papillose; costa percurrent or ending 1–4 cells below
apex, **semicircular in cross section**, sometimes dorsally papillose, with 4 fully included guide cells, 2(−4) ventral and 2−3(−6) dorsal layers of stereid cells; upper laminal cells subquadrate, 11−15μ in diameter, lumens rounded-rectangular in cross section, walls moderately thickened, **papillae crowded, multifid, 2−4 over each lumen**; inner basal cells rectangular, mostly 9−11 × 45−65μ, scarcely papillose, walls thin or laterally thickened and porose, **alar region often differentiated as a group of yellowish-brown, short-rectangular cells with thick and porose walls**.

Apparently dioicus, perigonia not seen, perichaetial leaves 7–8 mm long. Seta 10–11 mm long, brown, twisted counterclockwise above, clockwise below, 1–2 from a perichaetium. Urn cylindrical, 0.3–0.5 × 1.50–1.75 mm, erect, rugose when dry, blackish-brown; exothelial cells short-rectangular, 20–30 × 30–45 μm; annulus of 4–5 rows of reddish-brown cells. Divisions of peristome teeth linear, 15–20 μm wide at the mouth of the capsule, 310–375 μm long, yellowish-orange, indistinctly striated, with about 10–12 articulations, preperistome sometimes present, very short. Spores 17–20 μm in diameter, dark brown, very papillose. Operculum conic, about 0.8 mm long. Calyptra not seen.

Habitat: soil, rock.

Distribution: Mexico, Central America, Andes, Juan Fernandez, southern Brazil, Africa (Fig. 23). Frequently collected on volcanos and páramos at high altitudes, 1,100–5,300 m.

MEXICO. Ajusco, Reiche, 1913 (H). Dist. Fed.: Ojos de Agua, dry soil, 12,800 ft., Balls 4095 (FH, US). Near Contreras, lava of Pedrigal, 8,000 ft., Sharp 1173 (TENN). MÉXICO: Nevada de Toluca, volcano, shores of highest lake, 13,500 ft., Patrick 319 (FH). Mt. Popocatépetl, near tree line, soil, 13,000 ft., Sharp 4737, 4738, 4739 (TENN); N facing slope, alpine, soil, Delgadillo 2079 (TENN); soil among rocks, 4,000 m, Kiener 18543a, 18547 (FH); W slope, soil, 11,500 ft., Hermann 20813 (US). OAXACA: Cerro Zempoaltepetl, summit, 3,395 m, Hallberg 759 (CANN). PUEBLA: Iztaacihuatl, SW end, alpine, soil, Delgadillo 1327 (TENN).


VENEZUELA. Lara: Between Buenos Aires and Páramo de las Rosas, rock, 2,285–3,290 m, Steyermark 55492 (FH). MÉRIDA: Páramo between Apartaderos and El Aquila, terrestrial, 4,000 m, Steyermark & Rabe 97155 (US). Páramo de Muchchies, in small lake, 4,000 m, Alston 6647c (BM, FH). Páramo de Mucubají, Sierra de Sto. Domingo, alrededores de la Laguna Grande, soil, 3,600 m, Barclay & Juajibioy 9639 (CANN).


ECUADOR. Azuay: Cuenca, shore of Lake Slavio, 3,400 m, Harling 2197 (CANN, FH). Vicinity of Portovelo, Rose 24040 (FH, US). Cañar, Rose 23661 (NY). CHIMBORAZO: Chimborazo, Jameson, s.n. (BM); páramo region, 5,300 m, Meyer 5529 (JE). Pungor, ad rupes, Spruce 29 (BM, NY). El Altar, páramo region, 4,000 m, Meyer 5436, 5465 (JE, 5542 (H). COPÓPAXI: Without precise locality, ground, 3,500 m, Holdridge 1568 (FH). Crest above Pujili, W of Latacunga, grassy páramo, Barclay & Juajibioy 7979 (CANN). CAJAMARCA: 4,600 m, Meyer 5471 (JE); lava flow, 4,400 m, Grubb, et al. 2562 (BM); páramo, hillock, between grass on soil, Grubb, et al. 2517 (BM). PICHINCHA: Jameson 17ab (BM); Mt. Pichincha, Jameson, s.n. (FH); 4,000 m, Naundorff, 1955 (JE); 14,500 ft., Bell 369 (BM, FH); 15,000 ft., Bell 413 (BM, FH); tussocks around low shrubs, 14,500 ft., Bell 367a (BM, FH). Corazón, Westseite, Espinoza, 1933 (JE). Andes of Quito, Jameson 193a (BM). TUNGURAHUA: E shoulder Chimborazo, grassy slopes, 3,480 m, Barclay & Juajibioy 8821A (CANN).

PERU. Hacienda d’Angarmarca, Standaërt, 1904 (S-PA). Ancash: 5 km NE Huaraz, 3,100 m, Griffin, 1965 (TENN). Cordillera Blanca, 4,300 m, Lukes, 1932 (JE). Ancash–Huancuyo–Lima: Yerupaja, 4,700 m, Kinzi 2a (JE, S-PA). AREQUIPA: Hills back of Mollendo,
ZANDER: REVISION OF LEPTODONTIUM


JUAN FERNANDEZ. MASAFUERA: Las Torres, 1,350 m, Skottsberg & Skottsberg M159 (FH, S-PA).

