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A REVISION OF THE MOSS GENUS *ERYTHRODONTIUM* (ENTODONTACEAE)

By

Piers Majestyk

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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ABSTRACT

A REVISION OF THE MOSS GENUS *ERYTHRODONTIUM* (ENTODONTACEAE)

By

Piers Majestyk

Advisor: Dr. William Buck

A revision of the moss genus *Erythrodontium* recognizes eight species from the previously accepted 15 species. *Erythrodontium* is a mostly epiphytic genus in the family Entodontaceae. Members of the genus generally occur in somewhat mountainous regions throughout the tropics in both the Western and Eastern hemispheres. Taxonomic treatments, distribution maps and illustrations are given for each recognized species. Molecular and morphological data were analyzed in an attempt to better understand the phylogenetic relationships within the genus and family. Dubious, invalid and excluded names associated with the genus are discussed.

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me to reach this point and for my children that help to brighten each day.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

A taxonomic revision of *Erythrodontium* (Entodontaceae)

Introduction and history of the genus

This paper represents a world-wide taxonomic revision of the species of *Erythrodontium* Hampe, a genus of mosses in the family Entodontaceae. *Erythrodontium* consists of small to medium sized pleurocarpous mosses. The species are commonly corticolous but they can also be found growing on soil or rocks. Species of *Erythrodontium* generally occur in somewhat mountainous regions throughout the tropics in both the Western and Eastern hemispheres. *Erythrodontium* is a fairly well defined and seemingly natural group recognized by the following morphological features: 1) julaceous branches, 2) relatively broad, decurrent leaves, 3) numerous oblate alar cells, 4) erect capsules with deeply inserted peristome, 5) rudimentary endostome and 6) papillose spores (Figure 1).

The first species now placed in the genus *Erythrodontium* was described by Schwaegrichen (1828; as *Neckera julacea*) from a collection made in Nepal by Nathaniel Wallich, a Danish physician and botanist who collected in Nepal from 1820-22. G. E. L. Hampe (1870) erected the genus *Erythrodontium* to accommodate a single species collected in Brazil by Eugenius Warming, a Danish botanist who collected near Lagoa Santa from 1863-1866. The type of the genus, *E. warmingii* Hampe, was named in his honor. In his world-wide treatment of mosses Brotherus (1909) provided a circumscription that defined *Erythrodontium*, with 25 species, as one of 19 genera within the Entodontaceae. In Brotherus' (1925) second world-wide treatment of the mosses,

Erythrodontium with 31 listed species remained as one of 14 genera within the Entodontaceae. Nearly four decades after Brotherus' work the taxa he accepted within *Erythrodontium* remained largely intact, with the exception of the dioicous species that were moved into *Bryosedgwickia* and subsequently *Platygyriella*. Buck (1980), in his study of the Entodontaceae, was responsible for the reduction of several names into synonymy. Crosby et al. (2000) list of 15 species of *Erythrodontium* is largely made up of those names remaining after Buck's work. Of these 15 (ten occur in Africa/Asia and five in the New World) only three have been thoroughly treated with descriptions, illustrations, and discussions since the end of 1962 the closing date of *Index Muscorum*. Workers who have treated *Erythrodontium* on a regional basis include Bartram (1949; Guatamala), Buck (1998; West Indies), Churchill and Linares (1995; Colombia), Enroth (1991; Papua New Guinea), Gangulee (1980; India), and Sharp et al. (1994; Mexico). However, no one has attempted a revisionary work on a world-wide scale.

Critical examination of morphology and additional analysis by molecular sequencing of all species of *Erythrodontium* has resulted in the reduction of the New and Old World species to three and five taxa, respectively (Figures 2, 3).

Taxonomic treatment

ERYTHRODONTIUM Hampe

Erythrodontium Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn III, 2: 279. 1870.

Plants small to moderately robust, yellowish-green to red, usually densely matted, corticolous to saxicolous (less frequently on soil). Stems creeping, irregularly pinnately branched, with branches short to moderately long, branches straight to curved; in cross-section with small thick-walled colored cells (generally 2-4 layers) surrounding larger thinner-walled cells, central strand present, small; pseudoparaphyllia foliose; rhizoids yellow-orange, smooth, generally clustered on ventral surface; axillary hairs with a short brown-green basal cell and (1-)3(-4-5) larger hyaline rectangular cells. Stem and branch leaves slightly differentiated, crowded, stem leaves generally slightly larger and julaceous, branch leaves julaceous to imbricate when dry, somewhat spreading when wet, short- to long-oblong-ovate, abruptly or moderately apiculate, concave to cucullate, smooth, broadly decurrent; margins serrulate above, entire below, plain to rarely recurved; costa short and double to absent; cells rhombic, linear-rhomboidal or elongate, smooth, thin-walled, generally becoming shorter near the apex; alar cells differentiated, oblate to quadrate, extending 1/6 to 1/2 the leaf length up the margins, usually not reaching the costa. Asexual propagula none. Autoicous. Perichaetia small to large, along stems; leaves convolute, elongate, oblong-lanceolate, abruptly acuminate; margins entire to serrulate

above, entire below, plain; costa none; cells linear, straight, smooth, thin-walled, becoming shorter, thicker-walled and flexuose at the apex, becoming larger, lax and rectangular toward the insertion; alar cells not differentiated; archegonia numerous, paraphyses numerous, surpassing archegonia, composed of hyaline rectangular to flattened cells. Perigonia small, scattered along the stem near the perichaetia; antheridia numerous, subcylindric, light orange to brown; paraphyses numerous, surpassing antheridia, composed of hyaline rectangular to flattened cells. Sporophytes frequent; setae elongate, short to long, smooth, red-brown to yellow, slightly twisted; capsules exserted, erect, symmetric, short- to long-cylindric, yellow-brown to dark red-brown; exothecial cells quadrate to short rectangular, thin- to thick-walled, not collenchymatous, stomata few at base of urn; annulus not differentiated; operculum conic, short- to long-rostrate, straight; columella narrowly cylindric, sometimes exserted; peristome double, exostome teeth 16, narrowly triangular, yellow to orange-red, not shouldered, very narrowly bordered, on the front surface with a straight median line and relatively broad plates, smooth, striate or papillose below, smooth above, without prostome, not trabeculate at back, sometimes perforate along median line, smooth; endostome segments 16, rudimentary, with no basal membrane, segments smooth, linear, flat, not perforate, as long as the teeth, or more commonly discontinuous and adhering to the exostome, cilia none. Spores spherical, finely to coarsely papillose. Calyptra cucullate, naked or hairy (1 species), smooth.

Key to species

1. Plants from Central or South America 2

1. Plants from Africa or Asia 4

2. Leaves oblong-ovate, most > 1.0 mm long; seta yellow (rarely orange-light red in older collections) .....1. *E. longisetum*

2. Leaves suborbicular to shortly oblong-ovate, most < 1.0 mm long; seta red or yellow 3

3. Branch leaves generally tightly appressed; seta red; capsule not noticeably plicate ..... 2. *E. squarrosum*

3. Branch leaves not tightly appressed; seta yellow-brown; capsule somewhat plicate (known only from the type) .....3. *E. warmingii*

4. Branch leaves broadly oblong-ovate, generally > 1.0 mm long; calyptra naked or hairy 5

4. Branch leaves suborbicular to shortly oblong-ovate, generally < 1.0 mm; calyptra naked 7

5. Seta yellow; exostome yellow, smooth; calyptra naked; mid-laminal cells linear-elongate .....7. *E. engleri*

5. Seta yellow/brown to reddish; exostome light to dark orange, striate from base to at least middle of teeth; calyptra naked or hairy; mid-laminal cells rhombic to linear 6

6. Mid-laminal cells linear-elongate; seta short (most < 8 mm), yellow-brown; calyptra hairy .....8. *E. barteri*

6. Mid-laminal cells rhombic (sometimes somewhat linear-elongate); seta long (> 10 mm), light-dark brown; calyptra naked .....4. *E. julaceum*

7. Seta yellow to light brown; branch leaves shortly oblong-ovate to suborbicular; found in Asia .....5. *E. squarrosulum*

7. Seta red (although becoming fainter with age); branch leaves suborbicular to somewhat oblong-ovate; found in central to southern Africa ....6. *E. subjulaceum*

1. ***Erythrodontium longisetum*** (Hook.) Paris

Index Bryol. 436. 1896; *Neckera longiseta* Hook., Musci Exot. 1: 43. 1818. Type: [Colombia] Locis umbrosis, alsis montis Quindiu (Cordillera de los Andes de Cundinamara), *Humboldt & Bonpland* (lectotype BM!; isotype NY!).

