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A Revision of the Genus *Crossomitrium* (Musci: Hookeriaceae)

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Abstract. *Crossomitrium* is a genus of neotropical, essentially epiphyllous mosses. The genus consists of six species that are distributed in two sections: section *Crossomitrium* (*C. acuminatum*, *C. patrisiae*, and *C. scabrisetum*) and section *Cormophila* (*C. epiphyllum*, *C. saprophilum*, and *C. sintenisii*). Section *Crossomitrium* is characterized by 1. plants nearly always on leaves or twigs, 2. lateral leaves oblong-acuminate and widest below the middle, 3. leaves when dry that arch from an erect base downward to the substrate and, 4. the presence of specialized brood branches that are closely adnate to the substrate and have tightly imbricate leaves. Section *Cormophila* is characterized by 1. plants growing on rocks and tree trunks as well as on leaves, 2. lateral leaves oval to obovate, acute to apiculate and widest above the middle, 3. leaves when dry flattened to the substrate and, 4. the presence of erect, specialized brood branches that have leaves spreading on all sides. *Crossomitrium* is placed in the Hookeriaceae (sensu Whittemore & Allen, 1989) on the basis of its branched stems, ecostate leaves, straight, unbranched rhizoids that are tightly clustered just posterior to the leaf bases, 2-celled axillary hairs and weakly pigmented stem cortex. Within the Hookeriaceae *Crossomitrium* is considered close to the genus *Lepidopilum* by virtue of 1. its peristome which is hydrocastique and has a high basal membrane, 2. the spinose setae of *C. acuminatum* and *C. scabrisetum*, 3. the irregular subdivision of its stomatal guard cells (including the presence of stomates at the base of raised pustules), 4. leaves doubly serrulate by the projecting ends of contiguous marginal cells, 6. absence of a stem central strand. It differs from *Lepidopilum* in its 1. symmetric, ecostate leaves, 2. calyptra fimbriate by downward projecting, multicellular hairs that arise from the margins of the calyptra, 3. collenchymatous exothecial cells, 4. the presence of brood-bodies on specialized brood branches as well as in clusters just below the junction of the leaf with the stem.

Introduction and generic relationships

Crossomitrium is a genus of neotropic mosses endemic to the New World. It is one of the few mosses that grows consistently, indeed characteristically, on leaves. The oldest species now placed in *Crossomitrium* (*C. patrisiae*) was described by Bridel in 1827. Not surprisingly its generic placement presented difficulties that were compounded by the absence of capsules in the type collection. The genera *Hypnum*, *Pterygophyllum* and *Hypopterygium* were considered by Bridel who tentively placed it in *Hypnum* until the sporophyte became better known. Hampe (1844) transferred Bridel's species to *Hookeria* on the basis of a comparison with

Hookeria swartzii a species now placed in *Lepidopilum*. Hampe considered the fimbriate calyptrae of *H. patrisiae* to be its most notably feature. Montagne (1856) described the second taxon now placed in *Crossomitrium*. Like Hampe, Montagne placed his species in *Hookeria* (*H. splitgerberi*). Montagne was the first to note the vegetative propagulae of *Crossomitrium*, a characteristic feature of the genus.

Mitten (1869) initially viewed the species now placed in *Crossomitrium* as a unit when he transferred Bridel's and Montagne's species into *Lepidopilum* section *Tetrastichium* along with a newly described species, *Lepidopilum epiphyllum* Mitt. This unit of three neotropical species

along with three other newly described neotropical species (*Crossomitrium cruegeri* C. Müll., *C. sellowii* C. Müll., and *C. spruceanum* C. Müll.) constituted the genus *Crossomitrium* which Müller described in 1874. Although section *Tetrastichium* is commonly ascribed to *Crossomitrium* by way of Mitten's 1869 treatment, the section was actually established by Mitten in 1865 as a subdivision of *Lepidopilum* (without clear indication of rank) for the Macaronesian species *Lepidopilum fontanum* (see Allen et al. 1985).

Müller characterized *Crossomitrium* as having 1. a hookeriaceous habit, 2. dimorphic, ecostate leaves in four ranks, 3. a campanulate and fimbriate calyptra, and 4. a peristome that lack cilia, had weakly projecting trabeculae and an exostome composed of a single layer. He aligned *Crossomitrium* with *Lepidopilum*, from which it differed by its single layered peristome. Although the peristome in *Crossomitrium*, as in all other diplolepeidous mosses, is two layered Müller's observation of a peristomal difference between the two genera was correct. The peristomes of both *Crossomitrium* and *Lepidopilum* are of the hydrocastique-type (see Whittemore and Allen 1989), however, in *Crossomitrium* the inner layer of the exostome is often nearly as wide as the outer layer and since both layers are papillose and pale yellowish in color they appear as a single layer. In *Lepidopilum* the exostome has a dark red, narrow inner layer that contrasts sharply with the broad, yellowish outer layer.

For many years the systematic positioning of *Crossomitrium* received little consideration. The genus was placed in the Hookeriaceae by Brotherrus (1907, 1925) and Fleischer (1908) where it continued to be aligned with the genus *Lepidopilum*. In his 1907 treatment, Brotherrus established two sections for *Crossomitrium* Section *Phyllophila* (= sec. *Crossomitrium*) for epiphyllous plants with dimorphic branches and oblong, acuminate leaves that shrivel when dry and section *Cormophila* for corticolous plants with monomorphic branches and oval, acute to apiculate leaves that are unchanged when dry.

Conflicting views on the relationships of *Crossomitrium* began to appear in 1971 when Miller published an overview of the Hookeriaceae in which he placed *Crossomitrium* (because of its ecostate condition) in subfamily Hookerioideae along with *Hookeria*, *Tetrastichium*, *Schimperobryum* and *Calyptrochaeta*. Miller separated *Lepidopilum* (placing it in subfamily Hookeriopsidoideae) from *Crossomitrium* because of its long double costae.

In 1974, Crosby offered a new classification of the Hookeriales that established broad lines based on peristomal form and secondary divisions based on gametophytic characters. *Crossomitrium*, with a papillose exostome, was transferred to the Daltoniaceae and placed in an informal Actinodontioid group that consisted of *Actinodontium*, *Lepidopilum*, *Stenodesmus*, *Crossomitrium* and (with some reservation) *Iso-drepanium*. The Actinodontioid group consisted of 2-0-costate mosses with a lax areolation and variously complanate habit. Crosby's positioning of *Crossomitrium* was followed by Walther (1983) and Vitt (1984).

Buck (1987, 1988), in a rearrangement of the Hookeriales considered variation in exostome form within the order to be an unreliable indicator of family relationships. He divided the order into five families according to gametophytic features. In Buck's treatment *Crossomitrium* was placed along with *Lepidopilum* in the Callicostaceae on the basis of its ecostate leaves, two-celled axillary hairs, mitrate calyptra and the absence of a stem central strand.

Finally, Whittemore and Allen (1989) in their classification of the Hookeriales recognized only two families: Hookeriaceae and Daltoniaceae. Whittemore and Allen's classification returned *Crossomitrium* to the Hookeriaceae a family represented by plants with branched stems, bicostate to ecostate leaves, rhizoids straight, unbranched and tightly clustered just posterior to the leaf bases, axillary hairs 2- (rarely 3-) celled and the stem cortex weakly pigmented. Neither the classification of Buck nor of Whittemore and Allen considered the subfamilial or generic relationships of *Crossomitrium*.

There is little doubt that the genus *Crossomitrium* has been correctly placed in the order Hookeriales. This placement is supported by the presence of a character state group that includes the following: 1. a fringed, mitrate calyptra; 2. papillose exostome teeth; 3. stomatal guide cells that are secondarily divided; 4. absolutely ecostate leaves; 5. an absence of differentiated alar cells; 6. leaf cell that are laxly developed, particularly the median cells at the extreme base of the leaf; 7. two-celled axillary hairs; 8. stems that lack both paraphyllia and a central strand.

A positioning of *Crossomitrium* in the Daltoniaceae (sensu Whittmore and Allen 1989) is supported by the presence of three characters: 1. hydrocastique-type of peristome; 2. fringed calyptra; and 3. collenchymatous exothelial cells. Since peristome form has generally been considered a conservative and phylogenetically stable character, this is the most important character supporting a placement of *Crossomitrium* in the Daltoniaceae. However, as discussed by Whittmore and Allen (1989) the functional differences between the xerocastique- and hydrocastique-types of peristome are likely to be strong enough to provide the necessary evolutionary force for the multiple derivation of the hydrocastique-type of peristome. This view is supported by the presence of the two types of peristomes within a number of other pleurocarpous families. As regards the calyptra character, a fringed calyptra is a feature that occurs sporadically but widely in the mosses. Its presence in a number of clearly unrelated mosses indicates that the character has been independently derived a number of times and for this reason the character can not be used as a primary indicator of relationships. Likewise, seemingly identical types of collenchymatous exothelial cells are encountered in both the Daltoniaceae and the Hookeriaceae, which appears to indicate that the character is basal to the Hookeriaceae-Daltoniaceae group.

A placement of the genus *Crossomitrium* in the Hookeriaceae is supported by the presence of four characters: 1. branched stems; 2. ecostate leaves; 3. straight, unbranched rhizoids that are tightly

clustered just posterior to the leaf bases; 3. 2-celled axillary hairs; and 4. weakly pigmented stem cortex. These characters, when taken together, form a basic complex that is here interpreted as evidence for the placement of the genus in the Hookeriaceae.

Within the Hookeriaceae the relationships of *Crossomitrium* are more difficult to evaluate because many of its character states have reticulate distributional patterns within the family. There are, however, two characters that appear important in a consideration of the relationships of *Crossomitrium*, these are its hydrocastique-type of peristome and its ecostate leaves.

Although the hydrocastique-type peristome is not used here as an indicator of family relationships, as noted by Whittmore and Allen (1989), it may be important in determining infra-familial relationships. Within the Hookeriaceae this peristome type, as exemplified by that of *Lepidopilum*, has exostome teeth with narrow, strongly colored inner lamellae and broad flattened endostome segments that arise from a high basal membrane. The hydrocastique-type of peristome in *Crossomitrium* is variably developed. It differs from that of *Lepidopilum* in having both exostome layers pale-yellow to whitish and in having narrow, keeled endostomial processes. It does, however, share some features with the hydrocastique-type peristome of *Lepidopilum*. Generally the width of the inner layer of the exostome is nearly as broad as the outer layer, but it can be quite narrow in some collections of *C. patrisiae* (see e.g. Churchill et al 13892 in NY, MO). In addition, the basal membrane, which is low in *C. patrisiae* is relatively high in *C. epiphyllum* (see e.g. Buck 10562 in NY).

There are a number of other shared features supporting the peristomal evidence that *Crossomitrium* and *Lepidopilum* are close. For example, both *C. acuminatum* Bartr. and *C. scabrisetum* Bartr. have spinose setae. Both genera have irregularly subdivided stomatal guard cells (including the presence of stomates at the base of raised pustules). The leaves in some species of *Lepidopilum* are doubly serrulate by the projecting

ends of contiguous marginal cells: a generic character in *Crossomitrium*.

Conversely, *Crossomitrium* differs from *Lepidopilum* in a number of features. The leaves of *Lepidopilum* are asymmetric and although the costae may be very short they are always present. In *Crossomitrium* the leaves are symmetric and absolutely ecostate. In *Crossomitrium* the calyptra is fimbriate by downward projecting, multicellular hairs that arise from the margins of the calyptra. In *Lepidopilum* the calyptra may be hairy but the hairs arise from the surface of calyptra never from basal margin as in *Crossomitrium*. Indeed, the fimbriate calyptra of *Crossomitrium* is not found in any other genus of the Hookeriaceae (sensu Whittemore and Allen). It is however found in *Calypstrochaeta*, *Crosbya*, *Daltonia*, *Distichophyllum* and *Leskeodon*. In addition, the exothelial cells of *Crossomitrium* are variously collenchymatous while those of *Lepidopilum* are evenly thickened. Finally, the marginal leaf cells of *Crossomitrium* have from 1- several papillae per cell. In *Lepidopilum* the leaf cells are smooth.

The ecostate leaves of *Crossomitrium* point to a possible relationship with two other subgroups of the Hookeriaceae. The subgroup of genera centered on *Rhynchostegiopsis* (*Leucomium*, *Rhynchostegiopsis*, *Sauloma* and *Tetrastichium*) are ecostate, have lax leaf cells, serrate leaves (in *Rhynchostegiopsis* and *Tetrastichium*) and collechymatous exothelial cells (*Leucomium* and *Tetrastichium*). However, the exostome in this subgroup is striated with a well developed furrow and the calyptra is cucullate. Although the importance of the cucullate calyptra in this subgroup is lessened by the calyptra of *Sauloma* which technically is mitriate (see Allen 1987) the peristome and calyptra characters of this subgroup point to a more distant relationship with *Crossomitrium*.

The second subgroup of Hookeriaceae distinguished by the lack or very weak expression of a costa is the subgroup centered on *Hookeria*. This subgroup differs from *Crossomitrium* in its xerocastique, striated exostome, the presence of a weakly developed central strand in the stem, and a calyptra that in cross-section usually has 1

or more outer layers of enlarged, thin-walled cells.

Clearly, the alignment of *Crossomitrium* within the Hookeriaceae depends upon which characters are emphasized. In this treatment, the hydrocastique-type of peristome is considered of primary importance as an indicator of generic relationships. Thus, *Crossomitrium* is maintained within the Hookeriaceae near to *Lepidopilum*. At the beginning of this study there were 26 validly published species of *Crossomitrium*. The types of four of these species were unavailable for study. Of the remaining 22 species only six species are presently recognized.

Morphology

Stems

The stems of *Crossomitrium* are reddish-brown, (occasionally yellowish-green), creeping and irregularly pinnately branched. They are generally closely adnate to the substrate. The epidermal cells in surface view are elongate-rectangular and firm-walled. The stems have 1-2 rows of small, thick-walled epidermal cells but otherwise they lack internal differentiation. The cortical cells in cross-section are largest in the center of the stem. Paraphyllia and pseudoparaphyllia are absent, although at times the primordial leaves on branch buds may be mistaken for foliose pseudoparaphyllia.