ARGENTINA. CóRDOBA: Sierra Achala, Cerro do los Gigantes, Lapides, 2,000 m, Kurtz 6935 (H, S-PA); 2,000-2,379 m, Kurtz 4446 (H). POTOSI: Aquila, 5,200 m, Knoch 53 (JE). TUCUMAN: Cabrahoreco, 2,500 m, Lillo 995 (FH). Carapunco, 2,800 m, Lamb 5369, 5373, 5381 (FH). Cuesta de las Cañas, Cumbre de Calahue, Felsen, 3,000 m, Kühn, 1920 (JE). Montibus inter Siambon et Tafi, Lorentz, 1873 (S-PA).

BRAZIL. RIO GRANDE DO SUL: Bom Jesus, earth, 1,100 m, Sehnem 286 (CANM, FH, NY).

CAMEROON. Cameroons Mt., Mann, 1862 (NY). Kamerunberg, Aschenkegel, 4,550 m, Hintz 26c (H). In summo monte "Fako," 3,600-4,000 m, Bornmüller, 1898 (NY).

KENYA. CENTRAL: Mt. Kenya, western slopes, trail from West Kenya Forest Station to summit, 4,200 m, Mearns 1660 (FH, NY, US).


**Trichostomum wallisii** C. Müll., Linnaea 38: 603. 1874. Type: Colombia, Antioquia, Páramo de Ruiz, Wallis, 1872 (BM, JE, NY, S-PA—isodesotypes).


**Leptodontium variegatum** Herz., Arch. Bot. São Paulo 1: 62. 1925. Type: Brazil, Luetzelsburg, s.n. (JE—holotype; M—isodesotypes).


**Leptodontium anomalum** Dix. & Thér., Rev. Bryol. Lichénol. 9: 15, fig. 7. 1936. Type: Ecuador, Ladrillos, Benoist 2661 (BM—holotype).

Plants medium-sized, in mats, greenish- to yellowish-brown above, brown below; stems 2–10 cm long, fluted in cross section, tomentum reddish-brown, sparse or absent; leaves erect to spreading-recurved, twisted when dry, spreading-recurved to squarrose-recurved when wet, lanceolate to long-lanceolate, with a narrowly acute apex sometimes filled with scarcely papillose rhomboidal cells, 0.8–1.0 × 4.5–5.5 mm, carinate above, with an oblong, high-sheathing base, little decurrent, margins revolute and incurved submarginally in lower ¼–½, dentate in upper ¼–½, the marginal 1–3 rows of cells above often little papillose, elongated; costa percurrent or ending 1–3 cells below apex, dorsally not papillose, semicircular in cross section through the upper part of the leaf sheath, with 4 fully included guide cells, 2 ventral and 2–3 dorsal layers of stereid cells; upper laminar cells subquadrature, 8–11μ in diameter, lumens rounded-rectangular in cross section, walls evenly and moderately thickened; papillae crowded, simple to multifid,
usually fused into 2–4 groups over each lumen; inner basal cells long-rectangular, often porose, **basal submarginal cells of the sheathing base short-rectangular, 11–13 × 25–35μ, wider than the inner basal cells.**

Dioicous, perigonia and perichaetia terminal, perichaetial leaves 6–8 mm long.
Seta 8–10 mm long, yellowish-brown, twisted clockwise above, 1–3 from each perichaetium. Urn cylindrical, 0.7–0.9 × 2.0–2.2 mm, erect, yellowish-brown; exothecial cells subquadrate to short-rectangular, 20–25 × 20–40 μm; annulus of 4–6 rows of reddish-brown cells. Divisions of peristome teeth linear, 20–25 μm wide at the mouth of the capsule, 350–450 μm long, yellow to orange, lightly papillose-striated, with 10–15 articulations. Spores 25–30 μm in diameter, light brown, lightly papillose. Operculum conic-rostrate, 1.2–1.5 mm long. Calyptra about 4 mm long.

Habitat: soil, rock.

Distribution: Central America, Andes, southern Brazil, Africa. Infrequently collected; evidently restricted to high altitudes, from about 2,000–5,200 m.

Leptodontium wallisii is closely related to L. pungens, but differs mainly in the enlarged lower submarginal cells, and in the usually more highly sheathing leaf base. The costa may sometimes be red throughout most of its length, as in Bües 1457 (NY). The upper marginal cells in 1–2 rows may be little papillose and elongated, forming a distinct border, as in [no collector cited] Herb. Bescherelle, 1900, Colombia (BM).


ECUADOR. Rochers vers le Picado de Ladrillos, Benoist 2661 (BM). Pichincha: Páramo de Guamaní, vicinity of Ciénaga, grassy slopes, 4,050 m, Barclay & Juajibioy 8877 (CANN).

PERU. Ancash: Yerupajágruppe, Ostrand, gegen des Carniceropasses, 4,500 m, Kinzl 4c (JE, S-PA). Cordillera Blanca, Carniceropass, 4,500 m, Kinzl 7 (S-PA); Pico Rury, Felsritzen, 4,600 m, Luttas 3013 (JE). Cuzco: Maracapata, 12,000 ft., Stafford 1011 (BM). Province la Convencion, 13,000–14,000 ft., Bües 1454 (NY).

BOLIVIA. Cochabamba: Águila, Cordillera Real, 5,200 m, Knoche 53 (H). Nebelwald über Tablas, 3,400 m, Herzog 2873 (JE, M). La Paz: Yungas von Inquisive, Ceygurquet bei Negracota, Troll 82 (FH, JE); Troll 83 (JE).


CONGO. Nord-Kivu: Karisimbi, Sudkraterrand, 3,400 m, Mildbraed 2070 (H); Gipfelkegel, 4,000 m, Mildbraed 2090 (H).


Type: Bolivia, Cochabamba, San Benito, Herzog, 1908 (JE—holotype; S-PA—isotype).