Neckera teres Müll. Hal., Syn. Musc. Frond. 2: 98. 1850; *Entodon teres* (Müll. Hal.) Mitt., J. Linn. Soc., Bot. 12: 524. 1869; *Erythrodontium teres* (Müll. Hal.) Paris, Index Bryol. 437. 1896. Type: *Galeotti s.n.*, Mexico (isotype S!).

Neckera cylindricaulis Müll. Hal., Syn. Musc. Frond. 2: 100. 1850; *Leptohymenium cylindricaule* (Müll. Hal.) Hampe, Flora 45: 456. 1862; *Erythrodontium cylindricaule* (Müll. Hal.) Müll.Hal., Bull. Herb. Boissier 5: 208. 1897. Type: [Venezuela] Cumbre de Caracas, ad lapides, soc. *N. nigrescentis*, altitud. 5000 ft: *Wagner s.n.* 9 Sept. 1849 (lectotype NY!; syntype: Venezuela, Caripe: *Moritz 120,* BM!).

Leptohymenium consanguineum Hampe, Ann. Sci. Nat. Bot. sér. 5, 4: 373. 1865; *Erythrodontium consanguineum* (Hampe) Paris, Index Bryol. Ed.

2, 2: 157. 1904. Type: [Colombia] In Monte del Moro, 2200 m., *Lindig s.n.* (lectotype BM!, isotypes BM!, S!).

In the original description Hampe listed several collections made by Lindig as representing *L. consanguineum*. Of these collections some are *E. squarrosum* and some are *E. longisetum*. Amongst other things in the description is a reference to the yellow exostome teeth that makes it clear that Hampe was referring to the collections representing *E. longisetum*, thus *L. consanguineum* which has been recognized as a synonym of *E. squarrosum* is actually synonymous with *E. longisetum*.

Leptohymenium cylindricaule (Müll. Hal.) Hampe var. *rupestre* Hampe, Ann. Sci. Nat. Bot. sér. 5, 4: 372. 1865. Type: [Colombia] Bogota, Pacho, 1900 m., ad rupes. Julio, leg. *A. Lindig s.n.* (lectotype BM!, isotype BM!).

Pterigynandrum brasiliense Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 2: 280. 1870; *Erythrodontium brasiliense* (Hampe) Paris, Index Bryol. ed. 2, 2: 157. 1904. Type: [Brazil] Lagoa Santa ad arbores, 27 Jan.1864, leg. *E. Warming s.n.* (lectotype BM!).

Rhegmatodon hypnoides Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 232. 1872; *Cylindrothecium hypnoides* (Schimp. *ex* Besch.) Kiaer, Forh. Vidensk.-Selsk. Kristiania 1882(4): 43. 1883; *Entodon hypnoides* (Schimp. *ex* Besch.) Wijk & Margad., Taxon 8: 106. 1959. Type: Mexico, Mirador, *Liebmann s.n.* [type not seen].

Leptohymenium affine Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 246. 1872; *Erythrodontium affine* (Schimp. *ex* Besch.) Broth. *in* A. Engl. & K. Prantl, Nat. Pfl. 1(3): 888. 1907. Type: Orizaba, Mexico, *Lorentz s.n.* (lectotype NY!).

Leptohymenium myuroides Schimp. *ex* Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 246. 1872; *Erythrodontium myuroides* (Schimp. *ex* Besch.) Besch., J. Bot. (Morot) 15: 385. 1901. Type: Oaxaca, Cordillera, Mexico 1840, *Galeotti 6888* (lectotype BM!; isotype NY!).

Entodon argentinicus Müll. Hal., Linnaea 42: 432. 1879; *Erythrodontium argentinicum* (Müll. Hal.) Paris, Index Bryol. ed. 2, 2: 157. 1904. Type: Argentinia subtropica, Garone prope Salta inter alios muscos, cuesta de Siambon in Sierra de Tucuman et prope Siambon, fine March 1873, *Lorentz s.n.* (lectotype H-BR!, isotypes S! herb. numbers B36390, B36391).

Entodon germainii Müll. Hal., Nuovo Giorn. Bot. Ital. 4: 144. 1897; *Erythrodontium germainii* (Müll. Hal.) Paris, Index Bryol. Suppl. 1: 144. 1900. Type: Bolivia, prov. Cochabamba prope Choquecamata, *Germain 1128,* June 1881 (lectotype NY!).

Erythrodontium cylindricaule (Müll. Hal.) Müll. Hal. var. *pungenticaulis* Müll. Hal., Bull. Herb. Boissier 5: 208. 1897. Type: [Guatamala] In arboribus sylvae prope Coban, 4800 ped. altum, Febr. 1886: *H. v. Türckheim s.n.* [type not seen].

Erythodontium ochrocarpum Müll. Hal., *nom.nud.*, Hedwigia 38(Beibl.) 1: 59. 1899.

Erythrodontium minus Cardot, Rev. Bryol. 37: 11. 1910. Type: [Mexico] Orizaba in 1905, *W. Trelease 49* (lectotype MO!).

Erythrodontium macrocarpum Broth. *in* Herzog, Biblioth. Bot. 87: 127. 1916. Type: [Bolivia] In der Dornbuschsteppe von Comarapa, an Gesträuchwurzeln, alt. 1900-2000 m, *Herzog 4320* (isotype NY!).

Erythrodontium germainii (Müll. Hal.) Paris var. *brevipes* Broth. *in* Herzog, Biblioth. Bot. 87: 127. 1916. Type: [Bolivia] Bei Tres Cruces, Cordillere von Santa Cruz, ca. 1400 m, *Herzog 3490* [type not seen].

Erythrodontium andinum Müll. Hal. *in* M. Fleisch., *nom.inval. in synon.*, Hedwigia 59: 217. 1917.

Erythrodontium bescherellei (bescherellii) Müll. Hal. *in* M. Fleisch., *nom. inval. in synon.*, Hedwigia 59: 217. 1917.

Erythrodontium denticulatum Müll. Hal. *in* M. Fleisch., *nom.inval. in synon.*, Hedwigia 59: 217. 1917.

Plants medium to moderately robust, in mostly yellow-green, dense mats, corticolous to saxicolous, autoicous. Stems complanate to subjulaceous, densely foliate, pinnately branched; in cross section 3-4 layers of small, yellow, incrassate cells surrounding a cortex of 9-14 layers of larger thin-walled gray cells; rhizoids yellow-orange, smooth, in clusters on ventral surface; pseudoparaphyllia foliose. Axillary hairs composed of a small yellow basal cell and 3-4 larger rectangular-elliptical hyaline apical cells. Branches julaceous,

straight to slightly curved, ascending, generally all pointing the same direction, irregularly spaced, 7-10 mm long. Stem leaves 1-1.6 × 0.4-0.8 mm, broadly oblong-elliptical to broadly obovate-lanceolate, cuspidate, decurrent; margins entire to slightly serrulate at the apex; costa short, double or more frequently absent, extending 1/8 to 1/6 of leaf length; upper laminal cells linear-rhomboidal, thick-walled, 20-38 × 5.5-7.5 μm; median cells linear-rhomboidal, thin-walled, 70-130 μm long; alar cells oblate to quadrate, confined to leaf corners, extending 1/5 to 1/3 the leaf length, 7-24 × 16-28 μm. Branch leaves 1-1.6 × 0.33-0.75 mm, broadly obvate to oblong-lanceolate, acute, concave, decurrent, entire to slightly serrulate at the apex; costa short, double or absent, very pale, yellow, extending to 1/5 the leaf length; cells as in stem leaves. Perigonial leaves 0.6-1.2 × 0.25-0.4 mm, broadly oblong-lanceolate, entire, ecostate; basal cells rectangular, median upper cells linear-rhomboidal; antheridia light brown, slightly curved, 280-360 × 55-65 μm, cells rectangular, bulging; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, oblong-ovate lanceolate, inner leaves oblong-long lanceolate (3-4 mm long post-fertilization), entire to serrulate at the apex, ecostate; basal cells long-rectangular, crowded; median-upper cells linear-rhomboidal; archegonia 460-500 μm long, orange; paraphyses numerous. Setae yellow, turning darker with age, 0.8-2.3 cm long; capsules erect, cylindric, exserted, 2-3.5 × 0.7-1 mm, light brown, smooth; operculum dark yellow-brown, 0.8-1.1 mm long, conic, obliquely long-rostrate; exostome teeth 260-290 × 55-85 μm, yellow, smooth above, faintly striate in the basal area below the capsule mouth; endostome

segments rudimentary, yellow, smooth, composed of rectangular cells, approaching length of exostome teeth but frequently discontinuous; cilia absent. Spores spherical, yellow-orange, papillose, 17-37 μm. Calyptra, smooth, naked, pale yellow, 3-4 mm long.

Etymology. The specific epithet refers to the "long" seta.

Distribution. West Indies, Mexico, Central and South America except Chile, Figure 4.