Rhizoids

Rhizoids arise from cell initials that are grouped into discrete, roughly circular areas located on the stems immediately below the junction of the leaf and stem. Rhizoids may also arise from basal leaf cells that are contiguous to the stem rhizoidal initials. The stem rhizoidal initials appear to be restricted to the ventral region of the stem. The rhizoids are reddish-brown, have oblique end walls, and are unbranched until they make contact with the substrate. At the points of contact with the substrate the rhizoids may have numerous short branches. Frequently the rhizoids from one zone of rhizoidal initials, fuse along their distal lengths. Rhizoids fused in this manner have a

pad-like form that appears to aid in attaching the plants to the substrate.

Alternatively, the rhizoidal initials may give rise to a filament made up of short, quadrate cells with right-angled cross walls that bear brood-bodies in terminal groups of twos or threes. The developmental control over the fate of a rhizoidal initial appears to be weak as judged from the observation that some of the brood-body filaments have extremely long cells with oblique angled cross-walls. These long celled brood-body filaments appear to have begun their development as rhizoids, and only later became brood-body filaments. In some species the brood-body filaments appear to originate from the dorsal surface of the stem. A careful examination of the stems in these cases reveals that they have twisted 180 degrees thereby placing the morphologically ventral surface upwards.

Axillary Hairs

The axillary hairs of *Crossomitrium* are two-celled, or rarely three-celled. The basal cell is short, brownish and quadrate. The terminal cell is large, hyaline and elongate-oblong. All three-celled axillary hairs observed in this study consisted of two basal cells and a terminal cell.

Leaves

The leaves of *Crossomitrium* species have two basic aspects. They may be strongly flattened to the substrate or they may be erect at base then strongly curved downward toward the substrate in the upper part of the leaf. This leaf aspect is, in a general sense, a sectional character in *Crossomitrium*. However, *Crossomitrium* species are variable in their expression of this feature and nearly every species has some collections that are intermediate in expression.

Both within and between *Crossomitrium* species the leaves are variously dimorphic. The dorsal leaves of all species tend to broad, i.e. ovate to orbicular, while the lateral leaves vary from orbicular to lanceolate-oblong. Leaf shape appears to be a taxonomically useful characters only for the lateral leaves. A distinctive feature,

commonly encountered in section *Crossomitrium*, is found in the apical one-third of the leaves. In this region the leaves may be keeled or conduplicate. This feature appears to be positively correlated with a narrow leaf shape since it becomes weakly developed or absent in broad-leaved collections.

Leaf margins may vary from plane to strongly and narrowly recurved. Leaves with both plane and narrowly recurved margins can be found on single stems. The leaves in *Crossomitrium* are always serrate by the projecting end walls of the marginal cells. Characteristically, the margins are doubly serrate by the projections of the end walls of contiguous cells. The leaves are absolutely ecostate.

Leaf cells

The upper and median leaf cells in *Crossomitrium* are linear-flexuous to vermicular and firm- to lax-walled. In contrast, the extreme basal leaf cells at the middle of the leaf are enlarged, thin-walled to bulging and rectangular to pentagonal in shape. The cells in the alar regions are shorter than the median leaf cells and curved at the insertions, but otherwise they are identical to the median leaf cells.

The leaf cells in *Crossomitrium* have a distinctive ornamentation that represents a generic character. Nearly all the leaf cells are smooth, however, the marginal row of cells are papillose, with one to several papillae over the lumens on the outside margins of the cells. Some leaves may appear to be entirely smooth-celled, but, on careful examination at least some marginal papillae will be found.

Asexual reproduction

All species of *Crossomitrium* reproduce asexually by means of brood-bodies. Each brood-body is part of a complex consisting of a rhizoidal initial, a stalk, and two to many brood-bodies. The stalk is uniseriate and multicellular; generally the cells are short, quadrate and have right angled cross-walls. The number of cells in each stalk may vary widely. The brood-bodies are also uniseriate

and multicellular. They are smooth, reddish-brown, and made up of short, quadrate cells with end walls at right angles to the lateral walls. In form the brood-bodies are identical to the fringe hairs of the calyptra. Unless the collection is small or scappy, brood-bodies will be found in either of two locations: on the stem immediately abaxially to the ventral leaves or on specialized brood branches.

In section *Crossomitrium* the brood branches are closely adnate to the substrate and have tightly imbricate, broad, oval leaves. The brood branches of section *Cormophila* are erect to inclined (but never closely adnate to the substrate) and they have wide spreading, generally oval leaves.

Setae

Sporophytes are known from only four of the six species of *Crossomitrium*. In those four species the setae are red to reddish brown. The setae may be smooth in the lower 3/4 and papillose to scabrose in the upper 1/4 (*C. patrisiae* and *C. epiphyllum*) or densely scabrose throughout (*C. scabrisetum* and *C. acuminatum*). In length the setae can be phenomenally variable: even within a single collection. Seta length within the genus ranges from 4 mm to 12 mm. Although relative seta length has been used to separate some species, the character does not appear to be taxonomically reliable in this genus.

Capsules and opercula

Capsules in *Crossomitrium* are borne suberect to inclined, and are ovoid to elliptic in shape. The capsule neck is moderately differentiated. Some of the species of *Crossomitrium* have raised pustules at the base of the capsule. Immersed stomata can sometimes be found within the pustules. The guard cells of the stomata are secondarily subdivided, a feature also found in a number of other Hookeriaceae genera. The capsule exothecial cells are shortly rectangular and may vary from strongly to weakly collenchymatous. The opercula are conic-rostrate. They separate from the capsule mouth with the aid of a several layered annulus of thin-walled, quadrate cells. The annulus is non-revoluable

and annular cell fragments may remain attached to either the capsule mouth or the operculum after dehiscence.

Peristome

The peristome of *Crossomitrium* is diplolepidous. The exostome teeth are typically whitish-yellow on both surfaces (occasionally the inner surface is reddish-brown), and the trabeculae are weakly projecting. The lamellae on both surfaces are papillose. The outer layer of the exostome teeth is wider than the inner layer. Usually the inner layer is nearly as wide as the outer layer, however it may also be only one-third the width of the outer layer. The exostome teeth are of the hydrocastique type.

The endostome in *Crossomitrium* is yellow to hyaline. The basal membrane may be low or high and the well formed processes commonly extend just beyond the exostome teeth. The processes are moderately keeled and not noticeably perforate (although the inner layer of the process is deposited as a ring rather than a plate). Cilia are absent, but the inner layer of the basal membrane has cell columns in the region (i.e. between the processes) from which the cilia in mosses with perfect endostomes arise.

Calyptrae

The calyptrae of *Crossomitrium* are mitrate, reddish-brown, smooth to roughened above and fimbriate at the base. The hairs at the base of the calyptrae arise from marginal cells, they are reddish brown, uniseriate and multicellular. The cells are short and quadrate, the end walls are at right angles to the lateral walls. This type of fimbriate calyptra is unique in the Hookeriaceae (sensu Whittimore and Allen 1989). In those genera of the Hookeriaceae with hairy calyptrae the hairs arise from the sides of the calyptrae. As noted earlier, a fimbriate calyptra is a common feature of the Daltoniaceae (where the morphologically identical character state exists) as well as a number of other unrelated mosses (i.e. *Campylopus* and related genera).

Distribution

Crossomitrium is endemic to the New World. It is widely distributed within (and nearly restricted to) the neotropics. As is typical for mosses with this type of distribution the genus occurs outside the neotropics in southeastern Brazil. In the New World it is found throughout Central America (from southern Mexico to Panama), on all the major islands of the Caribbean (including Trinidad and Tobago and the Pacific islands of Cocos and the Galapagos), and in South America west of the Andes from Colombia to Bolivia and east of the Andes from Venezuela through Guyana, Suriname, French Guiana and the Amazonian regions of Brazil, Peru and Bolivia to the Rio de Janeiro region of Brazil.

Taxonomic Treatment

Crossomitrium C. Müll., *Linnaea* 38: 611. 1874. Type species *C. patrisiae* (Brid.) C. Müll. (designated here)

Plants procumbent, forming dense or thin, glossy, yellowish-green (occasionally reddish-yellow) mats. Stems creeping, tightly adherent to the substrate; irregularly pinnately branched; epidermal cells elongate, in cross-section with an outer layer of small, firm-walled cells, a cortex of thin-walled, hyaline cells (the largest cortical cells occupying the center of the stem), central strand absent; epidermal cells elongate-rectangular (except for discoid areas of quadrate cells just below the junction of the leaf and stem). Rhizoids reddish-brown, smooth, restricted to the substrate side of the stem arising from discoid areas of epidermal cells or from contiguous basal leaf cells. Pseudoparaphyllia absent, paraphyllia absent. Leaves in four rows, variously dimorphic, densely foliate, typically complanate; apices frequently carinate, margins plane or recurved, biserrate or bidentate by projecting end walls; cells smooth except for the marginal cells that have 1-4 low papillae per cell over the lumen, upper and median cells linear to elongate-rhomboidal, basal median cells enlarged, hexagonal to pentagonal; alar cells not differentiated, absolutely ecostate. Axillary hairs two-celled: basal cell quadrate, red-brown, terminal cell elongate-oblong, hyaline. Reproducing

asexually by means of elongate, uniseriate, multicellular brood-bodies originating from rhizoidal initials either at the base of the leaves or on specialized brood branches.

Dioicous. Perigonia and perichaetia numerous along branches and stems. Setae elongate, red to red-brown, smooth below and papillose to scabrose above or scabrose throughout; capsules suberect to inclined, ovoid to elliptic, stomata present in the neck, stomatal guard cells irregularly secondarily divided, exothecial cells short-rectangular, collenchymatous; annuli nonrevolvable, consisting of 3-4 layers of quadrate, thin-walled cells that cling to the operculum or capsule mouth after dehiscence; opercula shortly conic-rostrate; peristome diplolepidous and double, exostome teeth 16, yellowish-white, hydrocastique, dorsal and ventral lamellae papillose, dorsal and ventral trabeculae weakly projecting; endostome longer than the exostome, white to yellowish, papillose, basal membrane high or low, processes keeled, cilia absent. Spores spherical, lightly papillose. Calyptrae mitrate, reddish-brown and smooth to roughened above, fimbriate at base by uniseriate, multicellular hairs.

Etymology. The combination *crosso-* (Greek 'krossos' a fringe or tassel) and *-mitrium* (Greek 'mitra' cap) refers to the characteristic fringed calyptra of the genus.

Distribution. CENTRAL AMERICA: Mexico, Belize, Guatemala, Honduras, Nicaragua, Costa Rica (including Cocos Island) and Panama. CARIBBEAN: Cuba, Jamaica, Haiti, Dominican Republic, Puerto Rico, Saba, Montserrat, Guadeloupe, Dominica, Martinique, Grenada, Tobago and Trinidad. SOUTH AMERICA: Colombia, Ecuador, (including the Galapagos Islands) Peru, Bolivia, Venezuela, Guyana, Surinam, French Guiana and Brazil.

Brotherus (1907) established two sections of *Crossomitrium*: section *Phyllophila* (= sect. *Crossomitrium*) and section *Cormophila*. These sections appear to represent natural groupings. They are maintained in this study.

The species of section *Crossomitrium* are commonly epiphyllous. They have narrow leaves with nearly parallel sides that are erect at base when dry. The leaves are widest below the middle. Species of this section have specialized brood branches that are tightly adherent to the substrate and have broad, rigidly imbricate leaves.

Section *Cormophila* consists of species that more commonly are found on rocks or tree trunks. Occasionally species of this section may be epiphyllous. These species have broad leaves with convex sides that are flattened to the substrate when dry. The leaves are widest above the middle. Species of this section have erect specialized brood branches that have leaves spreading on all sides.

Five of the six *Crossomitrium* species fall cleanly within these two sectional groups. The sixth species (*C. sintenisii*) is difficult to place because it lacks specialized brood branches and is intermediate in a number of sectional features. This species is treated in section *Cormophila* on the basis of its broad leaves that are flattened to the substrate when dry. Some collections of *C. sintenisii*, however, grade closely into the jamaicense-expression of *C. patrisiae*, and in fact on the island of Hispaniola the two are virtually unseparable.

The species of *Crossomitrium* represent a very close, tightly marked group. For that the reason the generic description is lengthy and includes statements on many single state characters. All single state characters given in the generic description are found in every species of the genus.

Key to the species of Crossomitrium

- 1. Setae spinose to scabrose throughout 1
- 1. Setae smooth in lower 2/3 and papillose to scabrose in upper 1/3 OR setae absent 3
 - 2. Leaf margins dentate and strongly recurved throughout *C. acuminatum*

- 2. Leaf margins serrate to serrulate and plane to weakly recurved at the middle *C. scabrisetum*

- 3. Lateral leaves less than 1.2 mm long 4

- 3. Lateral leaves greater than 1.3 mm long, commonly longer than 1.5 mm long 6

- 4. Lateral leaves lanceolate-oblong, erect at base then arching downward to the substrate; brood-bodies on specialized brood branches that tightly adhere to the substrate and have closely spaced and rigidly overlapping leaves *C. patrisiae*

- 4. Lateral leaves oval-acute, flattened to substrate; brood bodies on erect specialized brood branches, brood leaves loosely spreading on all sides 5

- 5. Brood bodies clustered in terminal groups at apex of specialized brood branches *C. saphophilum*

- 5. Brood-bodies borne on all sides and along the length of specialized brood branches *C. epiphyllum*

- 6. Leaf margins dentate and strongly recurved throughout *C. acuminatum*

- 6. Leaf margins serrate, plane or weakly recurved 7

- 7. Lateral leaves widely spaced on the stems not overlapping, with parallel sides, widest below the middle; commonly with specialized brood branches that tightly adhere to the substrate and have closely spaced, rigidly overlapping leaves *C. patrisae*
(*C. scabrisetum* without sporophytes keys here)

- 7. Lateral leaves closely spaced on the stems and overlapping at base with the leaves above and below, with convex sides, widest above the middle; specialized brood branches absent, brood-

bodies borne in dense reddish-brown clusters on the stem abaxially to the leaves *C. sintenisii*
(see also jamaicense-expression of *C. patrisiae*)

Section *Crossomitrium*

Crossomitrium section *Phyllophila* Broth., Nat. Pflanzenfam. 1(3):957. 1907.

Plants mostly epiphyllous, leaves when dry erect at base; lateral leaves with nearly parallel sides and widest below the middle. Specialized brood branches tightly adherent to the substrate with broad, closely imbricate leaves.

I. Crossomitrium acuminatum Bartr., Rev. Bryol. Lichénol. 22: 157. 1953. Types. Panama, Western arm of Quebrada, Salamanca, Canal Zone, Dodge, Steyermark & Allen Dec. 16 1934. (FH holotype; MO lectotype). Panama, Canal Zone, Pelucca station, Rio Boqueron, Chickering, July 26 1950 (MICH paratype).