Plants medium-sized, in dense mats, light brown above, reddish-brown below; stems mostly 2–3 cm long, fluted in cross section, without tomentum; leaves appressed, slightly incurved, scarcely incurved when dry, spreading-recurved when wet, lanceolate, with an acute or narrowly obtuse, incurved apex, 0.8–1.0 × 2.5–4.0 mm, carinate above, with a moderately sheathing base, little decurrent, margins recurved in lower ½–⅔, weakly dentate in upper ⅓–½; costa red throughout, ending 2–3 cells below apex, smooth, semicircular in cross section, with 4–6 fully included guide cells, 2–3 ventral and 2 dorsal layers of stereid cells; upper laminal cells subquadrate, 9–11 μm in diameter, lumens rounded-rectangular in cross section, walls moderately and evenly thickened, papillae crowded, bifid or much fused, 4–6 over each lumen; inner basal cells long-rectangular, mostly 9–11 × 65–75 μm, scarcely papillose, walls slightly thickened laterally, scarcely porose.
Dioicous, perigonia and perichaetia terminal, perichaetial leaves to 5 mm long. Seta 15–16 mm long, yellowish-brown, twisted clockwise. Urn cylindrical, 0.6–0.8 × 1.8–2.0 mm, erect, brown; exothecial cells short-rectangular, 25–35 × 45–65 μ; complete annulus not seen. Complete peristome not seen. Spores 22–42 μ in diameter, yellowish-brown, papillose.

Habitat: rock.

Distribution: Andes, collected only from very high elevations, 3,500–7,700 m.

Specimens of L. wallisii may occasionally have red costae, and, upon superficial examination, may be confused with L. erythroneuron.

COLOMBIA. CUNDINAMARCA: Boquerón, Bogotá, Felsen, 7,700 m, Troll 2173b (JE, S-PA). Chiquinguiva, près de Bogotá, Apollinaire 2343 (DUKE).

PERU. HUANUCO–ANCASH–LIMA: Cerro Yerupajá, 4,700 m, Kinzl, 1936 (JE, s-PA); Kinzl 2b (s-PA).


Type: Peru, Yerupajá, Kinzl, 1936 (JE—holotype; s-PA—isotype).

Plants medium-sized, in dense mats, greenish- to yellowish-brown above, brown below; stems 4–7 cm long, fluted in cross section, with dense reddish-brown tomentum; leaves appressed, incurved and slightly twisted when dry, spreading-recurved when wet, oblong-lanceolate with an acute apex, 0.75–1 × 3–4 mm, carinate above, with a high sheathing base, not decurrent, margins recurved in the lower ½–¾, minutely crenulate above by projecting cell walls and papillae, occasionally denticulate near apex; costa ending 6–10 cells below apex, dorsally smooth, semicircular in cross section, with 4 fully included guide cells, 2 ventral and 2 dorsal layers of stéreid cells; upper laminal cells subquadrate, 10–12 μ in diameter, lumens rounded-hexagonal in cross section, walls moderately and evenly thickened, bulging; papillae crowded, simple to multifid, usually centrally grouped over each lumen; inner basal cells rectangular, mostly 9–11 × 50–65 μ, scarcely papillose, walls thin or slightly thickened laterally, scarcely porose.

Apparently dioicous, perigonia not seen, perichaetia terminal. Sporophytes not seen.

Habitat: not given.

Distribution: Andes of Peru. Known only from two collections, 4,700 m elevation.

Leptodontium subintegrifolium is distinguished from other New World species of the section by the leaf margins above being minutely crenulate and seldom denticulate near the apex (Fig. 111, 114). Leptodontium interruptum (Mitt.) Broth., of Australia, New Zealand, and New Amsterdam Island, seems closely related, but differs by the short stems, mostly 2–3 cm long, with crowded, falcate leaves with short sheathing bases.

PERU. ANCASH–HUANUCO–LIMA: Yerupajá Cruppe, 4,700 m, Kinzl, 1936 (JE, s-PA); Ostrand, gegen der Carnicero-Pass, Kinzl, 1936 (JE, s-PA).
IV. **Leptodontium** sect. **Coronopapillata** Zander, sect. nov.  

Type species: *L. longicaule* Mitt.

Planta robusta, fola ovato- ad longo-lanceolata, papillae humiles, applantae vel ramosae, plerumque coronam formantes; perigonia lateralia.


Plants medium-sized to large, in loose mats, greenish- to yellowish-brown above, brown below; *stems* 3–20 cm long, *fluted in cross section*, without tomentum; leaves erect to spreading, twisted when dry, spreading-recurved when wet, *lanceolate with a narrowly obtuse apex*, 1–1.75 × 4–8 mm, slightly carinate above, *with an elliptical sheathing base*, short decurrent, margins revolute in the lower 1/4–1/3, dentate to near the insertion, often becoming erose below, often differentiated by 1–5 rows of short-rectangular, thick-walled cells, *occasionally enlarged below*; costa ending 2–4 cells below apex, sometimes dorsally papillose, reniform in cross section, with 4 fully included guide cells, 1 ventral and 1–2 dorsal layers of stereid cells; upper laminar cells subquadrate to short-rectangular, 9–11 × 9–13μm, lumens rounded-rectangular in cross section, walls evenly and slightly to moderately thickened, *papillae crowded, low*, delicate, *simple to multiform or often flattened*, usually 4–6 over each lumen; inner basal cells rectangular, mostly 7–11 × 35–65μm, thinly papillose, walls laterally thickened, scarcely porose.

Propagula occasionally present, obovate, 30–40 × 45–65μm, with mostly 2 transverse septa, borne on short stalks on the stem above.