Illustrations. Bartram (1949, Fig. 161, D-E); Buck (1998, Plate 114 (1-7)); Hooker (1818, table XLIII (1-9)); Sharp et al. (1994, Fig. 715, A-G); Figure 5.

Ecology. On bases and branches of trees and on rocks, generally between 1200-2800 m.

The frequently fruiting *E. longisetum* can be easily recognized from the other two taxa in the New World by its yellow seta and smooth, yellow exostome teeth. The leaf morphology of *E. longisetum* is quite variable as can be attested by the fairly lengthy list of synonyms attributed to it. *Erythrodontium argenticum* is representative of a robust expression of *E. longisetum* with some leaves reaching 1.5 mm in length. *Erythrodontium teres,* with its smaller area of alar cells, leaves generally near 1 mm long and short apiculate apex, is representative of a smaller expression of *E. longisetum.* Another notable phenotypic expression appears in a collection from Paraguay (*Buck 12149A*, NY), in which the branch leaves have an extremely long acuminate apex, which makes up nearly half of the leaf's length.

The one species likely to be confused with *E. longisetum* when sterile is *Platygyriella pringlei* (Cardot) W. R. Buck. The leaves of *E. longisetum* are generally oblong compared to the more ovate leaves of *P. pringlei*. The decurrent leaf cells of *P. pringlei* generally have a few enlarged cells which generally remained attached to the stem when the leaves are stripped from it whereas the decurrent leaf cells of *E. longisetum* are not differentiated. The dioicous sexual condition of *P. pringlei* along with the red seta and exostome teeth when sporophytes are present are also characters that can aid in distinguishing the two. *Platygyriella pringlei* is usually rupestral while *E. longisetum* is more frequently corticolous although it also occurs on rock.

Representative specimens examined.

ARGENTINA. Jujuy [23°00'S, 66°00'W]: Chaco-Andinis, *Fries 6, 44* (S); Misiones: Posadas [27°22'S, 55°52'W], *Ekman 2078* (FH); Salta: Dept. Orán, San Andres, 1540 m, 23°04'S, 64°50'W, *Churchill & Schiavone 20007* (MO), Dept. La Caldera, 24°35′S, 65°21′W, 1340 m, *Buck 26236A* (NY); Tucumán: Chicligasta [27°28'S, 65°07'W], Alpachiri, 600 m, *Venturi 1844* (FH), El Indio, 27°03′S, 65°40′W, 960 m, *Buck 26032* (NY).

BELIZE. Cayo: Caracol ruins, ca. 14 km W of Las Cuevas Field Station, 16°46'N, 89°07'W, 520 m, *Allen 18191* (MO).

BOLIVIA. Chuquisaca: Prov. Jaime Mendoza, 19°33′S, 64°09′W, ca. 1620 m, *Lewis 84-821* (NY); La Paz: Polopolo, bei Coroico [16°10'S, 67°43'W], *Buchtien 37* (S); Santa Cruz: bei Comarapa [17°53'S, 64°28'W], ca. 2000 m,

Herzog 4320 (BM); Tarija: Prov. Gran Chaco, 21°26′S, 63°55′W, ca. 1460 m, *Lewis 84-2889* (NY).

BRAZIL. Ceará: Sitio Uruguaiana, 4 km W of Guaramiranga [4°15'S, 38°55'W], 700 m, *Cutler 8316* (BM); Minas Gerais: Caldas [21°55'S, 46°22'W], *Regnell s.n.* (S), Parque Nacional do Itatiaia, 22°22′S, 44°45′W, 1900 m, *Vital & Buck 19417* (NY); Paraná: Mun. Foz do Iguaçu, Parque Nacional do Iguaçu, 100-200 m, 25°40′S, 54°25′W, *Vital & Buck 12070* (NY); Rio de Janeiro: Brasilia, Nova Friburgo [22°16'S, 42°31'W], *Dusén s.n.* (NY), Serra do Itatiaia [22°00'S, 42°30'W], *Dusén 1602, 1655* (S), Praça D. Affonso, Petrópolis [05°52'S, 36°42'W], *Bandeira 209* (NY); Santa Catarina [27°00'S, 50°00'W]: Serra Geral, Capãos, *Ule 184* (BM); São Paulo: Santa Rita do Passa Quatro, Santa Albertina [21°16'S, 47°58'W], *Hemmendorff 106* (NY, S).

COLOMBIA. Antioquia: Municipio Medellín, Corregimiento de San Antonio de Prado, ca. 10 km de San Antonio, 06°10′N, 75°35′W, *Churchill et al. 14005* (NY), Municipio de Sonson, 05°41′N, 75°21′W, 2420 m, *Churchill et al. 15533* (NY); Cauca [03°00'N, 77°00'W]: 6000-7000 ft, *Steere 7850* (NY); Cundinamarca: Municipio de El Charquito, ca. 04°32′ N, 74°18′ W, 1930-1940 m, *Linares & Churchill 3755* (NY); Nariño: Municipio de Yacuanquer, ca. 4 km N of Río Guaitara, ca. 01°04′ N, 77°24′W, 2000 m, *Churchill & Rengifo 17586* (NY); Santander [07°00'N, 73°00'W]: Vicinity of Sarantá, 1600-1800 m, *Killip & Smith 16501* (NY); Tolima: Municipio de Ibagué [04°27'N, 75°14'W], 1800 m, *Morales 57* (NY); Valle: Municipio de Cali, ca. 03°15-20′ N, 75°30′ W, 1050-1090 m, *Churchill et al. 15264* (NY).

COSTA RICA. Cartago: Tapantí Forest Reserve ca. 25 km SE of Cartago [09°40'N, 83°40'W], 1000-1500 m, *Griffin & Eakin 19958* (NY); San José: vicinty of Zapote [09°52'N, 84°19'W], 1200 m, *Standley 40272* (NY), vicinity of San Sebastián [09°55'N, 84°04'W], 160 m, *Standley 49370* (NY).

CUBA. Las Villas: Trinidad mountains, Santa Clara [22°24'N, 79°58'W], *Britton 5432* (NY).

DOMINICAN REPUBLIC. Prov. Azua: Cañada Miguel Martín, 18°39'N, 70°43'W, 1500-1600 m, *Mejía & Zanoni 8271, 8275* (both NY); Prov. La Vega: Vicinity of Constanza [18°55'N, 70°45'W], 1000-1600 m, *Allard 17563a, 17589, 17597g* (all NY).

ECUADOR. Guayas: Vicinity of Huigra [02°46'S, 79°25'W], *Rose 23658* (NY); Napo: Banks of River Napo [00°30'S, 77°00'W], *Villavencia 140* (FH); Pichincha: Quito [00°13'S, 78°30'W], *Jameson 87* (NY).

GUATAMALA. Alta Verapaz: Cobán [15°28'N, 90°22'W], 1350 m, *Türckheim 6907, 6674* (BM, NY, S); Huehuetenango [15°19'N, 91°28'W]: near ruins of Zaculeu, ca. 1800 m, *Standley 82776* (NY); Quiché: Uspantán [15°22'N, 90°49'W], 6400 ft, *Hermann 26369* (NY, S).

HAITI. Dept. de l'Artibonite: Vicinity of Ennery [19°28'N, 72°28'W], 325 to 900 m, *Leonard 9523* (NY); Near Douz[y]ette [18°21'N, 74°04'W], 800 m, *Ekman 642* (NY, S).

HONDURAS. Comayagua: near Siguatepeque [14°32'N, 87°49'W], 1050 m, *Yuncker et al. 6540* (NY), Quebrada Agua Helado, above San José Del Los Planes, ca. 1000 m, 14°47'N, 87°51'W, *Allen 13728* (MO); Intibucá: El Cayo

District, San Agustin [14°07'N, 88°16'W], *Mains 4039* (NY); Olancho: Slopes of Montana Peña Blanca, 980-1000 m, 14°57'N, 86°08'W, *Allen 12414* (MO).

JAMAICA. Farm Hill [18°01'N, 76°37'W], *Orcutt 3461* (NY); Blue Mountains, Chestervale [18°04'N, 76°40'W], *Britton 1050* (NY, S); near Trafalger Gap [18°21'N, 77°10'W], Port Royal Mountains, 1125 m, *Maxon 8736* (BM, NY).