Plants slender to medium sized; stems up to 4 cm long, 1-3 mm wide, specialized brood-branches adnate to the substrate, with closely imbricate leaves. Lateral leaves erect at base and arching downward toward the substrate above, frequently overlapping at base; oblong to oblong-lanceolate, 1.0-2.0 mm long, 0.3-0.5 mm wide, with nearly parallel sides, short acuminate to acute, often carinate at apex; dorsal leaves shorter and broader, sub-ovate, erected spreading when dry. Leaves on specialized brood-branches orbicular, apiculate, cordate at base, closely imbricate giving the branches a julaceous appearance. Leaf margins tightly and narrowly recurved for most of the leaf length, sharply and coarsely doubly dentate by projecting cell end walls, the teeth frequently recurved. Upper and median leaf cells linear to vermicular, 60-160 µm long, 3-5 µm wide, firm-walled; median cells at the extreme base 30-60 µm long 12-35 µm wide, Setae 5 mm long, densely scabrose to tuberclose throughout. Capsules inclined, ovoid to elliptic, 1.0 mm long the neck

moderately developed; stomata poorly differentiated at the base of the capsule. Opercula 0.7 mm long. Exostome teeth 0.3 mm long, outer plates quadrate to shortly rectangular, papillose, trabeculae weakly projecting; inner plates nearly are wide as the outer but one-half as high, lightly papillose, trabecular moderately projecting. Endostome 0.35 mm long, basal membrane low, 0.05 mm high, segments densely spiculose. Spores 10-13 µm. Calyptra not seen.

Etymology. The name *acuminatum* refers to the shape of the lateral leaves.

Distribution. Central and South America: Nicaragua, Panama and Colombia. Fig. 22.

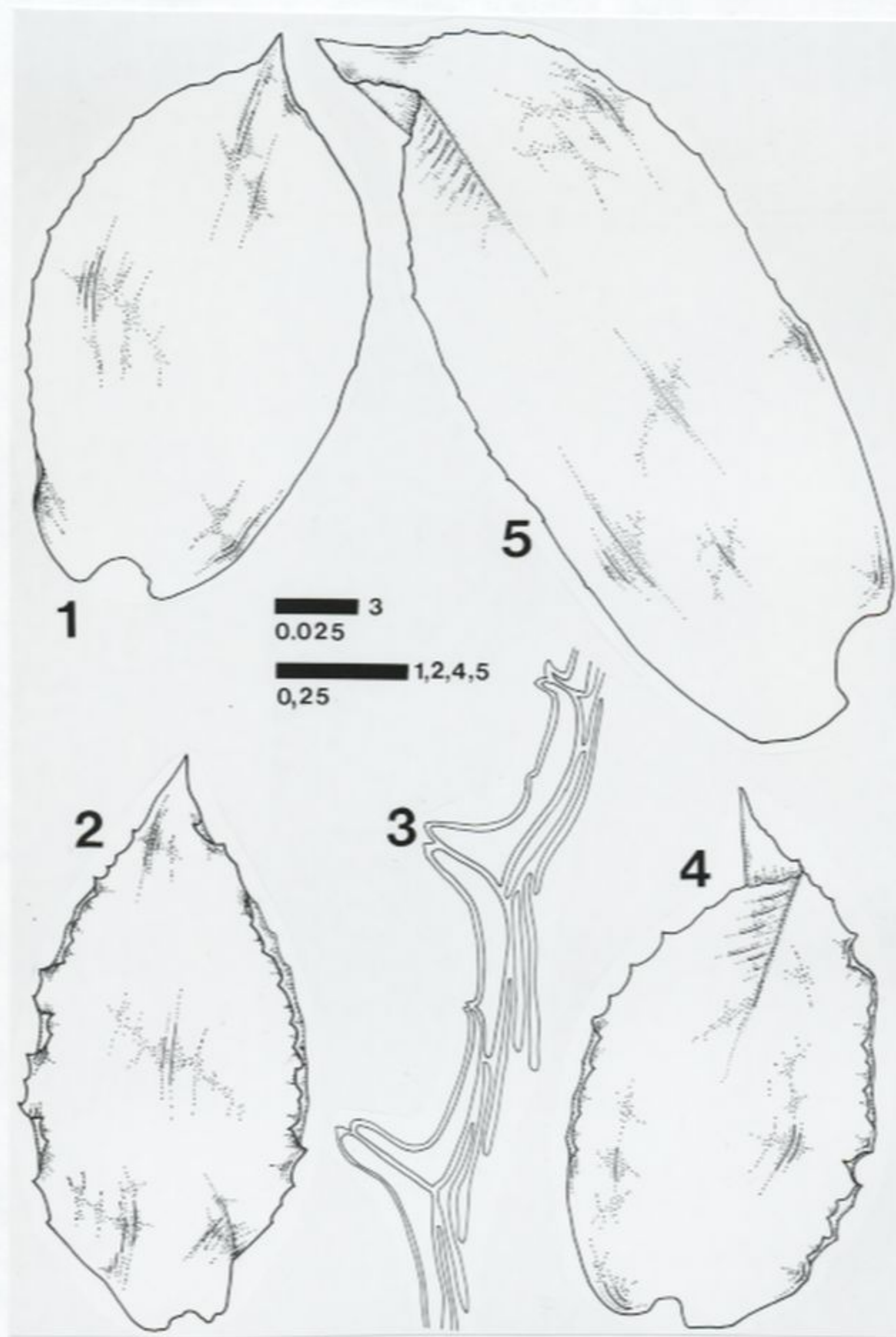
Illustrations. Welch (1974, Figs 73-78); Figs. 2-4.

Ecology. Epiphyllous; sea level-1650 m.

Specimens examined.

NICARAGUA. Zelaya: along Cano Majagua, 13°45'N; 85°00-01'W, *Stevens 6945* (MO). **PANAMA.** Bocas Del Toro: vicinity of Fortuna Dam, 8°55'N; 82°08'W, *Allen 5582* (CANM, MO, NY); Panama: Quebrada Salamanca, *Dodge et al. 17018*, (FH, MO), Rio Boqueron, Pelucca Station, Chickering (MICH); Veraguas: 5.4 km NW of Santa Fe, 8°30'N; 81°05'W, *Crosby 10163* (MO, PMA), along Rio Caloveborita, near Santa Fe, *Nee & Mori 14315, 14316* (MO). **COLOMBIA.** Choco: Municipio de Novita, Cerro Torra, Rio Surama, *Forero et al. 3112* (MO), El Valle, *Killip 11478* (NY); Valle: Rio Calima, *Cuatrecasas 16864b, 21079b, 21174b, 26039b, 26082b* (all US), confluencia del rio Pichindecito con el Pichinde, *Cuatrecasas 18753b* (US).

Plants of *C. acuminatum* have acuminate, lanceolate-oblong lateral leaves. Characteristically the leaves when dry are erect at base and arch downward to the substrate in the upper part. The *patrisiae*-type of specialized brood-branch is commonly found in *C. acuminatum*. From *C. patrisiae* this species differs by its leaf margins that are sharply denticulate and tightly, narrowly recurved nearly the length of the leaf. The marginal teeth on the leaves of *C. patrisiae* can be sharply serrate, however, they are never developed to the degree seen in *C. acuminatum*. When sporophytes



Figures 1 & 5. Leaves of *Crossomitrium scabrisetum*. Figures 2-4. *Crossomitrium acuminatum*.
Figures 2 & 4. Leaves. Figure 3. Leaf margin.

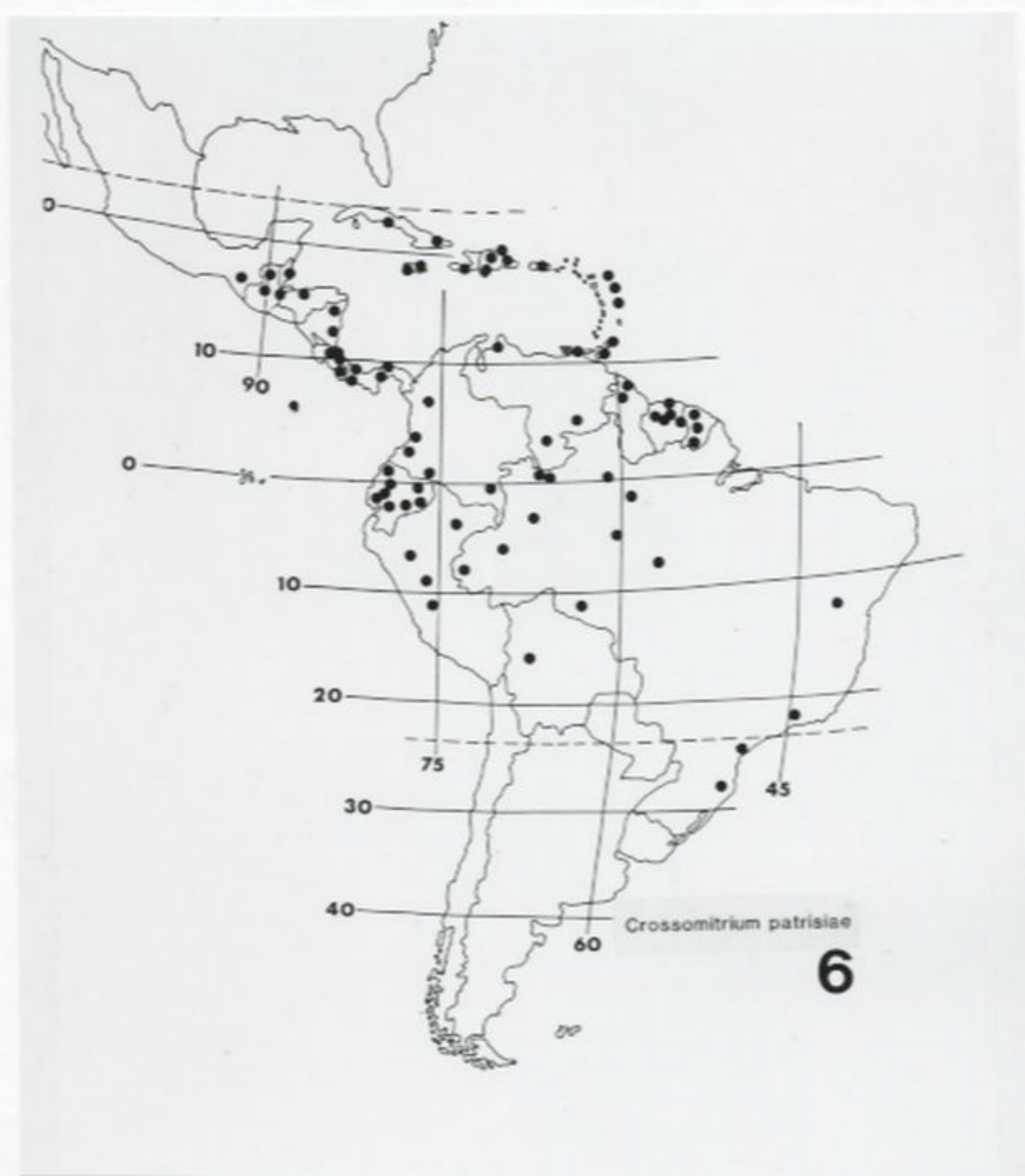


Figure 6. Distribution of *Crossomitrium patrisiae*.

ge et al. 17018, (FH, MO), Rio Boqueron, Pelucca Station, Chickering (MICH); Veraguas: 5.4 km NW of Santa Fe, 8°30'N; 81°05'W, Crosby 10163 (MO, PMA), along Rio Caloveborita, near Santa Fe, Nee & Mori 14315, 14316 (MO). COLOMBIA. Choco: Municipio de Novita, Cerro Torra, Rio Surama, Forero et al. 3112 (MO), El Valle,

Killip 11478 (NY); Valle: Rio Calima, Cuatrecasas 16864b, 21079b, 21174b, 26039b, 26082b (all US), confluencia del rio Pichindecito con el Pichinde, Cuatrecasas 18753b (US).

Plants of *C. acuminatum* have acuminate, lan-

from *C. sintenisii* in its smaller size, narrower leaves, and its denticulate, strongly recurved leaf margins. *Crossomitrium epiphyllum* and *C. saprophyllum* are similar to *C. acuminatum* in size their erect brood branches and moderately serrate, broadly oval to orbiculate leaves make confusion with *C. acuminatum* unlikely.

2. *Crossomitrium patrisiae* (Brid.) C. Müll., Linnaea 38: 612. 1874. *Hypnum patrisiae* Brid., Bryol. Univ. 2: 539. 1827. *Hookeria patrisiae* (Brid.) Hampe, Icon. Musc. 1. 1844. *Lepidopilum patrisiae* (Brid.) Mitt., J. Linn. Soc., Bot., 12: 369. 1869. Type. French Guiana, Cayenne in foliis Patrisiae periferiae, *Fée s.n.* (B holotype).

Hookeria splitgerberi Mont., Syll. 14. 1856. *Lepidopilum splitgerberi* (Mont.) Mitt., J. Linn. Soc., Bot. 12: 370. 1869. *Crossomitrium splitgerberi* (Mont.) C. Müll., Linnaea 38: 613. Type. Surinam, in folio coriaceo ad Surinam, *Splitgerber 1205* (PC holotype).

Crossomitrium cruegeri C. Müll., Linnaea 38: 611. 1874. Type. Trinidad, monte Tamanaco, *Crueger s.n.* (BM lectotype designated here; NY isotype).

Crossomitrium sellowii C. Müll., Linnaea 38: 612. 1874. Type. Brazil, in foliis coriaceis adnatum, *Sellow (sic.) s.n.* (BM lectotype designated here; NY, S isotypes).

Crossomitrium spruceanum C. Müll., Linnaea 38: 613. 1874. Type. Ecuador, Andes Quitenses, ad flumen Bombonasa, 1200 ft., *Spruce 790*. (NY lectotype designated here; BM, F, FH, G, H, MICH, S, US isolectotypes).

Lepidopilum subepiphyllum Besch., Ann. Sci. Nat. Bot. ser 6, 3: 228. 1876. *Crossomitrium subepiphyllum* (Besch.) Jaeg., Ber. Tätigk. St. Gallischen Naturwiss. Ges. 1875-76: 337. 1877. Type. Guadeloupe, sur les feuilles tombées à terre, *L'Herminier* (BM holotype; H isotype).