Dioicus, perigonia lateral, perichaetial leaves 7–8 mm long. Setae 1–5 per perichaetium, 12–17(−30) mm long, yellowish-brown, twisted clockwise. Urn cylindrical, 0.4–0.5 × 2–3 mm, erect, yellowish-brown; exothecial cells rectangular, 25–45 × 70–80μm; annulus of about 6 rows of reddish-brown cells. Divisions of peristome teeth linear, 15–20μ wide at the mouth of the capsule, 550–650μ long, reddish-orange, obliquely striated, with mostly 10–15 articulations. Spores 12–14(−20)μ in diameter, brown, lightly papillose. Operculum conic, 1.0–1.5 mm long. Calyptra about 4 mm long.

Habitat: soil, rock.

Distribution: Andes, Africa. Collected mostly on volcanos and páramos, 1,830–4,000 m elevation.

*Leptodontium luteum* is distinguished by its large size, elliptical leaf base dentate to erose along the lower margin, and the usually thin-walled leaf cells. The dentition may be obscure along the lower margins of plants in which these margins are greatly rolled. The laminar cells of this species characteristically have flat surfaces and low, simple to multiform papillae, which often become flat and plate-like (Fig. 4). Occasional specimens of *L. araucarieti*, a related species with usually bulging upper laminal cells, and small, delicate, simple to bi- or trifid papillae grouped over the center of each lumen (Fig. 5), may have similar areolation and papillae structure, but may be distinguished by the lack of dentition on the lower leaf margin. *Leptodontium aggre-
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Leptodontium gatum C. Müll. of Java seems closely related to L. luteum, but is distinguished by the smaller, more recurved leaves, dentate only in the upper half, with laminal walls usually greatly thickened at the angles.


Plants medium-sized, in loose mats, greenish- to yellowish-brown; stems mostly 6–9 cm long, fluted in cross section, without tomentum; leaves spreading-recurved, contorted and twisted when dry, spreading- to squarrose-recurved when wet, lanceolate to ovate-lanceolate with an acute apex, 0.8–1.2 × 3–4 mm, carinate above, with a high sheathing base, little decurrent, margins recurved in the lower 1/2–1/4, dentate in the upper 1/4–1/4; costa ending 4–8 cells below apex, dorsally papillose, reniform in cross section, with 4 fully included guide cells, 1–2 ventral and 1–2 dorsal layers of stereid cells; upper laminal cells subquadrate to occasionally longitudinally elongated, 9–11 × 9–11 (–17) μ, lumens rounded-hexagonal in cross section, walls little and even
thickened, somewhat bulging, papillae simple to multifid, scattered or grouped over the center of each lumen; inner basal cells rectangular, 9–11 × 20–60μ, thinly papillose, walls thin to laterally thickened. Stalked, rudimentary leaves, lanceolate to linear-lanceolate, usually costate, mostly 0.5–1.0 mm long, occasionally present on the stem.

Propagula obovoid, 30–50 × 55–65μ, with mostly 2 transverse septa, borne on short stalks on the stem.

Dioicous; perigonia lateral, perichaetia terminal, perichaetial leaves 5–6 mm long. Setae 1–6 from a perichaetium, 15–20 mm long, yellowish-brown, twisted clockwise above. Urn cylindrical, 0.5–0.6 × 2.0–2.5 mm, erect, yellowish- to reddish-brown; exothecial cells short-rectangular, 20–30 × 35–55μ; annulus of 4–6 rows of reddish-brown cells.


Habitat: soil, rock.

Distribution: Andes, southern Brazil. Found mostly at lower altitudes than are most species of the genus, 300–2,000 m, but sometimes as high as 2,600–3,000 m.

Leptodontium araucarieti is close to L. luteum, but differs by the shorter, ovate leaf base, and in the absence of dentition along the lower leaf margin. The upper laminal cells are usually somewhat bulging, with small, delicate papillae grouped over the center of each lumen (Fig. 5) but the areolation and papillae of occasional specimens appear to intergrade with those typical of L. luteum (Fig. 4). Flattened papillae of the L. luteum kind are also found in some specimens of L. capituligerum, e.g., the type of Williamsiella tricolor. Sterile plants of Streptotrichum ramicolum Herz. of Bolivia may be confused with L. araucarieti, but differ in the larger, quadrate upper laminal cells, mostly 11–15μ in diameter.

In certain collections, e.g., Bandeira 480 (NY) and Schiffner 1868 (S-PA), both from Brazil, occasional small leaf-like bodies (Fig. 19–20), usually stalked and costate, often contorted, are found along the stem. In many cases, these appear to arise from the same mass of rhizoids as do the propagula. These phylloid s have not been noted in other species of the genus.

PERU. PUNO: Sandia, Erde, 2,600–3,000 m, Weberbauer 794 (H).

BOLIVIA. COCHABAMBA: Uber Comarapa, Bergen, 2,400 m, Herzog 3806 (JE). SANTA CRUZ: Florida de San Mateo, Holz, 1,800 m, Herzog 3638 (JE).


Type: Ecuador, Pichincha, Spruce 30b (NY—holotype; BM—isotype).


Plants large, in loose mats, greenish- to yellowish-brown above, brown below; stems to 12 cm long, flushed in cross section, without tomentum; leaves spreading-recurved, flexuose when dry, spreading-recurved when wet, ovate-lanceolate, with an acute apex, 1.0–1.5 × 3–5 mm, carinate above, with a broad sheathing base, scarcely decurrent, margins recurved to revolute in the lower 1/4, dentate in the upper 1/4; costa ending 4–6 cells below apex, dorsally papillose, reniform in cross section, with 4 fully included guide cells, 1–2 ventral and 1–2 dorsal layers of stereid cells; upper laminal cells subquadrate, 11–15 µm in diameter, lumens rounded-hexagonal in cross section, walls evenly and moderately thickened, bulging, papillae spiculate, branching, arranged in a crown-like ring over the cell lumen, raised on the salient of the bulging cell wall; inner basal cells short- to long-rectangular, 8–13 × 30–55 µm, thinly papillose, walls evenly or laterally thickened.