MEXICO. Chiapas: Yerba Buena, Pueblo Nuevo [15°31'N, 92°34'W], ca. 6800 ft, *Sharp et al. 4228* (NY); Guerrero: Chilpancingo [17°33'N, 99°40'W], 6000 ft, *Sharp 1063* (NY), ca. 25 km west of Michoacán, Ixtlán [20°10'N, 102°24'W], Sierra Juarez, 7800 ft, *Hermann 26252* (NY); Hildago: along Hwy 85, ca. 6 mi N of Jacala [21°01'N, 99°10'W], *Norris 17243, 17284* (NY); Michoacán: Lake Patzcuaro [19°31'N, 101°36'W], *Frye & Frye 2786* (NY); Oaxaca [17°00'N, 96°30'W]: Cordillera, *Galeotti 6888* (BM); Queretaro: west of Jalpan [21°13'N, 99°28'W], *Webster et al. 180a* (NY); San Luis Potosi: Tamasopo [21°55'N, 99°28'W], 1000 ft, *Pringle 766* (BM, NY, S), San Luis Potosí: ca. 4.0 km W of centre of Xilitla [21°20'N, 98°58'W], elev. 2600-2900 ft, *Vitt 17873* (NY); Tabasco: Jalapa [17°43'N, 92°49'W], 5000 ft, *Murrill & Murrill 27* (NY); Veracruz: Orizaba [18°51'N, 97°05'W], *Borgeau 3291* (BM).

NICARAGUA. Madriz: lower slope of Cerro Volcán de Somoto, 900-1300 m, 13°25'N, 86°35'W, *Stevens 16433* (MO); Matagalpa [13°00'N, 85°30'W]: Hamonia, Selva Negra, 1220 m, *Granzow de la Cerda 2145a* (MO, NY); Matagalpa: Santa María [12°40'N, 86°09'W], 1500 m, *Seymour 2160a* (MO).

PANAMA. Chiriquí: Alto Quiel [08°48'N, 82°28'W], Finca La Fortuna, *Salazar et al. 862* (MO), Finca de Cora Sasse, Boquete [08°46'N, 82°25'W], ca. 3474 m, *Beliz & Correa 889* (MO).

PARAGUAY. Alto Paraná: Cuidad Nueva, 250 m, 25°30′S, 54°41′W, *Buck 12285* (NY); Caaguazú: Coronel Oviedo [25°25'S, 56°27'W], Barrio Azucena, *Bordas 109* (NY); Guará: Parque National Ybycuí, 200 m, 26°05′S, 56°53′W, *Buck 12112* (NY); Itapúa: 200 m, 27°08′S, 55°45′W, *Buck 12197* (NY).

PERU. Amazonas: Prov. of Chachapoyas [06°13'S, 77°50'W], 2400 m, *Hutchison & Wright 4802* (NY); Ayacucho: Aina, between Huanta [12°55'S, 74°15'W] and Río Apurimac, 750-1000 m, *Killip & Smith 22527a* (NY); Cajamarca: Prov. Celedín [06°52'S, 78°09'W], 2500 m, *Sagástegui et al. 8445* (NY); Cuzco [12°30'S, 72°30'W]: Provencia La Convencion, 5500 ft, *Bües 1134* (NY); Libertad: Prov. Otuzco [07°07'S, 78°27'W], 2050 m, *Hegewald 5229* (NY); Pasco: Prov. Oxapampa, Piña Flor 12 km von Oxapampa [10°34'S, 75°24'W] in Richtung Tarma, 1750 m, *Hegewald 8425* (NY); San Martín: Tarapoto [06°30'S, 76°25'W], *Spruce 1023* (NY).

URUGUAY. [33°00'S, 56°00'W] *Felippone s.n.* (S).

VENEZUELA. Distrito Federal: El Paraíso, Caracas [10°30'N, 66°55'W], 850 m, *Pittier 13780* (NY); Lara: near San Angelito on road to Guarico [09°37'N, 69°47'W], 1000 m, *Steyermark & Rabe 97460* (NY); Mérida [83°00'N, 71°10'W]: Hacienda Lourdes, Sierra Nevada, 1750-1850 m, *Chardon s.n.* (NY), vicinity of Timotes [08°58'N, 70°43'W], 2000-2050 m, *Pittier 12697, 12949* (NY); Monagas [09°20'N, 63°00'W]: 1220 m, *Pursell 8467* (NY).

2. ***Erythrodontium squarrosum*** (Hampe) Paris

Index Bryol. ed. 2, 2: 159. 1904; *Leptohymenium squarrosum* Hampe, Flora 45: 456. 1862; *Neckera squarrosa* Müll. Hal., Syn. Musc. Frond. 2: 100. 1850; *Entodon squarrosus* (Hampe) Mitten, J. Linn. Soc. Bot. 12: 524. 1869; *Pterigynandrum squarrosum* (Hampe) Hampe, Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 2: 281. 1870. Type: Brasilia, Serro do Santa Brida, prov. Goyaz: *Gardner 77.* Febr. 1840 (lectotype BM!, isotypes BM!, NY!); .

Pterigynandrum latifolium Ångstr., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 33(4): 45. 1876; *Erythrodontium latifolium* (Ångström) Müll. Hal. in Paris, Index Bryol. 436. 1896. Type: St. Salvador in Honduras (lectotype S!, isotype BM!).

Leptohymenium squarrosum Hampe var. *griseum* Besch., Mém. Soc. Sci. Nat. Cherbourg 21: 268. 1877; *Erythrodontium setulosum* Müll. Hal. var. *griseum* (Besch.) Paris, Index Bryol. ed. 2, 2: 159. 1904. Type: [Paraguay] Assomption, *Ch. D' Orbigny 1262* (lectotype BM!).

Erythrodontium griseum Müll. Hal. *in* M. Fleisch., *nom.inval. in synon.*, Hedwigia 59: 217. 1917. I have not seen the specimen to which this name is attached.

In the original description, Ångström described the leaves of *E. squarrosum* (which is sterile) but the seta of *E. longisetum* (both of which appear side by side in the BM collection but only *E. squarrosum*

is present in the S collection). According to Article 9.12 of the 2000 ICBN when a type specimen contains more than one taxon the name must remain attached to that part which corresponds most nearly with the original description. It is my opinion that the original description is most closely associated with *E. squarrosum*.

Plants small, green to reddish brown, corticolous, saxicolous or terrestrial, autoicous. Stems complanate to subjulaceous, densely foliate, pinnately branched; in cross section composed of 3-4 layers of small, yellow incrassate epidermal cells surrounding 5-6 layers of larger, gray cortical cells, central strand not evident; rhizoids light to dark orange, smooth, in clusters on the ventral surface; pseudoparaphyllia foliose. Branches julaceous, ascending, curved, generally all pointing the same direction, densely foliate, 5-9 mm long. Axillary hairs composed of a short, yellow-orange basal cell and 3 elliptical-rectangular, hyaline apical cells. Stem leaves 0.65-0.9 × 0.35-0.62 mm, tightly imbricate with retrorse apices, concave, suborbicular to short oblong-ovate, abruptly rounded to an apiculus, cordate at base, decurrent; margins entire to faintly serrulate at apex; costa yellow, short and double, reaching 1/3 of the leaf length; upper laminal cells linear-rhomboidal, thick-walled, 23-34 × 5-6 μm; median cells linear-rhomboidal, 32.5-62 × 4.4-6.7 μm; alar cells differentiated, oblate near margins, becoming ± quadrate near costa, extending 1/4 to 1/2 the leaf length, 5.2-22.2 × 12.6-23.7 μm. Branch leaves 0.6-0.9 × 0.25-0.5 mm, in other respects very similar to stem leaves. Perigonial leaves 0.5-0.75 × 0.16-

0.32 mm, oblong-cuspidate, entire to serrulate at apex, ecostate; lower cells rectangular, bulging, upper-median cells linear-rhomboidal; antheridia light brown, straight to slightly curved, 290-310 × 65-70 μm, cells bulging, rectangular; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, oblong-cuspidate, inner leaves oblong-lanceolate (2.5-2.8 mm long post-fertilization), entire to slightly serrulate at the apex, ecostate; basal cells rectangular, bulging; middle and upper cells linear-rhomboidal; archegonia 275-325 μm long, orange; paraphyses numerous. Setae red, becoming lighter (yellowish) with age, 1-1.7 cm, smooth; capsules erect, short, smooth to slightly plicate, cylindric, exserted, 1.5-2.5 × 0.5-0.6 mm, light brown-green; operculum light to dark brown, 0.5-0.8 mm long, conic, obliquely rostrate; exostome teeth 310-365 × 87-135 μm, light to dark orange, striate and papillose almost to the apex; endostome segments rudimentary, yellow, composed of rectangular to elliptical cells, smooth, almost reaching length of exostome teeth but frequently discontinuous; cilia absent. Spores spherical, orange, papillose, 20-35 μm. Calyptra smooth, naked, yellow, 2.5-3 mm long.

Etymology. The specific epithet squarrosum presumably refers to the nature of the leaf attachment when moistened.

Distribution. Mexico, Central America, Argentina, Bolivia, Brazil, Colombia, Paraguay, Peru, Figure 6.

Illustrations. Bartram (1949, Fig. 161, A-C); Sharp et al. (1994, Fig. 716, A-G); Figure 7.

Ecology. On rocks, soil and bases of trees, 100-2200 m.