Lepidopilum herminieri Schimp. ex Besch., Ann. Sci. Nat. Bot. ser. 6, 3: 228. 1876. *Crossomitrium*

herminieri (Schimp. ex Besch.) Jaeg., Ber. Tätigk. St. Gallischen Naturwiss. Ges. 1875-76: 337. 1877. Type. Guadeloupe, *L'Herminier* (BM holotype; G, NY isotypes).

Crossomitrium heterodontium Ren. & Card., Bull. Soc. Roy. Bot. Belgique 32: 195. 1894. Type. Costa Rica, Bois du Rio Tuis, *Tonduz s.n.* [Pittier 5664] (PC holotype; NY isotype).

Crossomitrium ramulicola C. Müll., Malpighia 10: 514. 1896. Type. Guyana, prope Georgetown ad cataractas (Marshall Falls) fluvii Mazaruni, *Quelch 1276* (BM lectotype designated here; NY isolectotype).

Crossomitrium radulaeforme C. Müll., Malpighia 10: 514. 1896. Type. Guyana, prope Georgetown ad cataractas (Marshall Falls) fluvii Mazaruni, *Quelch 1274* (BM lectotype designated here; NY isolectotype).

Hookeria splitgerberi Mont. ex Par., Ind. Bryol. 585. 1896. err. pro *H. splitgerberi* Mont.

Crossomitrium jamaicense C. Müll., Hedwigia 37: 245. 1898. Type. Jamaica, in montis humidis, *Hansen s.n.* (FH lectotype designated here; C, H, NY, S isolectotypes).

Crossomitrium ulei C. Müll., Hedwigia 37: 245. 1898. Types. Brazil, Santa Catharina, Nova Venezia, ad folia fruticum in silva, *Ule 156* (BM lectotype designated here; C, FH, G, GOET, H, JE, L, M, MICH, MU, NY, S, UPS isolectotypes); Santa Catharina, Tubarao, *Ule 958* (H syntype); Santa Catharina, Nova Venezia, *Ule 1032* (syntype, not seen).

Plants slender to medium sized, stems 2-5 (8) cm long, 2-4 mm wide; irregularly pinnately branched, specialized brood branches with closely imbricate leaves commonly present. Leaves variously dimorphic. Lateral leaves 0.8-2.0 mm x 0.2-0.8 mm, well spaced on the stem, not or just barely overlapping with the lateral leaf next above, erect at base and arching toward the substrate above when dry; complanate when wet; oblong-subovate to lanceolate- oblong with

nearly parallel sides, widest below mid-leaf, short acuminate or acute, carinate. Dorsal leaves ovate, shorter and broader than the lateral leaves, widest at mid-leaf, erect spreading when dry, flattened to the stem when wet. Brood branch leaves orbicular, apiculate, cordate at base; closely imbricate, all leaves laterally positioned thereby giving the brood branches a julaceous appearance. Leaf margins plane or narrowly recurved at the middle, uni- or bi-serrate above by projecting, frequently recurved, cell end-walls; weakly serrate or entire at base. Upper and median leaf cells variable in size (even within the same leaf) 50-160 μm long, 5-10 μm wide; median cells at the extreme base 30-60 μm long, 12-35 μm wide; Propagulae on brood- branches occurring between the imbricate lateral leaves and a dense mat of rhizoids originating from initials at the ventral leaf bases. Setae 4-12 mm long, length variable even within a single collection, smooth at base, scabrose to papillose above, occasionally smooth throughout. Capsules 0.5-1.5 mm long, neck weakly to moderately differentiated, exothelial cells weakly or strongly collenchymatous; Opercula 0.5-1.5 mm long. Exostome teeth 0.45-0.60 mm long; outer plates quadrate to shortly rectangular, inner plates and outer plates similar in size and ornamentation. Endostome 0.50-0.65 mm long, basal membrane low, 0.10-0.20 mm, segments linear, 0.30-0.45 mm long, carinate, usually perforate along the keel. Spores 10-20 μm .

Etymology. *Patrisia* refers to the plant (*Patrisia pyrifera*) on which the type collection was made.

Distribution. In Central America from southern Mexico, Belize, Guatemala, Nicaragua, Costa Rica and Panama; in the West Indies from Cuba, Jamaica, Haiti, Dominican Republic; Puerto Rico, Guadeloupe, Dominica, Martinique, Tobago, and Trinidad; and in South America from Colombia, Venezuela, Guyana, Surinam, French Guiana, Brazil, Ecuador, Peru and Bolivia. Fig. 6.

Illustrations. Hampe (1844, Pl. 1, 1-10); Brotherrus (1907, Fig. 697, A-E); Brotherrus 1925 (Fig. 610, A-E); Bartram (1949, Fig 142, A-D); Welch 1966 (Figs. 47-65); Welch (1969, Figs. 39-45); Welch (1972, Figs. 26-36); Florschütz-de Waard

(1986, Fig 112, a-e). Figs. 7-12, 13, 14, 18, 20, 21.

Ecology. Nearly always on leaves or twigs, occasionally on branches and tree trunks, rarely on rotting logs; sea level to 2000 m.

Selected specimens examined.

MEXICO. Chiapas: Las Palmas, La Rue (MICH), near Pueblo de Vientes above Pueblo Nuevo, *Robinson 9876* (US); Calipa, *Lieberman 8103* (C). **BELIZE.** Stann Creek: Big Eddy Valley, *Gentle 3498c* (MICH). **GUATEMALA.** Alta Verapaz: Cubilguitz, *Turckheim 6905* (H, NY); Izabal: Puerto Barrios, *Standley 72881* (CANM, FH, MICH); Peten: La Libertad, Santa Teresa, *Lundell 2707* (FH), Libertad, *Lundell 2499* (FH, MICH). **HONDURAS.** Atlantida: Lancelilla Valley near Tela, *Standley 54901* (FH, US), south of San Alejo, *Standley 7613* (FH). **NICARAGUA.** Zelaya: vicinity of El Recreo on Rio Mico, *Standley 19567* (MICH), Comarca del Cabo, Miguel Bikou, *Seymour 5878* (MO), southeast of Cerro Isidro, 12°05'-12°N; 83°20'-45°W, *Proctor 26949* (H, MO, NY). **COSTA RICA.** Alajuela: Monte Verde, 10°15'N; 85°05'W, *Crosby 9996* (MO); Cartago: 15 km ESE of Cartago, 9°45'N; 83°47'W, Crosby & Crosby 5819 (MO); Heredia: Finca La Selva, ca 7 mi S of Puerto Viejo, *Koch 4946a* (MICH); Limon: between Turrialba & Siquirres, *Crosby 3686* (MO); Puntarenas: Rincon de Osa, Osa Peninsula, 8°42'N; 83°31'W, *Gentry & Burger 2791B* (MO); Cocos Island, Chatham Bay, *Weber B-14268* (C, CANM, FH, H, MICH, MO, NY, UPS, US). **PANAMA.** Bocas Del Toro: Isla de Colon, *Crosby 4088a* (MO); Chiriqui: Pedro Miguel, Boquete, *Corman 3038* (FH); Colon: Rio Guanache as it enters sea, 7 km SW of Portobelo, 9°20'N; 79°45'W, *Crosby 10767* (MO); Panama: Barro Colorado Island, Willis 47 (FH, MO), along the El Llani-Carti road, 9°15'N; 79°00'W, *Crosby 10420* (MO). **CUBA.** Las Villas: Trinidad Mountains, Santa Clara, *Britton 5117*, 5429 (NY); Oriente: Baracoa, El Yunque Mountain, *Underwood & Earle 1028* (H, MO, NY). **JAMAICA.** Clarendon Parish: W of Trout Hall, *Hermann 22939* (BM); Portland Parish: 7 mi NW of Muirton, 18°03'N; 76°20'W, *Crosby 13722* (MO); St. Mary Parish: Castleton Gardens, *Griffin 311* (FLAS); St. Thomas Parish: Sulphur River, 1 mi NNW of Bath, 17°53'N; 76°22'W, *Crosby 3246* (MO); Trelawny Parish: vicinity of Windsor Cave, 18°21'N; 77°39'W, *Crosby 13924* (C, G, M, MO). **HAITI.** Sud: Massif de la Hotte, Grand Anse, *Zanoni 25670c* (NY). **DOMINICAN REPUBLIC.** Barahona: Sierra de Baoruco, 18°07'N; 71°07'W, *Zanoni 25186n* (NY); El Seibo: 30 km from El Seibo, *Norris 7035c* (NY); La Vega: ESE of Bonao, 18°50'N; 70°05'W, *Zanoni et al. s.n.* (NY); Pacificado: Pimentel, *Abbott 718c* (NY, US); Samana: Parque Nacional Los Haitises, along trail of Naranjo, *Smith 10424* (MO, NY, U). **PUERTO RICO.** Luquillo Mountains, Yunque Range, Mt. Britton, *Steere 4219* (G, MO, S),

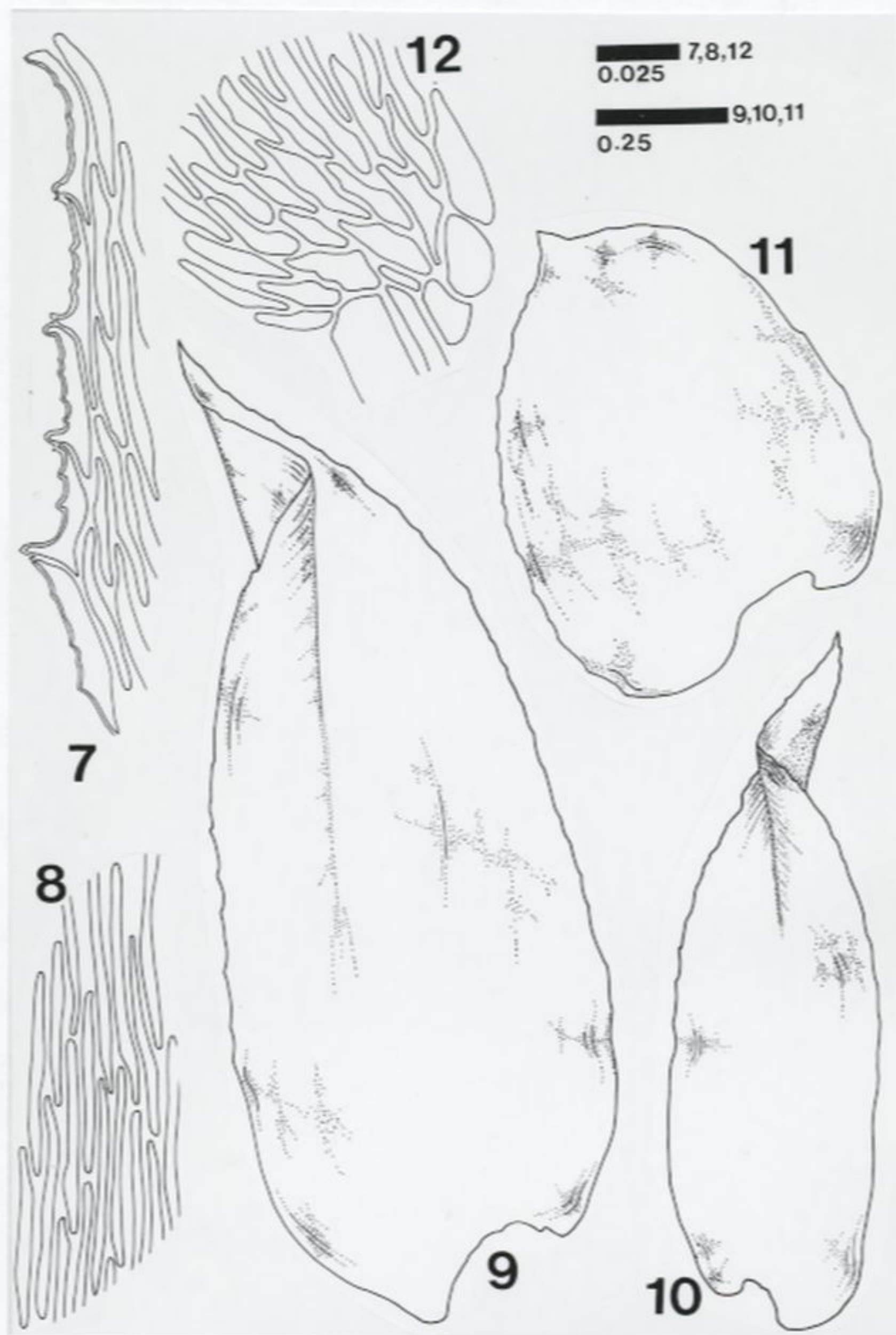


Figure 7-12. *Crossomitrium patrisiae*. Figure 7. Leaf margin. Figure 8. Median leaf cells. Figures 9 & 10. Lateral leaves. Figure 11. Lateral leaf from specialized brood branch. Figure 12. Basal leaf cells.