Propagula obovoid, mostly 25–33 × 45–55 µm, with usually 2 transverse septa, borne on short stalks on the stem.

Dioicus, perigonia lateral, clustered, perichaetial terminal, perichaetial leaves 6–7 mm long. Setae 1–4 per perichaetium, 10–15 mm long, yellowish- to reddish-brown, twisted clockwise above. Urn cylindrical, 0.3–0.4 × 2.0–2.5 mm, erect, yellowish- to reddish-brown; exothecial cells short-rectangular, 20–25 × 30–55 µm; annulus of 4–6 rows of reddish-brown cells. Divisions of peristome teeth linear, 15–20 µm wide at the mouth of the capsule, 440–460 µm long, reddish-orange, spirally lightly striate, with 8–10 articulations. Spores 13–17 µm in diameter, brown, papillose. Operculum conic-rostrate, 0.75–1.0 mm long. Calyptra about 3 mm long.

Habitat: soil.

Distribution: Central America, Andes, Africa, Réunion (Fig. 24 gives known range of both varieties of *L. longicaule*). Frequently collected in mountainous regions, 2,700–4,200 m elevation.

**Leptodontium longicaule** and the closely related *L. syntrichioides* have rather large bulging laminal cells, 12–15 µm in diameter, usually with spiculate branching papillae (Fig. 6, 138) occurring in a crown-like ring over the center of each lumen. These coroniform papillae usually cover little of the lumen. The two species are scarcely distinguishable unless sections of the stem are made. The laminal papillae of *L. longicaule* var. *microruncinatum* are often low, thickened and lens-shaped, and usually cover much of the lumen. Occasional specimens of *L. longicaule* may have laminal cells which are little bulging. These forms may be confused with *L. araucarieti*, but are generally more robust and have “fleshy” leaves with larger upper laminal cells. *Leptodontium latifolium* Broth., from the Eastern Congo, is closely related to *L. longicaule*, but differs in the thin-walled, bulging inner basal cells which are rather sharply demarcated. Perigonia were found in only one specimen of *L. longicaule*, Williams 2848 (nM) of Bolivia.
GUATEMALA. Quetzaltenango: Volcán Santa María, ground, 3,000–4,200 m, Steyermark 34185a (FH).

COSTA RICA. Heredia: Volcán Barba, 2,800 m, Valerio B27 (US); 3,000 m, Valerio 117 (FH, US); ground, 2,800 m, Valerio 27 (FH, US). San José: Cerro de las Vueltas, wet bank, 2,700–3,000 m, Standley & Valerio 43805 (FH, NY, US).


16b. Leptodontium longicaule var. microruncinatum (Dus.) Zander, comb. nov.

Leptodontium microruncinatum Dus., Ark. Bot. 6(8): 10, pl. 5, fig. 1–3. 1906. Type: Chile, Chiloé, Guaitecas, Dusén, 1897 (S-PA—lectotype; FH—isolectotype).


Diffs from the typical variety by the long-lanceolate leaves, to 6 mm, dentate in the upper ½; the upper laminal cells with thickened walls, papillae often obscure or fused into an irregular lens-shaped cap over each lumen (Fig. 7, 149, 155); the capsules larger, to 3.5 mm long, and the spores somewhat larger, 18–22 in diameter.

Habitat: soil, trees, rock.

Distribution: Andes, Juan Fernandez, Tristan da Cunha, Crozet Islands, Réunion, at 1,150–4,000 m elevation.

The var. microruncinatum lacks the “fleshy” appearance of var. longicaule, and has a wider austral distribution. In habit, var. microruncinatum is rather similar to L. luteum.

Zaruma, no collector cited, s.n. (FH). NAPO: Antisana, 4,600 m, Meyer 5560 (JE). Quilindaña, 4,000 m, Meyer 5475 (JE, H); Meyer 5478 (JH).

PERU. Prope Agapata, Leckler, 1852 (s-PA). CUSCO: Quebrada de Quispicanchi, Hacienda Chiraura, 3,250 m, Herrera 2625 (NY). JUNIN: Huancayo, 3,317–4,000 m, Soukup 2715 (FH).
BOLIVIA. COCHABAMBA: Im oberen Coranital, 2,600 m, Herzog 3368 (JE). Nebelwald über Comarapa, Baumästen, 2,600 m, Herzog 4277a (FH, JE). Bergkaum über Comarapa, Knieholz, 2,600 m, Herzog 4277 (JE, M, s-PA). Cerros de Malaga, torfigen Boden, 4,000 m, Herzog 4362 (BM, FH, H, JE, M, s-PA).


JUAN FERNANDEZ ISLANDS. MASAFUERA: Correspondencia, Skottsberg & Skottsberg 105 (BM, FH, s-PA). La Mona, N of the Correspondencia Camp, alpine heath, 1,150–1,200 m, Skottsberg & Skottsberg M188 (FH, s-PA). Los Innocentes, 4,000 ft., Hatcher & Engel 236 (US).

TRISTAN DA CUNHA. In pascuis, frequens, Milne, s.n. (NY). 2,200 ft., Dyer 3589, 3592b (BM). Above Burntwood, Rumex meadow, 1,100 m, Christopherson & Mejland 781 (BM); the Knobs, 1,100 m, Christopherson & Mejland 1661 (BM). Settlement, grassland, 30 m, Christopherson & Mejland 247c (BM). Above Camp, meadow, 50 m, Christopherson & Mejland (BM).