Erythrodontium squarrosum is a fairly distinctive moss that is unlikely to be confused with other taxa. It can be characterized by its small size, tightly imbricate leaves, frequent fertility, red seta and cylindrical capsule with orange-red striate exostome teeth. *Erythrodontium squarrosum* and *E. longisetum* show roughly the same distribution. Several times I have found them in the same collections intertwined with each other although *E. squarrosum* is generally found at lower elevations than *E. longisetum*.

Representative specimens examined.

ARGENTINA. Misiones: Posadas [27°22'S, 55°52'W], *Ekman 2066* (FH); Salta: Nueva Orán, Misión de Zenta [23°07'S, 64°22'W], *Sleumer 1981* (S), La Candalaria [26°06'S, 65°05'W], *Hosseus 603A* (S).

BOLIVIA. Beni: Ballivian, Estación Biológica del Reni near Porvenir, 14°30'S, 66°30'W, 200-250 m, *Lewis 89-037 d3* (MO); La Paz: Apolo [14°43'S, 68°31'W], 1500 m, *Williams 1974* (NY); Santa Cruz: Prov. Cordillera, 19°48′S, 63°43′W, 1560 m, *Lewis 84-1070A* (NY).

BRAZIL. Goiás: 50 km N of Corumbá de Goiás [15°55'S, 48°47'W], *Irwin et al. 21793* (NY), Côrrego Landim [15°10'S, 48°00'W], ca. 25 km N of Brasília, 950 m, *Irwin et al. 13983* (NY, S); Mato Grosso: 5 km E of town of Chapada do Guimarães [15°25'S, 55°45'W] on road to Embratal, 720 m, *Prance et al. 19377* (NY); Minas Gerais: Mun. São Roque de Minas, ca. 23 km NE of São Roque de Minas, ca. 600 m, ca. 20°10′S, 46°15′W, *Vital & Buck 11875* (NY); Pará: Serra do Cachimbo, ca. 20 km N of border of Mato Grosso, ca. 09°22′S, 54°54′W, ca. 430-480 m, *Reese 16129* (NY); Paraná: Mun. Foz do Iguaçu, Parque Nacional

do Iguaçu, 100-200 m, 25°40′S, 54°25′W, *Vital & Buck 12075* (NY), prope Castro [24°46'S, 50°00'W], 2000 ft, *Weir 57* (BM); Rio de Janeiro [22°00'S, 42°30'W]: *Glaziou 7927, 9287* (BM, NY); Rio Grande do Sul: 1 km W of Sobradinho [07°07'S, 42°00'W], ca. 1100 m, *Irwin et al. 33250* (NY, S).

COLOMBIA. Antioquia: Municipio de Valparaíso, 700 m, 05°44′N, 75°35′W, *Churchill & Marulanda 15662* (NY), Santa Fé de Antioquia [06°33'N, 75°49'W], via Uramita - Sta. Fé, 13 km S de Uramita, 1080 m, *Callejas et al. 5143* (NY), Municipio Liborino, 910-1030 m, 06°40′N, 75°45′W, *Churchill et al. 14600, 14648, 14652* (all NY); Atlantico: Municipio Sabanalarga, 1100 m, 06°45′N, 75°45′W, *Churchill et al. 14679* (NY); Huila: Transecto Neiva-San Vicente del Caguán, 02°56′N, 75°11′W, 680 m, *Churchill & Betancur 16763, 16768e* (both NY); Nariño: Mpio. del Tablón, Río Juanam bú, Buesaco-Tablón, 01°23′N, 77°04′W, 1500 m, *Ramírez 3722* (NY).

COSTA RICA. Alajuela [10°30'N, 84°30'W]: Entre Ríos Itiquis y Poas, *Brenes 17347* (NY).

EL SALVADOR. La Libertad: 870 m, 13°42'N, 89°15'W, *Renderos 504* (MO); San Salvador [13°41'N, 89°12'W]: 650-850 m, *Standley 22456* (MO, NY).

GUATAMALA. Jalapa: La Laguna [14°38'N, 89°59'W], at base of Volcán Jumay, 1 mile north of Jalapa, 1400-1600 m, *Steyermark 32245* (NY).

HONDURAS. [15°00'N, 86°30'W] *Hjalmarsson s.n.* (S).

MEXICO. Chiapas [16°30'N, 92°30'W]: 6100 ft, ca. 20 mi SE Teopisca, *Hermann 26376* (NY); Guerrero: 25 km west of Chilpancingo [17°33'N,

99°40'W], 6000 ft, *Sharp 1029* (NY); Nayarit: Cerro de San Juan [21°30'N, 105°00'W], W of Tepic, 1000 m, *Mexía 695-b* (NY).

PARAGUAY. Amambay: Parque Nacional Cerro Corá, along trail up Cerro Muralia, ca. 300 m, ca. 22°40′S, 56°00′W, *Buck 12481* (NY); Central: Asunción, Jardin Botánico y Zoológico, 25°16'S, 57°40'W, *Zardini & Aquino 32309* (MO).

PERU. Cuzco [12°30'S, 72°30'W]: Prov. La Convención, 1000 m, *Mexia 8092* (BM, NY, S); San Martín: Tarapoto [06°30'S, 76°25'W], *Spruce 138* (NY).

VENEZUELA. Distrito Federal: vicinity of Caracas [10°30'N, 66°55'W], *Rose 21679* (NY); Monagas: Caripe [10°10'N, 63°28'W], *Moritz 117* (NY); Miranda: La Malva, near Las Mostazas [10°19'N, 67°04'W], 1100 m, *Allart 280* (NY).

3. ***Erythrodontium warmingii*** Hampe

Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn ser. 3, 2: 279. 1870; *Entodon warmingii* (Hampe) Müll. Hal., Linnaea 42: 434. 1879; *Leptohymenium warmingii* (Hampe) A. Jaeger, Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1877-78: 479. 1880. Type: Brazil, Lagoa Santa, in silvis ad arbores, *Warming s.n.* (lectotype BM!, isotype NY!)

Plants small, yellow to light green, corticolous, autoicous. Stems adnate to the substrate, complanate to subjulaceus, densely foliate, pinnately branched; in cross section with 2-3 rows of small, incrassate, yellow epidermal cells

surrounding a cortex of 6-7 rows of larger, thin walled gray cells, central strand not evident; rhizoids yellow-orange, smooth, in clusters on the ventral surface; pseudoparaphyllia foliose. Branches julaceous, ascending, generally all pointed the same direction, mostly straight to curved, densely foliate, laxly imbricate, 4-6 mm long. Axillary hairs composed of one short, yellow-green to brown basal cell and 2-3 elliptical-rectangular hyaline apical cells. Stem leaves 0.65-1 × 0.4-0.7 mm, oblong-ovate to elliptical, loosely arranged, most slightly concave, acute to apiculate, apex curved, cordate at base, more or less clasping the stem, decurrent; margins reflexed, entire to weakly serrulate near the apex, costa double, pale yellow, straight, extending 1/4 to 1/3 the leaf length; upper laminal cells linear-rhomboidal, thick-walled, 14.8-24.5 × 5.9-9 μm; median cells linear-rhomboidal, 46.5-74(-89) × 7.4-9 μm; alar cells differentiated, oblate to quadrate nearer the costa, extending 1/4 to 1/3 the leaf length, not reaching the costa, 9.5-13.3(-17.75) × 13.3-15.6 μm. Branch leaves 0.8-1 × 0.33-0.72 mm, oblong-ovate to elliptical, laxly appressed dry, erect-spreading when moist, mostly slightly concave, acute or apiculate, apices slightly twisted, decurrent; margins reflexed, entire to slightly serrulate near apex; costa double or occasionally absent, pale yellow, straight, extending 1/4 to 1/3 the leaf length; cells as in stem leaves. Perigonial leaves 0.65-1 × 0.25-0.35 mm, ovate-lanceolate, apex slightly to moderately curved; margins serrulate; costa none; laminal cells linear-rhomboidal, alar cells quadrate in small area; antheridia light brown, slightly curved, 270-325 × 55-60 μm, cells rectangular, bulging; paraphyses numerous. Perichaetial leaves tightly convolute, outside leaves shorter, widely ovate-

lanceolate, inner leaves oblong-lanceolate (2.5-3 mm long post-fertilization), acuminate, entire to serrulate at apex, ecostate; basal cells subrectangular, apical cells densely aggregated, narrow, linear, clear; archegonia 250-300 μm long, orange; paraphyses numerous. Setae yellow to brown, 5-7 mm, smooth; capsules erect, short, cylindric, exserted, 1.5-2(2.5) × 0.5-1 mm, copper-brown, plicate. Opercula copper-brown, 0.8-1 mm long, conic-rostrate; exostome teeth 220-250 × 80-90 μm, light to dark orange (blood red in protologue), occasionally fenestrate, papillose at base, striate to apex; endostome segments rudimentary, composed of rectangular cells, as long as the exostome teeth, lower half striate, upper portion smooth; cilia absent. Spores spherical, orange, papillose, 18-26 μm. Calyptra campanulate, smooth, naked, yellow, 2.5-3 mm long.