Steere 4243 (CANM, MICH, MO). **GADELOUPE.** Capesterre, *Gallo 1714* (MICH). **DOMINICA.** Grand River, *Fishlock 27b* (NY). **MARTINIQUE.** L'Alma, 14°02'N; 61°06'W, *Crosby 4745* (CANM, MICH, NY, U, US). **TOBAGO.** Eggers 5852 (FH). **TRINIDAD.** St. George: trail to Morne Bleu, *Crosby 2100* (MO). **COLOMBIA.** Amazonas-Vaupes: Rio Apaporis, Soratama, 0°05'N; 7040'W, *Schultes 15126* (CANM, FH); Antioquia: Municipio Santo Domingo, 06°30'N; 75°10'W, *Churchilletal. 14740* (NY); Cauca: Los Gallera, Micay Valley, *Killip 11879a* (NY); Putumayo: 15 kms NW of Puerto Asis, *King C-1126* (US); Valle: Costadel Pacifico, Rio Cajambre, Barco, *Cuatrecasas 17178b* (US). **VENEZUELA.** Amazonas: along Rio Mawarimuma, just outside of Canon Grande, 00°50'N; 66°10'W, *Buck 11272* (NY); Bolivar: Rio Caura, arriba del Salto Para, *Steyermark & Dunsterville 112929A* (MO); Falcon: Sierra de San Luis, via Coro-Uria, *Griffin & Lopez PV-1604* (FLAS; MO); Sucre: Los Mangos, *Griffin & Bermudez.s.n.* (FLAS). **GUYANA.** Essequibo: Bartica, *Hartley 1408* (NY), Cuyuni River, Akarabice Creek, *Tutin 449* (BM). **SURINAM.** Brokopondo: Brokopondo, Marshall Creek, *Macgillavry.s.n.* (L), *Florschütz 1806* (U); Marowijne: Marowijne, *Wullschlaegel.s.n.* (S); Nickerie: Kabalebo Dam project, 4°00'N; 58°00'W, *Florschütz-de Waard 5415* (U); Paramaribo: prope Paramaribo, *Kegel 741 p.p.* (L); Saramacca: Bakhuis Mountains, Coppename River, *Florschütz & Maas 2720A* (U). **FRENCH GUIANA.** Cayenne: Kourou, Montagnes des Singers 5°07'N; 52°42'W, *Gradstein 5834* (U); Inini: Tumac Humac, *Granville 1293B* (U), Saul, *Cremers 3912b* (FLAS). **BRAZIL.** Acre: vicinity of Serra da Moa village, *Prance et al. 12473* (C, NY); Amazonas: slopes and summit of Serra Curicuriari, 00°20'S; 66°50'W, *Buck et al. 2505* (FLAS, MICH, MO, NY, US); Bahia: Rio Grongogy basin, *Curran 162* (NY, US); Para: Serrado Cachimbo, 974-1024 km N of Cuiaba, 7°40'S, 55°15'W, *Reese 16729* (MO, NY); Rio de Janeiro: near Jacarpoqua, *Ule 2087* (FH, H); Rondonia: 128 km SW of Ariqueaes at Mibrasa mining camp, *McFarland 182* (MO, NY, US); Roraima: Manaus- Venezuela highway Acampamentodo 6 BEC-Jundia at km 328, *Buck et al. 1854* (NY); Sao Paulo: near Santos, *Schiffner 1548* (BM, M, H); Santa Catharina: Nova Venezia, *Ule 156* (BM, C, FH, G, GOET, H, JE, L, M, MICH, NY, S, UPS). **ECUADOR.** Azuay: Gualaquiza, prope scaturiginem saloam ad rivum El Salado, *Allioni 8405* (H); Esmeraldas: Rio Grande, *Harling 4628* (MICH; NY); Guayas: in sylvia Guayas, *Allioni s.n.* (BM); Morona-Santiago: Pachicutza at km 140 on road Loja-Gualaquiza, 3°37'S; 78°34'W, *Holm-Nielsen 4592* (MO, S, US); Los Rios: Rio Palenque Science Center, 47 kms by road south of Santo Domingo, *Crosby 14740* (MO); Napo: south of Rio Napo at Anangu, halfway between Coca & Nueva Rocafuerte, 0°30'S; 76°25'W, *Brako 5159f* (NY); Pastaza: Valley of Rio Pastaza, Basnos-Puyo road ca 10 km below El Topo, *Steere E-54* (NY); Pichincha: 18 km

NW of San Miguel de los Bancos, 0°05'N; 78°55'W, *Buck 10370* (NY). **PERU.** Huanuco: *Weberbauer 3659a* (H); Junin: Puerto Bermudez, *Killip 26505* (NY, US); Loreto: Soledad on Rio Itaya, *Killip 29626a* (FH, US); San Martin: Strasse Yurimaguas- Tarpoto km 107, *Frahm et al. 1368* (B, G, H, MO, NY, U). **BOLIVIA.** La Paz: Coroico, *Mahunka s.n.* (MO).

Crossomitrium patrisiae is the most common species of *Crossomitrium*. Although it is as broadly distributed as the genus and has been collected from sea level to 2000 m, *C. patrisiae* is essentially a tropical lowland species. Most collections have been made from either the coastal regions or the Amazonian region of South America.

In its typical expression *C. patrisiae* is a medium sized plant with well spaced lateral leaves that do not overlap. The lateral leaves are lanceolate-oblong with nearly parallel sides and an acuminate apex. When dry the lateral and dorsal leaves are stiffly erect at base but curved strongly above so that the lateral leaves arch downward to the substrate and the dorsal leaves arch downward to the stem. This aspect of the leaves has been described as "leaves shriveled or contorted when dry".

In its typical expression *C. patrisiae* is nearly always found with brood branches at the tips of the stems or branches. These brood branches have been described as julaceous, but this is somewhat misleading. The leaves on these branches are oval, they are borne roughly perpendicular to the substrate and are tightly overlapping or imbricate giving the branch a smooth aspect. When well-developed the brood branches consist of three layers: a dense lower layer of rhizoids, a middle layer of brood-bodies that originate from rhizoidal initials on the stem abaxially to the lateral leaves, and an outer layer of imbricate leaves. Florschütz-de Waard (1986) has reported sporophytes from these brood-branches, however, when they are well-developed these structures function only in asexual reproduction. As suggested by Florschütz-de Waard (1986) the formation of brood-branches appears to be environmentally induced and in some cases branch tips that have begun to develop as brood branches appear to be arrested in mid-development. It is on these intermediate

branch tips that sporophytes may be found.

The typical expression of *C. patrisiae* is the common form of the species in the Amazonian region of South America. This expression is likely to be confused only with *C. scabrisetum* or *C. acuminatum* which are similar to *C. patrisiae* in habit, leaf shape and in having the same type of brood branch. *Crossomitrium scabrisetum* is in fact gametophytically identical to *C. patrisiae*. In *C. scabrisetum* the seta is scabrose throughout while in *C. patrisiae* it may be roughened or papillose above and smooth below or entirely smooth.

Crossomitrium acuminatum differs from *C. patrisiae* in its tightly recurved leaf margins and its stout, strongly recurved marginal dentations. In *C. patrisiae* the leaf margins are generally plane and while the marginal teeth are variably developed they are never as strong or recurved as in *C. patrisiae*.

In Central America the common expression of *C. patrisiae* is a larger plant with longer, broader leaves that have a tendency when dry to be flattened rather than arching. This expression is also encountered in the West Indies. Furthermore, the lateral leaves in this expression are closer together and frequently overlap on the upper parts of the stems and branches. This expression generally does not produce brood branches. Instead, brood-bodies occur in dense clusters on the stems abaxially to the ventral leaves. Frequently, the stems bearing brood-bodies are twisted 180 degrees so that the ventral leaves are borne on the upper surface and the brood-bodies exposed. This expression of *C. patrisiae* has been described as *C. jamaicense*, *C. cruegeri* and *C. ramulicola*.

In 1957, Crum and Steere synonymized *C. jamaicense* with *C. sintenisi* C. Müll., and indeed the two taxa are remarkably similar in size, habit, and the manner in which brood-bodies are borne. At first glance, *C. jamaicense* appears to be closer to *C. sintenisi* than to the typical expression of *C. patrisiae*. However, there are a number of collections that bridge the gap between *C. jamaicense* and *C. patrisiae*. The best of these

collections is Florschütz-de Waard & Zielman 5415 (U). This collection contains a few twigs and their attached leaves on which is found a large population of *Crossomitrium*. The plants on the twigs are identical to *C. jamaicense* while the organically connected plants on the leaves are identical to the typical expression of *C. patrisiae*. It thus appears that *C. jamaicense* is an environmentally induced expression of *C. patrisiae*. In fact, most herbarium specimens of the *jamaicense*-expression examined were found growing on twigs and bark rather than on leaves.

The inclusion of *C. jamaicense* under *C. patrisiae* raises the question of whether or not *C. sintenisi* also belongs in the synonymy of *C. patrisiae*. This is the most difficult taxonomic problem in the genus. In this study *C. sintenisi*, which does not produce sporophytes, is maintained as distinct on the basis of its broader lateral leaves that overlap at base and are distinctly flattened when dry. The problem is complex and frankly, separating the two taxa on the island of Hispaniola has not always been possible.

Crossomitrium patrisiae is distinguished from *C. epiphyllum* and *C. saprophilum* by its larger, narrower leaves that arch downward to the substrate and by its typical brood branches. In *C. epiphyllum* and *C. saprophilum* the leaves are smaller, ovate to oval in shape, strongly flattened to the substrate and its brood-bodies are borne on all sides of erect brood branches.

3. *Crossomitrium scabrisetum* Bartr., Bryologist 49: 119. 1946. Type. Guatemala, Dept. Izabal, damp forest slopes and barrancas, *Steyermark 41879* (FH holotype; F, MICH, S isotypes).

Plants slender, stems irregularly pinnately branched, up to 3 cm long. Specialized brood-branches as in *C. patrisiae*. Lateral leaves not or just barely overlapping with the leaf next above, erect at base and arched downward toward the substrate when dry, complantate when wet, oblong-subovate to lanceolate-oblong with nearly parallel sides, widest below mid-leaf, short acuminate or acute, carinate, 1.4-1.7 mm long, 0.4-0.5 mm wide. Dorsal

leaves erect spreading when dry, flattened to the stem when wet, subovate, widest at the middle. Leaf margins plane or shortly and narrowly recurved at the middle. Upper and median leaf cells 60-125 μm long, 7-10 μm wide, cells are extreme base 50-90 μm long, 15 μm wide, Setae up to 5 mm long, densely tuberculose above, rough at base. Capsules 0.5-1.0 mm long, tuberculate at base, exothecial cells moderately collenchymatous; Opercula 0.4-0.5 mm long. Exostome teeth 0.25-0.30 mm long, outer plates shortly rectangular, inner plates 2/3 as wide and nearly as broad as the outer plates. Endostome 0.35-0.40 mm long, basal membrane low, 0.10 mm high, segments entire or perforate along the keel. Spores 12-15 μm . Calyptrae 1.0 mm long.

Etymology. Scabrisetum refers to a densely tuberculose setae.

Distribution. Guatemala (Izabal). Fig. 22.

Illustrations. Bartram (1949, Fig. 142, E-H); Welch (1974, Figs. 86-100. Fig. 1, 5, 15, 16, 17 & 19.

Ecology. Epiphyllous; 300-900 m.

Specimen examined.

GUATEMALA. Izabal: Cerro San Gil, Steyermark 41879 (F, FH, MICH, S).

Crossomitrium scabrisetum is presently known only from the type collection. Vegetatively the species appears distinctive due to its leaves that are generally crowded and flattened at the tips of the stems and branches. However the gametophytically variable *C. patrisiae* has expressions that are nearly the same as *C. scabrisetum*. The two species can not be distinguished when sporophytes are absent. Thus it is likely that many sterile collections named as *Crossomitrium patrisiae* from Central America are actually *C. scabrisetum* (see for example Griffin et al. 221 (FLAS) from Costa Rica). Bartram emphasized the short setae of *C. scabrisetum* as one means of distinguishing *C. scabrisetum* from *C. patrisiae* but, the seta length of *C. scabrisetum* falls within the range of variation exhibited by *C. patrisiae*. Presently, the only way to separate *C. scabrisetum* from *C. patrisiae* is by the strongly tuberculose

setae and capsule neck of *C. scabrisetum*. Curiously, the stomata of *C. scabrisetum* are immersed in the tubercular swellings on the neck of the capsule.

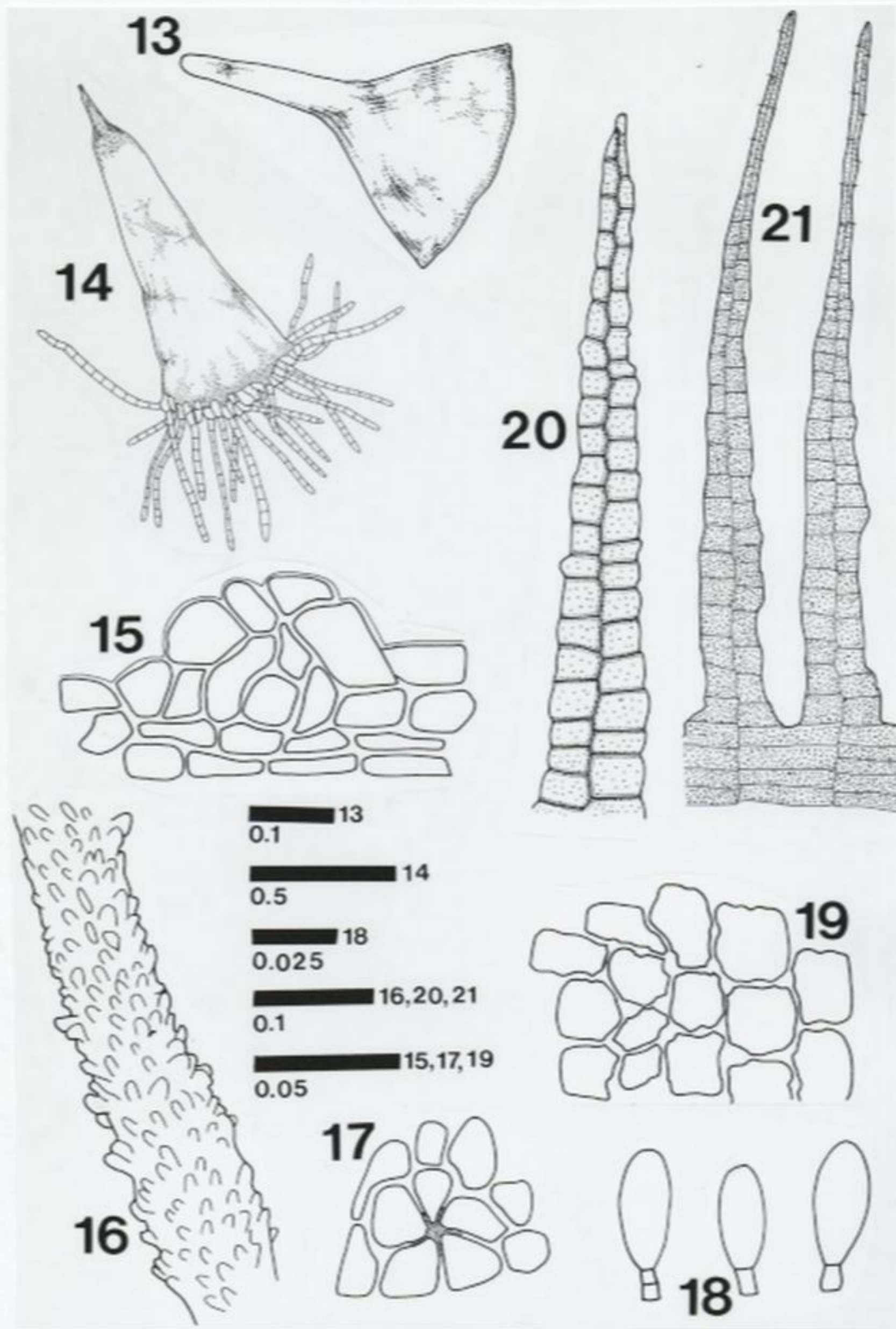
There is some doubt as to whether or not *C. scabrisetum* and *C. patrisiae* are distinct species. Setae ornamentation in *C. patrisiae* can be extremely variable and although I have neither observed tuberculate seta nor setae roughened at base in *C. patrisiae*, there are some collections in which the upper parts of the seta could be described as scabrose. The presence of tuberculose neck swellings with stomata at base would appear to be a distinctive character, however the stomata of *C. patrisiae* (which also are irregularly divided as in *C. scabrisetum*) are frequently surrounded by bulging cells. It may be that the distinctive features of *C. scabrisetum* represent extreme expressions of characters present in *C. patrisiae*. On the other hand, the presence of a similar type of setae ornamentation in *C. acuminatum* supports the recognition of *C. scabrisetum* at the specific level.