GOUGH ISLAND. Above Nellie’s Hump. Rumex zone, 2,500 ft., Gough Island Scientific Survey T547 (BM).

KENYA. Wandanyi Hill, forest, Amani 8975 (US).

SOUTH AFRICA. TRANSVAAL: Driekop Gorge, Graskop, Wages 1932 (US).

REUNION. Mafate, Rodriguez, 1889 (FH).

CROZET ISLANDS. POSSESSION ISLAND: Doctor’s Bay, Ring & Raknes 24, 50 (BM).

17. **Leptodontium syntrichioides** (C. Müll.) Kindb., Enum. Bryin. Exot. 63. 1888. Fig. 142–146

*Dichostomum syntrichioides* C. Müll., Linnaea 38: 602. 1874. Type: Colombia, Antioquia, Sonson, Wallis, 1872 (NY—epitype).


Plants large, in loose mats, greenish- to yellowish-brown; stems to 10 cm long, not fluted in cross section, without tomentum; leaves spreading-recurved, flexuose to contorted when dry, spreading recurved when wet, ovate- to oblong-lanceolate, with a narrowly obtuse apex, 1.0–2.0 × 4–7 mm, carinate above, with a broad sheathing base, scarcely decurrent, margins broadly recurved to revolute in the lower ±1/3, dentate in the upper 1/4; costa ending 4–8 cells below apex, dorsally papillose, reniform in cross section, with 4 fully included guide cells, 1 ventral and 1–2 dorsal layers of stereid cells; upper laminar cells subquadrate, 13–17 μ in diameter, walls moderately thickened, bulging, papillae spicate, branching, occurring in a crown-like ring over the center of each cell lumen, raised by the bulging salient of the cell wall; inner basal cells short- to long-rectangular, mostly 11–15 × 40–80 μ, lightly papillose, walls evenly to laterally thickened.

Apparently dioecious, perigonia not seen, perichaetial leaves 7–8 mm long. Seta about 20 mm long, yellowish-brown, twisted clockwise above. Urn cylindrical, 0.7–0.8 × 3.4–3.6 mm, erect, reddish-brown; exothecial cells short-rectangular, mostly 22–33 × 55–75 μ; annulus of 4–6 rows of reddish-brown cells. Divisions of peristome teeth linear, 15–22 μ wide at the mouth of the capsule, 420–470 μ long, reddish-orange, spirally ridged, with about 7 articulations. Spores 22–24 μ in diameter, papillose. Operculum and calyptra not seen.

Habitat: soil.
Distribution: Central America, Andes. Rarely collected, mostly from volcanos and páramos, 2,000–3,650 m elevation.

Plants of this species can be distinguished from *L. longicaule* with assurance only by the non-fluted stem (Fig. 80). Other characters which seem to distinguish *L. syntrichioides* from *L. longicaule* are the narrowly obtuse apex (Fig. 142), similar to that of *L. luteum*, the larger sporophyte with peristome teeth deeply ridged, rather than lightly striate, and the spores larger, 22–24 μ in diameter. So few sporophytes of either species were seen, however, that the latter characters are perhaps of little value.

**COSTA RICA.** Cartago: Volcán de Turrialba, S slope, near the Finca del Volcán de Turrialba, 2,000–2,400 m, *Standley 35251a* (US); wet bank, 2,000–2,400 m, *Standley 35277* (FH, US). Ojo Agua, near Cerro La Vuelta, wet open meadow, 3,000 m, *Holm & Ilits 1170a* (FH).


**COLOMBIA.** Antioquia: Sonson in Páramonibus cum Sphagnis, 10,000–12,000 ft., *Wallis, 1872* (NY).

**PERU.** Puno: Sandía, Erde, 2,600–3,000 m, *Weberbauer 805* (H, s-PA).

18. Leptodontium brachyphyllum Broth. & Thér. Bull. Acad. Int. Geogr. Bot. 16 (196): 40. 1906. **Fig. 130–135**


*Plants slender to medium-sized, in loose mats, greenish- to yellowish-brown; stems to 8 cm long, fluted in cross section, without tomentum; leaves erect, twisted when dry, squarrose-recurred when wet, ovate-lanceolate with an acute to broadly acute apex, 0.8–1.0 × 2.5–3.5 mm, carinate above, with a short sheathing base, scarcely decurrent, margins recurved in the lower ½–⅔, dentate in the upper ⅔; costa percurrent or ending 1–3 cells below apex, dorsally papillose, reniform in cross section, with 4 fully included guide cells, 1 ventral and 2 dorsal layers of stereid cells; upper laminal cells subquadrate, 9–11 μ in diameter, lumens rounded-hexagonal in cross section, walls evenly and moderately thickened, bulging, *papillae simple to bifid, usually centrally grouped in a crown-like ring over each lumen*; inner basal cells differentiated in the lower ⅖–⅔ of the sheathing base, short-rectangular, 10–15 × 30–45 μ, scarcely papillose, walls thin to moderately thickened.

Sterile.

Habitat: soil, rock, trees.

Distribution: Mexico, Central America, Andes. Found mostly at high elevations, 3,550–4,000 m, but infrequently as low as 200 m.

This species differs from other species of the section by the mostly ovate-lanceolate leaves, erect when dry, with a short sheathing base. The upper laminal cells are small, usually 9–11 μ in diameter, and the hyaline inner basal cells are restricted to the lower ⅖–⅔ of the sheathing base.