Etymology. The specific epithet warmingii honors Eugenius Warming (1841-1924), a Danish botanist who collected the type specimen while working in Lagoa Santa, Brazil (1863-1866).

Distribution. Brazil, Figure 8.

Illustrations. Figure 9.

Ecology. The single known specimen was collected on a tree trunk in Lagoa Santa, Brazil.

Erythrodontium warmingii can be characterized by its short yellow-brown seta, plicate capsules when dry, orange-red exostome, recurved leaf margins and oblong-ovate to elliptical, faintly plicate leaves with an apiculate apex. The only other member of the genus with a short yellow-brown seta and plicate brown capsule is *E. barteri* from the central west coast of Africa. In addition to the

geographic difference *E. barteri* has a hairy calyptra and longer attenuate leaf apices.

4. ***Erythrodontium julaceum*** (Hook. *ex* Schwägr.) Paris

Index Bryol. 436. 1896. *Neckera julacea* Hook. *ex* Schwägr., Sp. Musc. Suppl. 3(1): 245. 1828; *Leptohymenium julaceum* (Schwägr.) Hampe, Linnaea 20: 83. 1847; *Pterogonium julaceum* (Schwägr.) Hook. *in* Müll. Hal., Syn. Musc. Frond. 2: 101. 1850; *Platygyrium julaceum* (Schwägr.) Bosch & Sande Lac., Bryol. Jav. 2: 107. 1864; *Entodon julaceus* (Schwägr.) Müll. Hal., Linnaea 42: 435. 1879; *Erythrodontium juliforme* (Mitten) Paris, Index Bryol. 436. 1896. Type: Nepal, leg. *Wallich 3647* (lectotype BM!).

Pterogonium squarrosum Griff., Cal. J. Nat. Hist. 3: 63. 1843. Type. [India] Super arbores sylvarum Tingrei vicinitatisque Suddiyae (lectotype BM!).

Erythrodontium lacoutourei Renauld & Cardot, Prodr. Fl. Bryol. Madag. Suppl. 74: 1909. Type: Madagascar: Fianarantsoa, *Rev. Villaume s.n.*, 1905 (lectotype H-BR!, isotype FH!).

Erythrodontium lamoruense Thér., Bull. Mus. Natl. Hist. Natur. 30(3): 244. 1924. Type: British East Africa [Kenya]: Lamoru, plateau Kikuyu, 2000 m, Mission Gromier-Le Petit, 1911 (lectotype H-BR!).

Plants medium, olive-green to reddish brown, corticolous or saxicolous, autoicous. Stems complanate to subjulaceous, densely foliate, in mats, pinnately

branched; in cross section somewhat flattened, composed of 3-4 layers of small, yellow incrassate epidermal cells surrounding 8-12 layers of larger, gray cortical cells, central strand poorly differentiated; rhizoids light-dark orange, smooth, in clusters on the ventral surface; pseudoparaphyllia foliose. Branches julaceous, ascending, curved, densely foliate, 4-10 mm long. Axillary hairs composed of a short yellow-orange basal cell and 2-3 rectangular, hyaline apical cells. Stem leaves 1-1.6 × 0.7-1 mm, loose to tightly imbricate, plane to slightly concave, oblong-ovate, acute to acuminate; margins entire to faintly serrulate near apex; costa yellow, very short and double or frequently absent; upper laminal cells linear to linear-rhomboidal, thick-walled, 40-85 × 7.4-9.25 μm; median cells linear, 50-97 × 7.4-9.25 μm; alar cells oblate, extending 1/3 to 1/2 the leaf length, 7.4-18.5 × 13-24 μm. Branch leaves (0.9-)1-1.5 × 0.6-0.8 mm, in other respects very similar to stem leaves. Perigonial leaves 0.6-1 × 0.35-0.85 mm, oblong-cuspidate, entire to serrulate at the apex, ecostate; lower cells rectangular, bulging, upper-median cells linear-rhomboidal; antheridia light brown, straight to curved, 280-315 × 74-110 μm, cells rectangular, bulging; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, oblong-cuspidate, inner leaves oblong-lanceolate (2.7-3 mm long post-fertilization), entire to slightly serrulate at the apex, ecostate; basal cells rectangular, bulging; median and upper cells linear; archegonia 190-325 μm long, orange; paraphyses numerous. Seta light to dark brown, 1.3-2 cm, smooth, slightly twisted; capsules erect, cylindric, smooth, exserted, 2.3-3.5 × 1-1.25 mm, light to dark brown; operculum light to dark brown, 0.85-1 mm long, conic,

obliquely rostrate; exostome teeth 265-290 × 70-100 μm, light to dark orange, striate to middle or higher, fenestrate above middle, upper portion striate or occasionally smooth; endostome segments rudimentary, yellow, composed of rectangular to elliptical cells, smooth, almost reaching length of exostome teeth but frequently discontinuous; cilia absent. Spores spherical, orange, papillose, 22-41 μm. Calyptra smooth, naked, yellow, 3-3.5 mm long.

Etymology. The specific epithet julaceum presumably refers to the julaceous nature of the branches, particularly when moist.

Distribution. Burma, China, Ethiopia, India, Malawi, Nepal, New Guinea, Philippines, Tanzania, Thailand, Vietnam, Figure 10.

Illustrations. Schwaegrichen (1828, Tab. CCXLV, Fig. 1-15), Renauld and Cardot (1909, Plate XVII, Fig. 1, a, a', b; as *Erythrodontium lacoutourei*); Gangulee (1980, Fig. 910); Figure 11.

Ecology. Approximately 77% of collections corticolous, 14% saxicolous, 9% terrestrial; 300-2500 m.

Erythrodontium julaceum is currently the only known member of the genus to occur on two continents. Branch leaf length is fairly variable in *E. julaceum.* Smaller expressions of *E. julaceum* tend to grade into the larger expressions of *E. squarrosulum.* This has led to confusion between the two by previous workers. Fleischer (1922) reduced *E. squarrosulum* to a synonym of *E. julaceum* where it has remained until present. *Erythrodontium julaceum* and *E. squarrosulum* exhibit roughly the same distribution pattern in Southeast Asia although *E. julaceum* generally reaches higher elevations than *E. squarrosulum.*

The leaves of *E. julaceum* for the most part tend to keep their oblong-lanceolate shape even when they are short whereas the leaves of *E. squarrosulum* are regularly suborbicular although the larger ones sometimes exhibit a shortly oblong-lanceolate shape. Alar cells of *E. julaceum* frequently are confined to the lower quarter of the leaf whereas the alar cells of *E. squarrosulum* very rarely fail to reach midleaf or higher. Another leaf character that seems to be fairly reliable is that the outer row of cells above the alar cells tend to be long rhombic to linear in *E. julaceum* versus quadrate or short rectangular in *E. squarrosulum* (Fig. 11, E-F). Approximately 25% of the collections of *E. julaceum* are saxicolous or terrestrial while *E. squarrosulum* is almost exclusively corticolous.

Representative specimens examined.

BURMA. Mandalay: Maymyo [22°01'N, 96°28'E], *Svihla 3196* (MO); Shan: Taunggyi [17°04'N, 97°10'E], *Svihla 3383* (MO).

CHINA. Hainan Island: Changjiang Co., 19°15'N, 109°15'E, 500-1000 m, *Reese 17490* (MO); Yunnan: Mangshui [24°53'N, 99°43'E], *Hsu 20* (NY), Mangla county, Hwy Menglun [21°55'N, 101°15'E] to Manbang, 980-1000 m, *Redfearn et al. 33864* (MO), Xishuanbanna, Menghai County [21°58'N, 100°28'E], *Magill et al. 7992* (MO), Kunking, 1850-2000 m, 24°56'N, 102°29'E, *Redfearn et al. 2109* (MO).

ETHIOPIA. Bonga [07°16'N, 36°15'E], *Friis et al. 149b* (NY).

INDIA. Madras: Madura dist., Palni Hills [10°28'N, 77°31'E], *Foreau 1033* (NY); Mussoorie [30°26'N, 78°04'E], Landour, 6-7000ft, *Stewart 14677* (NY);

Dehra Dun Valley [30°19'N, 78°01'E], 610 m, *Marsen 6398* (NY); Debidhura (Pithorågarh) [29°34'N, 80°13'E], 1800 m, *Srivastava 3909* (NY); Mahârâshtra: Kumaon, Dharchoola, Kali River [16°52'N, 74°34'E], 7000 ft, *Khan 1937* (NY).