Section *Cormophila* Broth., Nat. Pflanzenfam. 1(3): 957. 1907. Type species: *Crossomitrium orbiculatum* C. Müll. (designated here).

Plants typically on rocks or tree trunks, less frequently epiphyllous. Leaves flattened to the substrate, lateral leaves widest above the middle. Brood branches erect, leaves spreading on all sides.

4. *Crossomitrium epiphyllum* (Mitt.) C. Müll., Linnaea 38: 613. 1874. *Lepidopilum epiphyllum* Mitt., J. Linn. Soc., Bot. 12: 370. 1869. Types. Ecuador, Chimborazo, ad folia, *Spruce 801* (NY lectotype designated here; BM, S isotypes, see note 1) Andes Quitenses, in sylva Canelos, *Spruce 800* (NY syntype).

Crossomitrium oerstedianum C. Müll., Flora 58: 545. 1875. Type. Costa Rica, in folio coriaceo, *Oersted s.n.* (FH).



Figures 13, 14, 18, 20, 21. *Crossomitrium patrisiae*. Figures 15, 16, 17, & 19. *Crossomitrium scabrisetum*. Figure 13. Operculum. Figure 14. Calyptra. Figure 15. Tuberculose swelling on capsule neck. Figure 16. Upper part of scabrose seta. Figure 17. Stomate with secondarily divided guard cells. Figure 18. Axillary hairs. Figure 19. Collenchymatous exothecial cells. Figure 20. Exostome tooth, outer (dorsal) surface. Figure 21. Part of an endostome showing two processes and basal membrane, outer (dorsal) surface.

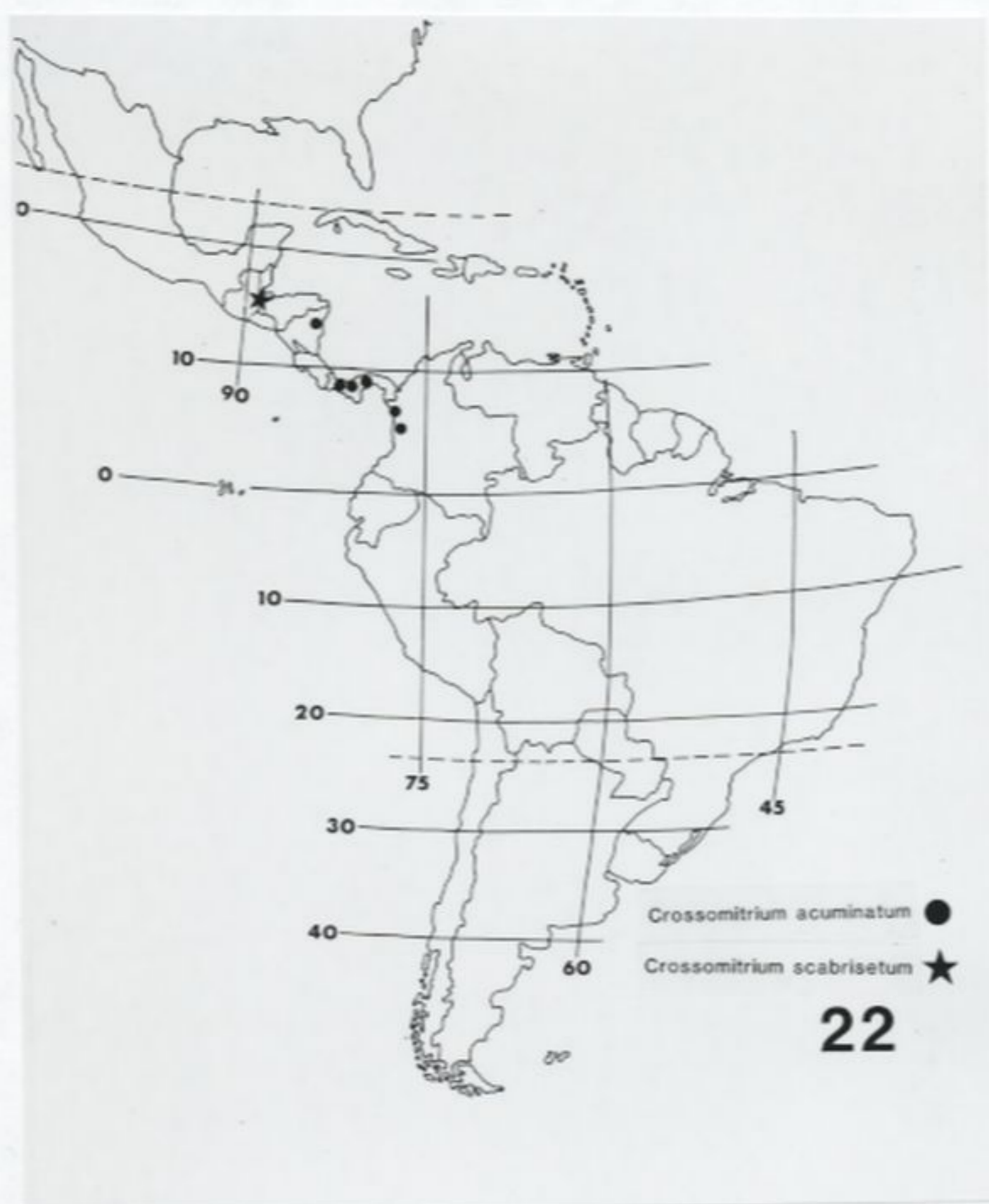


Figure 22. Distribution of *Crossomitrium acuminatum* and *C. scabrisetum*.

There is some doubt as to whether or not *C. scabrisetum* and *C. patrisiae* are distinct species. Setae ornamentation in *C. patrisiae* can be extremely variable and although I have neither observed tuberculate seta nor setae roughened at base in *C. patrisiae*, there are some collections in which the upper parts of the seta could be described as scabrose. The presence of tuberclose neck swellings with stomata at base would appear to be a distinctive character, however the stomata of *C. patrisiae* (which also are irregularly divided as in *C. scabrisetum*) are

frequently surrounded by bulging cells. It may be that the distinctive features of *C. scabrisetum* represent extreme expressions of characters present in *C. patrisiae*. On the other hand, the presence of a similar type of setae ornamentation in *C. acuminatum* supports the recognition of *C. scabrisetum* at the specific level.

Section *Cormophila* Broth., Nat. Pflanzenfam. 1(3): 957. 1907. Type species: *Crossomitrium orbiculatum* C. Müll. (designated here).

Picacho, 13°00'N; 85°55'W, *Stevens 22726* (MO). COSTA RICA. Alajuela: vicinity of Guatuso de San Rafael, 10°43'N; 84°48'W, *Holm et al. 1312*, (G); Cartago: vicinity of confluence of Rio Grande de Orosi and Rio Humo, 9°42'N; 83°47'W, *Crosby & Crosby 8574* (MO); Limon: 16 mi northeast of Guapiles, 10°23'N; 83°45'W, *Daly 103* (MO); Puntarenas: Rincon de Osa, *Liesner 1788* (MO); San Jose: La Palma area, 9 km NE of San Jeronimo, 10°03'N; 83°59'W, *Engel 8855a* (MO). PANAMA. Bocas Del Toro: vic. of Fortuna Dam, 8°55'N; 82°08'W, *Allen 5582 p.p.* (MO); Canal Area: experimental greenhouse, *Meyer 149* (MICH); Chiriqui: along Holcomb trail to Cerro Horqueta, *Crosby 4048b* (MO); Cocle: cloud forest above El Valle, *Luer et al. 10646* (MO); Colon: left bank of Rio Guanache, 7 km SW of Portobelo, 9°20'N; 79°45'W, *Crosby 10790* (MO); Panama: Cerro Campana, 8°40'N; 79°55'W, *Crosby 7213* (MO). CUBA. Oriente: Mt. Baracoa, El Yunque, *Underwood & Earle 1028 p.p.* (NY). JAMAICA. St. Thomas: N side of Cuna-Cuna Gap, *Britton 984* (H, NY). HAITI. Sud: Riviere Glace, Morne la Hotte, *Holdridge 3084a* (MICH). PUERTO RICO. Arecibo, Igartua trail, Rio Abajo Planting Project, *Steere 6698* (MICH, MO). SABA. Mt. Scenery, *Wiersma & van Slageren 230m* (U), in monte, *Suringar* (H, L). MONTSERRAT. Chances Pond, *Shafer 925b* (NY). GUADELOUPE. Morne l'Echelle, *Duss 208* (H, MICH, NY). DOMINICA. Windward slope of Morne Diablotin, *Elliott 224a* (BM, FH). MARTINIQUE. Morne Paillasse (Mont Pelee), *Duss 22* (H, NY). GRENADA. East ridge, Mt. St. Catharine, *Simmonds 514* (BM, CANM). TRINIDAD. Heights of Aripo, *Broadway 9988* (NY). VENEZUELA. Aragua: Nacional Parque H. Pittier, *Agostini & Cobo 189b* (MO). COLOMBIA. Antioquia: Campamento Municipio, 7°00'N; 75°15'W, *Churchill et al. 15027* (NY); Cauca: La Gallera, Micay Valley, *Killip 11880* (FH, NY, US); Choco: Novita Vereda Curundo Municipio, *Aguirre & van Reenen 3400* (U); Risaralda: Santa Rosa del Cabal Municipio, *van Reenen & Griffin 1769* (U); Valle: Hoyade Rio Digua, *Cuatrecasas 15137b* (US). ECUADOR. Galapagos: Santa Cruz, *van der Werff 2082* (U); Morona-Santiago: Gualaquiza, *Allioni 492* (H); Napo: Anangu, 70 km E of Coca on Napo River, *Brako 4619b* (NY); Pichincha: 18 km NW of San Miguel de los Bancos, 00°05'N; 78°55'W, *Buck 10562* (NY), N slopes of Mt. Pichincha, *Crosby 10734* (MO, NY). PERU. Junin: above San Ramon, *Killip 24807* (NY); Loreto: Gegend von Iquitos, 3°34'S; 73°00'W, *Doppelbaur p.p.* (M); San Martin: km 97 on strasse Chachapoyas-Moyobamba, *Frahm et al. 197* (B, MO, NY, U). BOLIVIA. Cochabamba: bei Tablas, *Herzog 4558* (FLAS, JE, L, M, S).

Crossomitrium epiphyllum is a commonly encountered species with a range nearly equal to that of the genus. In South America it is generally

found at higher elevations than *C. patrisiae* which is more common in the lowland tropics. Both species occur together and may even be mixed on the same leaf or twig. The species are best distinguished by their diagnostic brood branches. In *C. epiphyllum* the brood branches are erect with leaves erect to spreading and propagulae present on all sides. In *C. patrisiae* the brood branches are adnate to the substrate with imbricate leaves and propagulae present only on the lateral sides of the branch.

In its typical expression *C. epiphyllum* is separated from *C. patrisiae* (as well as *C. scabrisetum* and *C. acuminatum*) by its strongly flattened, obovate to orbicular lateral leaves that are less than 1.0 mm long. *Crossomitrium patrisiae* has arching, lanceolate-oblong lateral leaves that are greater than 1.2 mm long. When sporophytes are present the two species can be distinguished by examining the basal membrane of the endostome. In *C. epiphyllum* it is more than one third while in *C. patrisiae* it is one fourth or less the height of the endostome.

Crossomitrium epiphyllum has a troublesome expression that is found throughout its range but which is particularly common in the West Indies. This expression, described as *C. calomicron* and *C. cubense*, has small lateral leaves that are oblong and erect to erect-spreading rather than obovate to orbicular and flattened to the substrate. Furthermore, although typical erect brood branches are present, there is a tendency for the brood branches to be horizontal rather than erect. This expression grades closely into some forms of *C. patrisiae* and may cause confusion. The expression is linked to *C. epiphyllum* by a number of collections that vegetatively approach *C. patrisiae* but which on the basis of their specialized brood branches and sporophytes clearly belong to *C. epiphyllum*. The best of these critical calomicron-expressions is *Crosby 10734* (MO, NY). The proper assigning of many these calomicron-expressions relies almost entirely on the presence and recognition of epiphyllum-type brood-branches.

Crossomitrium saprophilum is vegetatively identical to some expressions of *C. epiphyllum*, the

Nomenclatural notes

1. Both Spruce 801 and Spruce 800 represent *C. epiphyllum*. The choice of Spruce 801 as lectotype is based on the completeness and size of the collection: sporophytes and specialized, erect, brood branches with brood-bodies on all sides and along the length of the brood branches are present.

2. Welch (1971) neotypified *C. orbiculatum* with "Heller & Heller 796b, Puerto Rico, N slope of Luquillo Mts, on stump, March 8 1899" (NY) and listed *Heller & Heller 796* (NY) as an additional specimen examined. *Heller & Heller 796b* (which has not been annotated by Welch as a neotype) bears the label information "on *Marcgravia sintenisii*", while *Heller & Heller 796* has a label reading "N. slope Luquillo Mts. Mar. 8 1899, on stump." Since there appears to have been a mix-up of collection numbers and label information, *Heller & Heller 796*, N. slope Luquillo Mts, Mar. 8 1899, on stump (NY) is here chosen as the neotype *C. orbiculatum*.

3. The protologue for *C. cubense* gives the type collection as Loma San Juan, epiphyte, leg. *Hioram 13748*. This is essentially in agreement with the information given on the holotype (PC) and an isotype (JE): 'Cuba: Guantanamo, Loma San Juan, 1100 m, *Hioram 13748*.' There are two collections (FH, NY) attributed to *Hioram 13748* that give the locality as 'Loma del Gato, Sierra Maestra (Oriente).' Although Loma San Juan appears to be a hill either in or near the Loma del Gato range, an eastern spur of the Sierra Maestra, *Hioram* (in Thériot 1940) used the names to indicate different localities. The plants from all four collections are identical and they were all collected on the same type of fern pinnae. Nevertheless, since the locality information on the material in FH and NY does not completely agree with the protologue they should be considered questionable isotypes.