**COLOMBIA.** Cundinamarca: Bogotá, *Apollinaire-Marie*, 1904 (FH, H, NY, s-PA). 1 km
ZANDER: REVISION OF LEPTODONTIUM

N of Guasca, 2,700 m, King C-649 (US). 22 km NE of Bogotá, 2,650 m, King C-645 (MICH, US).


BOLIVIA. COCHABAMBA: Cochabamba, 2,600 m, Julio 222 (FH, US).

19. Leptodontium capituligerum C. Müll., Linn. 1879. Fig. 159-171

Type: Argentina, Siambon, Lorentz, s.n. (NY-lectotype).

Leptodontium arachnoideum C. Müll., Linn. 1879. Type: Argentina, Boliviana Cordillerarum, Lorentz, s.n. (NY-isotype).


Leptodontium calymperoides Ther., Rev. Bryol. Lichénol. 9: 16, fig. 8. 1936. Type: Ecuador, Pichincha, Chemin de Tablahuasi, Benoist 4348 (BM-lectotype); Benoist, 1931 (S-PA-isolectotype).


Plants medium-sized to large, in mats, greenish- to yellowish-brown; stems mostly 2-9 cm long, fluted in cross section, tomentum brown, thick, thin or absent; leaves erect, flexuose to contorted when dry, squarrose-recurved when wet, ovate-lanceolate to lanceolate, with an acute to broadly acute apex, 1.0-1.5 x 3.5-4.0 mm, carinate above, with a sheathing base, decurrent, margins recurved in lower 1/2, dentate in the upper 1/3, the marginal row of cells above thinly papillose, below elongate; costa ending 2-5 cells below apex, dorsally papillose, reniform in cross section, with 4 fully included guide cells 1(--2) ventral and 2-3 dorsal layers of stereid cells; upper laminal cells subquadrate, 11-15 X 11-15 in diameter, lumens rounded-hexagonal in cross section, walls usually little thickened, or if thickened, with angular lumens, usually bulging; laminal papillae sometimes scattered, crowded, low, granular, but usually spiculate, in a crown-like ring over the cell lumens, raised on the salient of the bulging cell wall, often with a high columnar base; inner basal cells rectangular, mostly 11-14 x 50-70μ, scarcely papillose, thin-walled, forming large, sharply demarcated, hyaline fenestrations, sometimes iridescent.

Propagula obovoid, mostly 30-35 x 50-75μ, with mostly 2 transverse septa, borne on short stalks on the stem above.
Dioicus, perigonia lateral, perichaetia terminal, perichaetial leaves 6–7 mm long. Seta 11–14 mm long, brown, twisted clockwise. Urn cylindrical, 0.6–0.7 \( \times 2.4–2.6 \) mm; exothecial cells rectangular, 20–30 \( \times 55–70 \mu \); annulus of 3–4 rows of reddish-brown cells. Divisions of peristome teeth linear, 17–22 \( \mu \) wide at the mouth of the capsule, 600–650 \( \mu \) long, reddish-orange, essentially smooth, with mostly 12–15 articulations, preperistome occasionally present, short, adhering to the 4–5 lowest articulations. Spores 17–22 \( \mu \) in diameter, light brown, papillose. Operculum conic, about 1 mm long. Calyptra not seen.

Habitat: soil.

Distribution: Mexico, Central America, Andes, southern Brazil, Uruguay, Africa. Often collected, 2,600–3,270 m elevation.

*Leptodontium capituligerum* is distinguished from other species of the section by the sharply demarcated fenestrations in the leaves formed by the thin-walled inner basal cells. The papillae are usually coroniform, occurring over each lumen of the upper laminal cells, and often have a thick columnar base (Fig. 162), as in the lectotype of *L. capituligerum*. These raised papillae are reminiscent of those of *Thelia asprella* Sull. (Theliaceae). The type (Fig. 167–171) of *Williamsiella tricolor* differs from most other collections of *L. capituligerum* by the highly iridescent laminal fenestrations and in the low, granular or flake-like upper laminal papillae, similar to those of *L. luteum*. Intergrading specimens have been seen, however; *e.g.*, the isotype of *L. arachnoideum* (Lorentz, *s.n.* (NY)) of Bolivia has low, scattered laminal papillae and non-iridescent fenestrations, while *Grubb & Guymar B101 and B421 (BM)* of Colombia have coroniform laminal papillae and iridescent fenestrations.


**GUATEMALA.** Totonicapán: Chiu Jolom, mountains above Totonicapán, 2,800–3,200 m, damp thicket, Standley 84441 (FH, NY); moist rocky bank, Standley 84432, 84443 (FH, NY, s-PA); 2,500–2,800 m, moist shaded bank, Standley 84466 (FH, MICH, NY, s-PA). Desconsuelo, damp shaded bank, 3,000–3,240 m, Standley 62686 (FH), 62687 (FH, MICH).

**COSTA RICA.** Heredia: Faldas del Volcán de Barba, ground, 1,800 m, Valerio 131b (FH).

**COLOMBIA.** Páramo del Bouqueron, 3,700 m, Troll 2003 (s-PA). Boyacá: Lake San Paulin, humus, 4,100 m, Grubb & Guymar B22 (BM). Above Guican, roadside bank, 3,250 m, Grubb & Guymar B4 (BM). N of Farm Rítacuba, stream at top of ridge, 3,800 m, Grubb & Guymar B101 (BM). Above El Ployon, Valle de San José, damp margin of boulder-strewn boggy patch, Grubb & Guymar B421 (BM). Nevada de Cocaya, Lacia La Coeva, 3,700 m, Cuatrecasas 1639b (US). Cundinamarca: Monserrate, 9,000 ft, King C-736 (US); thicket at summit, 3,210 m, Cuatrecasas 7b (US). Along road to Chochí, 10 km SW of Bogotá, 9,000 ft, King et al. C-794, C-795, C-804, C-805 (US); 14 km SW of Bogotá, 9,200–9,300 ft, King et al. C-815 (MICH, s-PA, US). 2 km SE of Bogotá, 2,800 m, King C-744 (US). San Cristobal, Apollinaire-Marie, 1908 (BM, M).