MALAWI. Southern: NE side of Soche [15°48'S, 35°01'E] near Blantyre, 4200 ft, *Crundwell 355* (S).

NEPAL. Between Bir Gaon and Dingla [27°03'N, 87°01'E], 1400 m, *Iwatsuki 2148* (NY); Dhankuta [26°58'N, 87°19'E], 1200 m, *Hara et al. 235769* (NY).

PAPUA NEW GUINEA. Central: near Pt. Moresby, 450 m, 09°25'S, 147°27'E, *Hovenkamp 91/28* (MO); Eastern Highlands: Swiss Mission, Kassam Pass, 06°13′S, 146°01′E, 1520 m, *Streimann 18308* (NY); Morobe: 8 km NW of Bulolo, 07°09′S, 146°35′E, 950 m, *Streimann 14309* (NY).

PHILIPPINES. Benguet: northern Luzon, Baguio [16°25'N, 120°36'E], 1570 m, *Williams 1877* (NY); Cotabato: SE Mindanao, Todaya [06°58'N, 125°20'E], Mt. Apo, 850 m, *Williams 2653* (NY); Mountain: Baguio-Bontoc road [ca. 17°00'N, 120°50'E], 2100 m, *Lugod 10* (MO), Mt. Polis [ca. 17°10'N, 121°00'E], 2500m, *Pancho 4703* (MO); Rizal: [14°35'N, 121°10'E], Luzon, *Ramos s.n.* (NY), Bontoc subprov. [14°30'N, 121°05'E], Luzon, *Ramos & Edano 9086* (MO).

SRI LANKA. Central Prov.: Kandy Dist. [07°18'N, 80°38'E], *Townsend 73/738* (NY).

TANZANIA. West Lake: Bukoba [01°19'S, 31°49'E], *Stuhlmann 1600* (S); Tanga: Usambara [04°45'S, 38°30'E], Latiadi, *Holst s.n.* (S); Kilimanjaro [04°00'S, 38°00'E], *Harrington s.n.* (NY).

THAILAND. Phitsanulok [16°46'N, 100°16'E], Tung Salaeng Luang, *Larsen et al. 859* (NY); Do-Intanon [18°34'N, 98°28'E], 600 m, *Sørensen et al. 7855a* (NY); Payap: near Karen village of Sop Aep, 18°30′N, 98°35′E, 780-820 m, *Touw 9476* (NY); Nakhon Sawan, Langsang National Park W of Tak, 300 m, 16°50'N, 99°05'E, *Touw 8036* (MO); Chiang mai [18°46'N, 98°58'E], Mae rim, 750 m, *Maxwell B-77* (MO).

VIETNAM. Lam Dông, Bao Lôc [18°22'N, 105°46'E], 700 m, *Tixier s.n.* (MO).

5. ***Erythrodontium*** *squarrosulum* (Mont.) Paris

Index Bryol. 437. 1896; *Pterogonium squarrosulum* Mont., Lond. J. Bot. 4: 9. 1845; *Neckera squarrosula* (Mont.) Müll. Hal., Syn. Musc. Frond. 2: 101. 1850 "squarrulosa"; *Platygyrium squarrosulum* (Mont.) A. Jaeger, Ber. S. Gall. Naturw. Ges. 277. 1876-1877. Type: [Philippines] Ad cortices arborum, *Cuming 2201* (lectotype BM!).

Plants small to medium, yellow-green to brown, corticolous or rarely terrestrial, autoicous. Stems subjulaceus, densely foliate, pinnately branched; in cross section oval, composed of 2-4 layers of small, yellow incrassate epidermal cells surrounding 10-15 layers of larger, gray cortical cells, central strand not evident; rhizoids light to dark orange, smooth, in clusters on the ventral surface; pseudoparaphyllia foliose. Branches julaceous, ascending, curved, densely foliate, 3-6 mm long. Axillary hairs composed of a short yellow-orange basal

cell and 2-3 rectangular, hyaline apical cells. Stem leaves 0.67-1 × 0.45-0.8 mm, loose or infrequently imbricate, plane to slightly concave, suborbicular to short oblong-ovate, abruptly rounded to an apiculus; margins entire to faintly serrulate near apex; costa yellow, short and double; upper laminal cells short-linear to rhombic, thick-walled, 30-56 × 7.4-8.5 μm; median cells short-linear, 30-75 × 7.4-9.25 μm; marginal cells above alar region quadrate to short rectangular; alar cells oblate, extending 1/2 to 2/3 the leaf length, 6.5-15 × 13-26 μm. Branch leaves 0.65-0.9(-1) × 0.35-0.55 mm, in other respects very similar to stem leaves. Perigonial leaves 0.6-0.85 × 0.25-0.5 mm, oblong-cuspidate, entire to serrulate at the apex, ecostate; basal cells rectangular, bulging; middle and upper cells linear; antheridia light brown, straight to curved, 220-260 × 45-60 μm, cells rectangular, bulging; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, oblong-cuspidate, inner leaves oblong-lanceolate (2.5-3 mm long post-fertilization), entire to slightly serrulate at the apex, ecostate; basal cells rectangular, bulging; middle and upper cells linear; archegonia 250-300 μm long, orange; paraphyses numerous. Seta yellow to light brown, 9-15 mm long, smooth; capsules erect, cylindric, smooth, exserted, 1.8-2.8 × 0.6-1 cm, light to dark brown; operculum light to dark brown, 0.5-0.75 mm long, conic, obliquely rostrate; exostome teeth 200-270 × 55-85 μm, light to dark orange, striate nearly to apex, fenestrate above middle, upper 2-4 cells smooth; endostome segments rudimentary, yellow, composed of rectangular to elliptical cells, smooth, almost reaching length of exostome teeth but frequently

discontinuous; cilia absent. Spores spherical, orange, papillose, 18-37 μm. Calyptra smooth, naked, yellow, 2.3-3 mm long.

Etymology. The specific epithet squarrosulum presumably refers to the somewhat squarrose nature of the branch leaves when moist.

Distribution. Burma, China, India, Indonesia, Papua New Guinea, Philippines, Thailand, Vietnam, Figure 12.

Illustrations. Enroth (1991, Fig. 4, a-f; as *Erythrodontium julaceum*); Fleischer (1922, Fig. 189, a-e; as *Erythrodontium julaceum*); Figures 11F, 13.

Ecology. Almost exclusively corticolous, very rarely on soil; 40-1230 m.

See above discussion under *E. julaceum* for further details of *E. squarrosulum*.

Representative specimens examined.

BURMA. Mandalay: Maymyo [22°01'N, 96°28'E], *Svihla 3196, 3199* (MO).

CHINA. Hainan Island [19°00'N, 109°30'E]: Bawangling Mt., 200 m, *Expedition Team 3020* (NY); Yunnan: Ruili [24°01'N, 97°52'E], *Li 77-150* (NY), Anning county [28°34'N, 104°57'E], 2000 m, *Redfearn et al. 34332* (NY), Xishuanbanna, Menghai County [21°58'N, 100°28'E], *Magill et al. 7915* (NY).

INDIA. Assam: Khasia [25°34'N, 91°37'E], *Griffith 534* (NY).

INDONESIA. Borneo: [Sabah] Tenom [05°08'N, 115°55'E], *Binstead s.n.* (BM); Celebes: Piek van Bonthain [05°19'S, 119°55'E], *Fruhstorfer s.n.* (S); Java: Buitenzorg [06°34'S, 106°46'E], *Nyman 392* (S), Nordhang des Panperango bei Artja [06°54'S, 106°13'E], ca. 800 m, *Schiffner 10739a* (S), Papandayan [07°19'S, 107°43'E], ca. 1330 m, *Schiffner 11131* (NY, S);

Sumatra: Hariaran (Res. Tapanui) [02°51'N, 98°16'E], *Overdijkink s.n.* (S), Fort de Kock [00°19'S, 100°22'E], 920 m, *Jacobson 81* (NY).

PAPUA NEW GUINEA. Eastern Highlands: Swiss Mission, Kassam Pass, 06°13'S, 146°01'E, 1520 m, *Streimann 18308* (S); Morobe: Road 2, 3 km SW of Bulolo, 07°13'S, 146°37'E, 780 m, *Streimann 41825* (S).

PHILIPPINES. Bukidnon: [08°00'N, 125°00'E], *Weber 1508* (NY); Nueva Vizcaya: Luzon [16°00'N, 121°20'E], *McGregor s.n.* (NY); Tarlac: [15°28'N, 120°34'E], Luzon, *Merrill 3589* (NY).

THAILAND. Northern, 10 km W of Fang, 19°57'N, 99°11'E, *Larsen et al. 2700* (MO, NY).