Plants small, stems up to 7 cm long, 1-3 mm wide, irregularly pinnately branched; branches frequently ending in specialized, erect brood-

branches with erect-spreading leaves. Lateral leaves complanate, flattened to the substrate and overlapping with the leaf next above or erect spreading, obovate, orbicular, oval or sub-oblong, with convex sides widest above the middle, 0.5-1.0 (1.2) mm long, acute to shortly acuminate; dorsal leaves orbiculate, flattened to the stem. Leaves on specialized brood-branches oval to orbiculate, erect-spreading from all sides or moderately flattened. Leaf margins plane, weakly serrate at base. Upper and median leaf cells 50-150 µm long, 5-10 µm wide, median cells at the extreme base 50-70 µm long, 18 µm wide. Setae papillose above, smooth below, 4-7 mm long. Capsules inclined to sub-erect, ovoid to elliptic, 0.7-1.0 mm long, with a weakly differentiated neck, exothecial cells collenchymous. Opercula 1.0 mm long. Exostome teeth whitish yellow, occasionally with light reddish tint, 0.25-0.28 mm long; outer plates quadrate, inner plates as wide as and nearly as long as the outer plates. Endostome 0.30-0.32 mm long, basal membrane high, 0.12-0.13 mm, segments weakly carinate, slightly perforate along the keel. Spores 12-15 µm.

Etymology. *Epiphyllum* refers to a epiphyllous habitat.

Distribution. In Central America from Guatemala, Nicaragua, Costa Rica and Panama; throughout the West Indies: Cuba, Jamaica, Haiti, Puerto Rico, Saba, Montserrat, Guadeloupe, Dominica, Martinique, Grenada, and Trinidad; in South America from Venezuela, Colombia, Ecuador (including the Galapagos Islands) Peru, and Bolivia. Fig. 23.

Illustrations. Thériot (1940, Pl. 55, fig. 9 a-e); Bartram (1949, Fig. 142, I-K); Welch (1969, Fig. 24-31); Welch (1971, Fig. 72-95); Welch (1974, Fig. 79-85). Figs. 24-32, 34, 36-38.

Ecology. On leaves, twigs, tree branches and trunks, rotting logs, stumps and boulders; 100-2340 m.

Selected specimens examined.

GUATEMALA. Alta Verapaz: Pantín, below Tamahu, *Standley 70967* (FH). NICARAGUA. Matagalpa: W slope of Cerro El

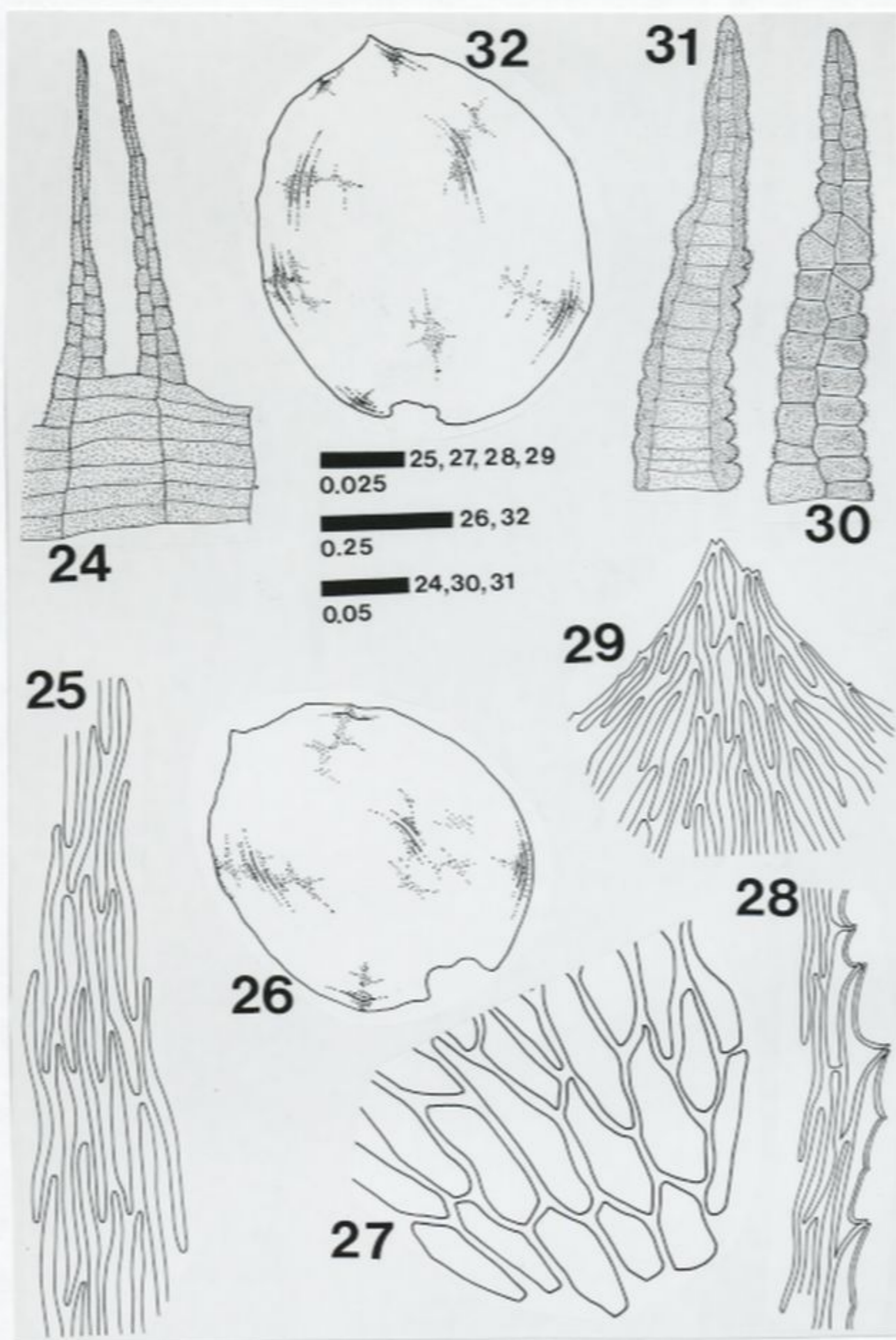


Figure 23. Distribution of *Crossomitrium epiphyllum*.

that of the genus. In South America it is generally found at higher elevations than *C. patrisiae* which is more common in the lowland tropics. Both species occur together and may even be mixed on the same leaf or twig. The species are best distinguished by their diagnostic brood branches. In *C. epiphyllum* the brood branches are erect with leaves erect to spreading and propagulae present on all sides. In *C. patrisiae* the brood branches are adnate to the substrate with imbricate leaves and propa-

gulae present only on the lateral sides of the branch.

In its typical expression *C. epiphyllum* is separated from *C. patrisiae* (as well as *C. scabrissetum* and *C. acuminatum*) by its strongly flattened, obovate to orbicular lateral leaves that are less than 1.0 mm long. *Crossomitrium patrisiae* has arching, lanceolate-oblong lateral leaves that are greater than 1.2 mm long. When sporophytes are present the two species can be



Figures 24-32. *Crossomitrium epiphyllum*. Figure 24. Part of the endostome showing two processes and basal membrane, outer (dorsal) surface. Figure 25. Median leaf cells. Figure 26. Dorsal leaf. Figure 27. Basal leaf cells. Figure 28. Marginal leaf cells. Figure 29. Apical leaf cells. Figure 30. Exostome tooth, outer (dorsal) surface. Figure 31. Exostome tooth, inner (ventral) surface. Figure 32. Lateral leaf.

Sebille s.n. (H holotype).

Nomenclature note.

The protologue for *C. rotundifolium* gives the collection number of the lectotype as *Herzog 2716*. The packets of *C. rotundifolium* in H, JE, and S marked 'species nova' and which otherwise agree in all particulars with the protologue bear the collection number *Herzog 2726*.

Plants medium to large; stems up to 6 cm long and 3-4 mm wide; irregularly and sparingly branched. Lateral leaves 1.3-2.0 mm long, 0.8-1.2 mm wide, moderately spaced on the stems, overlapping at base with the leaf next above, oblong-elliptic, rounded to the stem at base, with convex sides, generally widest above the middle, acute to shortly acuminate, flattened to the substrate when dry. Dorsal leaves broader, suborbiculate to oblong, acute, flattened to the stem when dry. Leaf margins plane, serrate above, weakly serrulate at base. Upper and median leaf cells 70-150 μm long, 7-10 μm wide; cells at the extreme base, 50-125 μm long, 17-25 μm wide, thinner walled. Asexual reproduction by brownish-red filamentous, septate brood-bodies in clusters of two or three on a common stalk arising from rhizoid initials abaxial on the ventral leaves, stems frequently turned 180 degrees thus exposed the brood-bodies. Specialized brood branches absent. Dioicous (?). Sporophytes unknown.

Etymology. Named for its collector Paul Ernst Emil Sintenis (1847-1907): German botanist and professional plant collector; Sintenis collected in Puerto Rico from 1884 to 1887 (Sayre 1975).

Distribution. In Central America from Guatemala, Nicaragua, Costa Rica and Panama, in the West Indies from Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Dominica and Martinique, and in South America from Surinam, Guyana, Venezuela, Colombia, Ecuador, Bolivia, and Brazil. Fig. 40.

Illustrations. Fig. 41-44.

Ecology. On tree trunks, branches and twigs, occasionally on leaves, rarely on rock; 200-1500

m.

Selected specimens examined.

GUATEMALA. Alta Verapaz: Cubilquitz, *Turckheim 6691* (H). NICARAGUA. Zelaya: 6.3 km south of bridge at Colonia Yolanía, 11°36'-37'N; 84°22'W, *Stevens 4894* (MO). COSTA RICA. Cartago: Reserva Forestal Tapanti, vertiente oriental del Río Macho, *Griffin 144* (FLAS); Puntarenas: Los Cruces, *Gomez 25370A* (MO); San José: General, *Alfaro 164* (FH, US); Floret de Talamanca, *Tonduz* (MO). PANAMA. Bocas Del Toro: 4 mi N of Almirante, *McDaniel 5080* (NY); Veraguas: 5.4 km NW of Santa Fe, 8°30'N; 81°05'W, *Crosby 10190* (MO). JAMAICA. Manchester Parish: Marshall's Pen 3 mi WNW of Mandeville, 18°05'N; 77°32'W, *Buck 5779* (NY); St. Catherine Parish: Mt. Diabolo, *Britton 775* (NY); Trelawny Parish: 0.5 mi from Winsor Caves, *Griffin 309* (FLAS). HAITI. Nord-Ouest: Morne Chavary, vicinity of St. Louis du Nord, *Leonard 14545* (BM, FH, NY, US); Sud: Massif de la Hotte, *Zanoni et al. 25670C* (NY). DOMINICAN REPUBLIC. La Vega: vicinity of Piedra Blanca, along Maimon River, *Allard 16662* (NY). PUERTO RICO. Maricao Insular Forest, stone observation tower, *Stimson 1447* (US). GUADELOUPE. Saint Claude sur des roches, *Gallo 911* (CANM). DOMINICA. Shawford Estate, *Elliot 894* (BM, FH). MARTINIQUE. Morne Rouge, *Duss 388* (H). SURINAM. Saramacca: Paka-paka, *Florschütz 1631* (U). GUYANA. Essequibo: Upper Mazaruni District, Jawalla at confluence of Kukui & Mazaruni rivers, 5°40'N; 60°29'W, *Gradstein 4951* (U). VENEZUELA. Nueva Esparta: Isla Maragita, Cerro Copey, *Sugden 1148* (NY). COLOMBIA. Antioquia, Jardín Municipio, Vereda El Salado, *Churchill 15883* (NY). ECUADOR. Los Ríos: Río Palenque Science Center, *Lojnant & Molau 15777* (NY); Morona-Santiago: Gualaquiza, *Allioni* (H); Napo: Cerro Antisana, 0°30'S; 78°00'W, *Grubb 2850* (BM); Pichincha: 2 km W of Tandape on Quito-Santo Domingo road, *Crosby 14753* (MO). BOLIVIA. Cochabamba: bei Tablas, *Herzog 4594* (JE); Pando: im feuchten Gebüsch bei San Miguelito, *Herzog 2726* (JE, H, S). BRAZIL. Bahia: locality uncertain, *Luetzelburg 2041* (B); Sao Paulo: Monastere de Maristella pres Tremembe, *Sebille* (H).

In its best development *C. sintenisii* appears to be a large expression of *C. epiphyllum*. The plants have leaves that are strongly flattened to the substrate and overlap at base with the leaf next above, the lateral leaves are broadest above the middle, and leaf apices are short and broad. In *C. epiphyllum* the leaves are usually less than 1.0 mm long (some leaves may be 1.2 mm long) while in *C. sintenisii* the leaves are greater than 1.3 mm long. In addition, *C. sintensisii* lacks specialized,

5. *Crossomitrium saprophilum* Broth., Rev. Bryol. 47: 38. 1921. Type. Ecuador, Prov. del Oriente, Gualaquiza ad truncos putrescentes in silva montis Guayusa, *Allioni* [611] (H holotype).

Plants small, stems up to 3 cm long; irregularly and shortly pinnately branched, branches (2-3 mm), erect brood-branches common. Leaves tightly flattened to the substrate, rounded to the insertion; lateral leaves obovate, oval or orbicular, 0.5-1.0 mm long, 0.3-0.7 mm wide, closely spaced and overlapping with the leaf next above, shortly acute to apiculate; dorsal leaves broader and wider. Leaves on erect brood branches erect-appressed, shorter than the vegetative leaves, orbiculate, those at the apex forming a cup like structure. Leaf margins plane. Upper and median leaf cells 50-125 µm long, 5-8 µm wide, median cells at extreme base 40-75 µm, 10-13 µm wide. Asexual propagulae in dense terminal clusters on short, erect brood-branches. Dioicous (?). Sporophytes unknown.

Etymology. Saprophilum - fond of things rotten - is a reference to the habitat of the type collection "ad truncos putrescentes."

Distribution. In Central America from Guatemala and Costa Rica; from Puerto Rico in the West Indies; and in South America from Colombia, Ecuador, Peru and Brazil. Fig. 39.

Illustrations. Figs. 33, 35.

Ecology. On leaves, twigs, tree trunks and rotting logs; 80-1100 m.