**ECUADOR.** Cotopaxi: Ground, 3,600 m, Holdridge 1568 (FH). Morona–Santiamago: Gualaquiza, 2,700 m, Allioni, 1910 (s-PA). Pichincha, around bases of shrubs, 11,500 ft, Bell 124 (BM, FH); páramo above Chillogallo, 11,300 ft, Rusby 3111 (BM, CANM, FH, NY). Chemín de Tablauasi, Benoist 4348 (BM); Benoist, 1931 (s-PA).

**BOLIVIA.** Mapiri, 5,000 ft, Rusby 3111 (BM, CANM, FH, NY). Toncoli, Felschlacht,

Herzog 4380 (FH). Cochabamba: Über Incaorral, grosse, liefe Rasem im alpinen Gebüscher, 3,000 m, Herzog, 1908 (M); unter Gestäuch an der Waldgrenze in den “Estradillas,” 3,200 m, Herzog, 1911 (FH). Bergkamm über Comarapa, 2,600 m, Herzog 4304 (H, JE, M, s-PA); Herzog 4304a (JE). Cochabamba, 2,600 m, Julio 271 (FH, US). La Paz: Pelechuco, ground,
Williams 2846 (NY). Sorata, 8,000 ft., Rusby 3108 (H). Pass over Andes, 4,000 m, Rogers Bib (NY). Unduavi, 3,500 m, Buchten 41 (H), 1908 (S-PA); 3,300-3,400 m, Buchten, 1910 (S-PA); 8,000 ft., Rusby 3109 (BM, NY).


Ethiopia. Bachit, feuchtem Boden, 3,600 m, Schimper, 1840 (H).

Species Excluded from Leptodontium by Transfer

Barbula integrifolia (Williams) Zander, comb. nov.


This species is close to *Barbula cebrynum* C. Müll., of central and southern Africa, from which it differs in the more longly excurrent and serrate costa bordered along the awn by non-papillose rhomboidal cells, the thin-walled basal cells of the lamina, and the absence of propagula.

Bryoerythrophyllum recurvifolium (Tayl.) Zander, comb. nov.


Though no fruiting plants have yet been seen, this species may be referred to the genus *Bryoerythrophyllum* by the following combination of gametophytic characters: the large, oblong, apiculate leaves bordered by thick-walled cells above, with sheathing bases filled with large rectangular hyaline cells, and the differentiated layer of enlarged, papillose epidermal cells on the ventral surface of the costa.

Gymnostomum valerianum (Bartr.) Zander, comb. nov.


This species is excluded from *Leptodontium* because of the presence of a central strand in the stem, and the enlarged epidermal cells of the costa. Evidently no fruiting material has yet been collected, but the gametophyte agrees in major respects with *Gymnostomum*, differing from previously reported species by the deeply dentate leaf margins.
SPECIES REFERRED TO OTHER GENERA


Leptodontium arsenii Thér., Smithsonian Misc. Coll. 85(4): 10, fig. 6. 1931. Type: Mexico, Michoacán, Morelia, Arsène 5073 (vs—holotype) ≡ Bryoerythrophyllum ferruginascens (Stirt.) Giac.—Mexican collections of this species represent a rather wide disjunction from its range in Greenland, northern Europe and the Alps, northwestern North America, and northern Asia.


Leptodontium bullockii Thér., Revista Chilena Hist. Nat. 33: 517, pl. 28, fig. 10–18. 1929 ≡ Leptostomum bullockii (Thér.) Thér.

Leptodontium canadense Kindb. in Macoun, Cat. Canad. Pl. 6: 45. 1892. Type: Canada, Ontario, Owen Sound, Macoun, 1890 (Macoun, Canadian Cryptogams 7) (ny—isotype) ≡ Hyophila involuta (Hook.) Jaeg. & Sauerb.

Leptodontium luteolum (Besch.) Par., Ind. Bryol. 731. 1897 ≡ Pleurochaete luteola (Besch.) Thér.


Leptodontium spinosum Williams, The Bryologist 33: 73, fig. 10. 1931 ≡ Zygodon pichinchensis (Tayl.) Mitt.


SPECIES NOT STUDIED

The types of the following New World species of Leptodontium have not been located, and no satisfactory disposition can be made on the basis of the original descriptions:


Leptodontium orthotrichoides (C. Müll.) Par., Ind. Bryol. Suppl. 224. 1900. Type from Colombia.—Malta (1926) said L. orthotrichoides is the same as Zygodon palmarum C. Müll. The isotype of the latter (Argentina Uruguaensis, Lorentz, 1876 (S-PA)), is orthotrichaceous, and is probably a Zygodon, though Malta thought not.

Leptodontium saxicola [C. Müll.] C. Müll. ex Par., Ind. Bryol. Suppl. 225. 1900. Syntypes from Brazil.

Leptodontium stellatum (Brid.) Ren., Rev. Bot. Bull. Mens. 9: 213. 1891. Type from Réunion.—The type of this species is not available, but in any case the species is not in the range of the present treatment as the single specimen reported (Beschereff, 1852) is L. viticulosoides var. exasperatum (Mexico, Orizaba, Müller, s.n. (NY)).


Leptodontium zygodontoides C. Müll., Linnaea 42: 326. 1879. Type from Argentina.

LITERATURE CITED