Specimens examined.

GUATEMALA. Solola: Ixtapafluss bei Chocola, *Morton* 4074 p.p. (JE, S). COSTA RICA. Cartago: Parque Arqueológico de Guayabo de Turrialba, *Infante* 83 (FLAS); Limón: Río Banano, *Gutierrez* (FH, US). PUERTO RICO. Luquillo Mts., El Verde rainforest, *Steere* s.n. (NY). COLOMBIA. Meta: Sierra del la Macarena, Río Guapaya, *Philipson* 2469 (BM, FH). ECUADOR. Los Ríos: Río Palenque Science Center, 47 km S of Santo Domingo, 0°30'S; 79°20'W, *Crosby* 14745; Morona-Santiago: Gualaquiza, *Allioni* 611 (H); Napo: NENuevo Rocafuerte, Río Braga, *Jaramillo* 4397 (NY); Pastaza: Puyo, *Steere* E-72 (NY).

PERU. San Martín: at km 409 Strasse Moyobamba-Chachapoyas, *Frahm et al.* 110 (B, MO). BRAZIL. São Paulo: Alto da Serra, *Gehst* (JE).

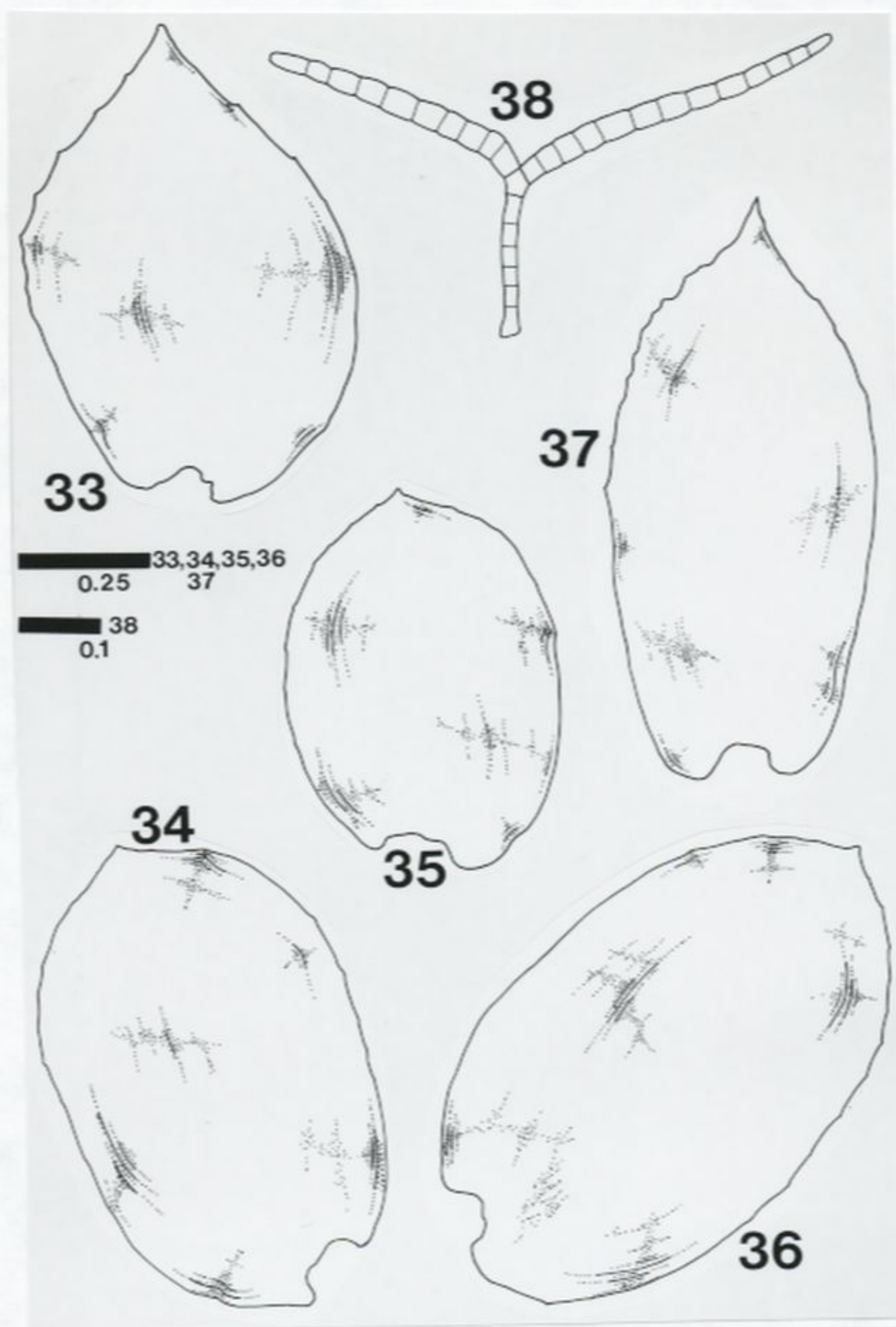
Crossomitrium saprophilum is a small plant with strongly flattened, orbicular to obovate leaves. It is vegetatively identical to some expressions of *C. epiphyllum*. Certainly its closeness to *C. epiphyllum* and its scattered occurrence over a broad range that completely overlaps with that of *C. epiphyllum* leads one to question its distinctiveness. The two taxa differ in several features of their brood branches. In *C. saprophilum* the brood branch leaves are erect-appressed and the uppermost leaves form a loose cup that surrounds a dense terminal cluster of propagulae. In *C. epiphyllum* the leaves on the brood branches are erect to erect-spreading, they do not form a terminal cup and the propagulae are borne along all sides of the brood branch abaxially to the leaves.

6. *Crossomitrium sintenisi* C. Müll., *Flora* 37: 244. 1898. Type. Puerto Rico, Sierra de Luquillo, regione media montis Hymene, Junio 1885, *Sintenisi* s.n. (BM, FH, G, H, MICH, NY, PC, S isotypes).

Crossomitrium rotundifolium Herzog, *Biblioth. Bot.* 87: 134. 1916. Types. Bolivia, auf Gersträuch; Ästen im feuchten Gebüsch bei San Miguelito, *Herzog* 2726 [sic] (JE lectotype designated here; H, S isolectotypes). Bolivia, Ästchen in der Talschlucht bei Tablas, *Herzog* 4594 (JE syntype).

Crossomitrium splendens Broth., Rev. Bryol. 47: 38. 1921. Types. Ecuador, Prov. del Oriente, Gualaquiza, in silva secus rivum 'El Salado', *Allioni* [8404] (H lectotype designated here). Ecuador, Prov. del Oriente, Gualaquiza, ad truncum Bixae orellanae secus rivum Gualaquiza, *Allioni* [525] (H syntype).

Crossomitrium paulense Broth. & Seville, Rev. Bryol. 52: 22. 1925. Type. Brazil, Etat de St.-Paul, monastere de Maristella pres Tremembe, 1922,



Figures 33 & 35. Leaves of *Crossomitrium saprophilum*. Figures 34, 36-38. *Crossomitrium epiphyllum*. Figures 34 & 36. Leaves *C. epiphyllum*. Figure 37. Leaf of the calomicron-expression of *C. epiphyllum*. Figure 38. Asexual brood-body complex showing a stalk and two brood-bodies.



Figure 39. Distribution of *Crossomitrium saprophilum*.

the West Indies from Jamaica, Hispaniola, Puerto Rico, Guadeloupe, Dominica and Martinique, and in South America from Surinam, Guyana, Venezuela, Colombia, Ecuador, Bolivia, and Brazil. Fig. 40.

Illustrations. Fig. 41-44.

Ecology. On tree trunks, branches and twigs, occasionally on leaves, rarely on rock; 200-1500 m.

discussion under *C. patrisiae*). The morphological intergradation between the two is complex and in Hispaniola, as well as some parts of Central America, there are a number of collections that have resisted sorting into one taxa or the other. In South America, *C. sintensisii* is distinct and on that basis *C. sintensisii* is recognized at the species level. It may be that the present treatment of *C. sintensisii* is too broad and that most of the Caribbean and Central American plants included here will eventually be found to be different from the South American plants. The sporophytes of *C. sintensisii* are unknown, the answer to this problem may lie in their discovery.

In South America *C. sintensisii* is generally found at higher elevations than *C. patrisiae*. Plants have broad lateral leaves that are clearly flattened, and much more rounded than the lateral leaves on plants of *C. sintensisii* from the Caribbean. The oldest South American name for the species is *Crossomitrium rotundifolium* Herzog.

Excluded species and types not seen

Lepidopilum filiferum Besch. in Fourn. Mexic. Pl. 1 (Crypt.): 42. 1872. *Lepidopilum piliferum* Besch., Mem. Soc. Sci. Nat. Cherbourg 16: 229. 1872. err. pro *L. filiferum*. *Crossomitrium piliferum* (Besch.) Broth., Nat. Pflanzenfam. 1(3): 957. 1907. Type. Mexico, Cordova, ad cortices arborum, Mart. 1866, *Bourgeau 2137*. (holotype PC, isotypes G, NY, S).

Although Bescherele considered this species nearest to *Hookeria patrisiae*, the leaves have a short double costae and the leaf cells are lax and bulging. As originally considered by Bescherele, this species belongs in *Lepidopilum*.

The types of the following species were not available for study. As judged from their descriptions there is nothing distinctive about them. Final disposition of these species, however, can not be made until their types are examined.

Crossomitrium goebelii C. Müll., Flora 83: 335. 1897. Type. Venezuela, Tovar, 1800 m altum Octobri 1890, in foliis adnatum, *Goebel s.n.* (K?,

RV?; not at M).

Crossomitrium phragmidiaceum C. Müll., Flora 83: 335. 1897. Type. Venezuela, Cumbre de Caracas, *Goebel s.n.* (K?, RV?; not at M).

Crossomitrium tenellum C. Müll., Flora 83: 335. 1897. Type. Venezuela, Tovar, 1800 m alt. in foliis adrepens, *Goebel s.n.* (K, RV?; not at M).

Crossomitrium wallisii C. Müll., Flora 58: 545. 1875. Type. Colombia, prov. Antioquia, Frontino, 8000 ped. altum in foliis repens, *Wallis* (not at H).

There is a collection in NY that appears to be a fragment of the type which was sent to Mrs. Britton. In annotations on the packet both Britton and Welch consider that the plants in the packet do not fit the description of *C. wallisii*. In view of Britton and Welch's doubts about the NY material it seems best to postpone a decision on this species until authentic type material is examined.

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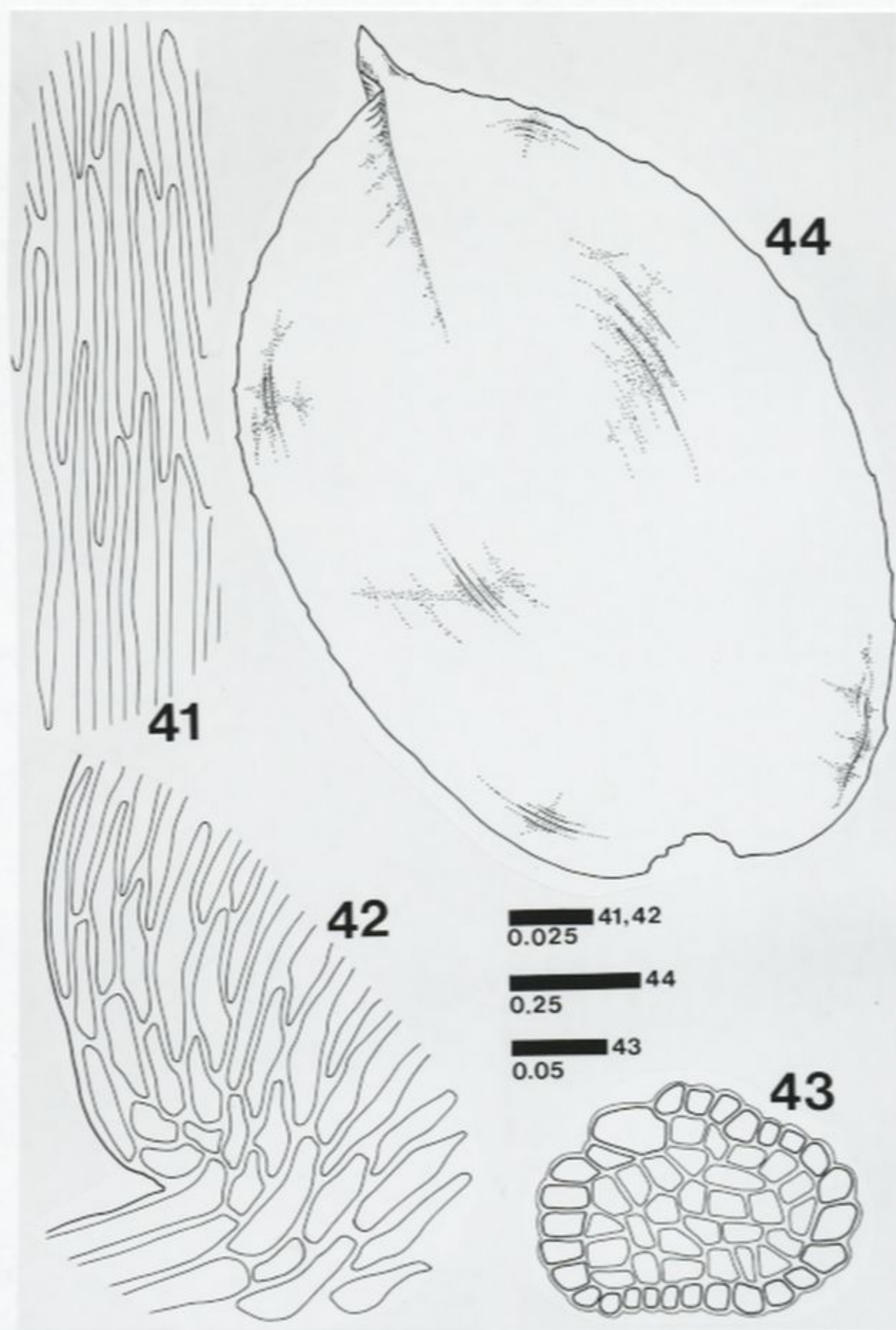
Figure 40. Distribution of *Crossomitrium sintenisii*.

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Figures 41-44. *Crossomitrium sintensisii*. Figure 41. Median leaf cells. Figure 42. Basal leaf cells. Figure 43. Cross section of stem. Figure 44. Lateral leaf