VIETNAM. Prov. Ninh-Binh, Chuc-Phuong [21°00'N, 105°00'E], 400 m, *Pócs 3058* (MO); Prov. Kontum [14°00'N, 108°00'E], Mgoc Linh mountain system, 800-1000 m, *Averyanov et al. B270* (MO).

6. ***Erythrodontium subjulaceum*** (Müll. Hal.) Paris

Index Bryol. 437. 1896; *Pterigynandrum subjulaceum* Müll. Hal., Linnaea 39: 453. 1875. Type: [Sudan] Niam-niam-regiones, ad rivulum (Chor) Boddo, Mbanga, Febr. 1870, *Schweinfurth s.n.* (lectotype NY!, isotype S!).

Entodon rotundifolius Müll. Hal., Flora 73: 494. 1890; *Erythrodontium rotundifolium* (Müll. Hal.) Paris, Index Bryol. 437. 1896, Type: Tanzania, in regione montis Kilima-Ndscharo [Kilimanjaro], Dschagga (Marango), 1300 m, *Meyer s.n.*, 1889 (lectotype H-BR!, isotype S!).

Pterogonium abruptum Wright, J. Bot. 30: 264. 1892; *Erythrodontium abruptum* (Wright) Broth. *in* A. Engl. & K. Prantl, Nat. Pfl. 1(3): 888. 1907. Type: Shiri Highlands, Zambesia, *Buchanan 32* (lectotype BM!).

Erythrodontium subjulaceum (Müll. Hal.) Paris var. *impolitum* Gepp *in* Hiern, Cat. Welwitsch Afr. Pl. 2(2): 298. 1901. Type: [Angola] on trunks and branches of *Edwardia lurida* in the forest of Quilombo-Quiacatubia, at an elev. of 2400 ft., *Welwitsch 164* [type not seen].

Erythrodontium setulosum Müll. Hal., *nom. inval. in synon.*, Hedwigia 59: 217. 1917.

Erythrodontium chalcophyllum Thér. & P. de la Varde, Bull. Soc. Bot. France 72: 359. 1926; *E. subjulaceum* (Müll. Hal.) Paris var. *chalcophyllum* (Thér. & P. de la Varde) P. de la Varde, Rev. Bryol. Lichénol. 20: 9. 1951. Type: [Congo] Riv. Dangara sur liane, *R.P.C. Tisserant s.n.*, 20 November 1923 [type not seen].

Plants small to medium, olive green to brown, corticolous or rarely saxicolous, autoicous. Stems julaceous, densely foliate, in mats, pinnately branched; in cross section composed of 2-3 layers of small, yellow, incrassate epidermal cells surrounding 7-12 layers of larger, gray, thin-walled cortical cells, central strand poorly differentiated; rhizoids light to dark orange, smooth, in clusters on ventral surface; pseudoparaphyllia foliose. Branches julaceous, ascending, curved, generally all pointed the same direction, densely foliate, 4.5-10 mm long. Axillary hairs composed of a small yellow basal cell and 2-3

larger rectangular-elliptical hyaline apical cells. Stem leaves 0.6-1.1 × 0.6-0.75 mm, tightly imbricate, decurrent, suborbicular to shortly oblong-ovate, cuspidate; margins entire; costa short, double, yellow, reaching 1/3 of the leaf length; upper laminal cells linear, 18.5-30 × 6.5-9.25 μm, median cells linear to linear-rhomboidal, 29-65 × 6.5-9.25 μm; alar cells oblate to quadrate, extending 1/4 to 1/3 of the leaf length, 6.5-20 × 14.5-18.5 μm. Branch leaves 0.75-1 × 0.45-0.65 mm, in other respects similar to stem leaves. Perigonial leaves 0.5-0.67 × 0.3-0.4 mm, oblong-suborbicular, cuspidate, entire to serrulate at the apex, ecostate; lower cells rectangular, bulging; upper-median cells linear-rhomboidal; antheridia light brown, straight to slightly curved, 280-340 × 59-100 μm, cells bulging, rectangular; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, oblong-cuspidate, inner leaves oblong-lanceolate (2.75-3.25 mm long post-fertilization), entire to slightly serrulate at the apex, ecostate; basal cells short-rectangular, bulging; upper median cells linear-rhomboidal; archegonia 260-320 μm long, orange; paraphyses numerous. Seta red but becoming paler (dark yellowish) with age, 9-13 mm, smooth; capsules erect, smooth to slightly plicate, cylindric, exserted, 1.9-3.2 × 0.85-1.15 mm, brown; operculum brown, 0.5-0.75 mm, conic, short-rostrate; exostome teeth 245-270 × 62-72 μm, light to dark orange, striate to upper 3/4, upper 1/4 smooth; endostome segments rudimentary, yellow, composed of rectangular cells, smooth, almost reaching length of exostome teeth but frequently discontinuous; cilia absent. Spores spherical, orange, papillose, 16.5-26 μm. Calyptra cucullate, smooth, naked, yellow, 2.5-3 mm.

Etymology. The specific epithet subjulaceum presumably refers to the species as being a smaller version of *E. julaceum*.

Distribution. Central African Republic, Comoro Islands, Democratic Republic of Congo, Guinea, Liberia, Kenya, Mozambique, Rwanda, Sudan, Tanzania, Uganda, Zimbabwe, Figure 14.

Illustrations. Potier de la Varde (1925, Fig. 12, A-E; as *Erythrodontium chalcophyllum*); Brotherus (1925, Fig. 700, A-E); Sim (1926, Fig. S, p. 407; as *Erythrodontium abruptum*); Figure 15.

Ecology. Almost exclusively corticolous, very rarely saxicolous; 540-2000 m.

Erythrodontium subjulaceum is unlikely to be confused with other members of the genus in Africa. The tightly imbricate, suborbicular leaves and distinct red seta help to separate it from all other members of the genus with the exception of *E. squarrosum*. Analysis of molecular data in combination with morphological characters suggests that these two may be closely related (Figure 26).

Representative specimens examined.

CAMEROON. Cameroun Occidental: Mukonji [04°37'N, 09°30'E] plantation, *Thobold 13* (MO); Cameroun Oriental: Batouri [06°54'N, 14°48'E], *Meijer 15194* (MO).

CENTRAL AFRICAN REPUBLIC. Ouaka: rochers près de Monduko, 40 km SE de Ippy [06°00'N, 21°30'E], *Tisserant 2124* (S).

COMORO ISLANDS. Ngazidja [11°41'S, 43°16'E], Grotto du Captain DuBois, 2.5 km E of Bahani village, 660 m, *Magill & Pócs 11753* (NY).

DEMOCRATIC REPUBLIC OF CONGO. Bandundu: Camp Lukuni [05°52'S, 17°11'E], Mt. Karisimbi, *Linder 2481* (FH).

GUINEA. [10°00'N, 10°00'W] *Pobeguin s.n.* (S).

LIBERIA. Central Province [07°00'N, 10°00'W], Sarokwele district, *Baldwin 13196* (FH).

KENYA. Nyanza: Morth Kavirondo, 1600 m, 00°14'N, 34°52'E, *Geesteranus 9300A* (MO); Rift Valley: ca. 3 km NW of Naro Moru, 00°09'S, 37°01'E, 6400 ft, *Crosby & Crosby 11012* (MO); Western: Mt. Elgon [00°52'N, 34°44'E], Kaimasi, *Lindblom s.n.* (NY); Central: Near Nairobi [01°17'S, 36°49'E], *Lönnberg 81* (S).

MALAWI. Southern: Zomba Moutain, 2000 m, 15°28'S, 35°28'E, *Magill 10875* (MO).

MOZAMBIQUE. Cabo Delgado: Zambézia [12°54'S, 39°42'E], Shiri Highlands, *Buchanon 32* (NY).

RWANDA. Near Rugarama [01°23'S, 29°43'E] at shore of Rwampanga Lake, 1300 m, *Fischer 8380* (NY); Butare [02°35'S, 29°44'E], 1800 m, *Frahm 8008* (NY);

SOUTH AFRICA. Transvaal: Duiwelskloof [23°41'S, 30°07'E], Westfalia Estate, 2750 ft, *Scheepers 1222* (MO).

SUDAN. Niam Niam region [08°00'N, 30°00'E], Mt. Boddo, *Schweinfurth s.n.* (NY, S).

SWAZILAND. Lubombo District, Blue jay ranch hills N of Siteki [26°26'S, 31°56'E], *Magill 3583* (MO).

TANZANIA. Arusha: S foothills of Mt. Meru, 17 km E of Arusha [03°22'S, 36°37'E], 1210 m, *Pócs & van Zanten 86125/E* (MO); Mbeya: Rungwe district, below Lugombo [09°09'S, 33°46'E], 1225 m, *Pócs 6768/FA* (MO); Morogoro: Uluguru mountains [07°02'S, 37°40'E], Kimboza forest reserve between Mkuyumi and Matombo, 300 m, *Pócs 6054/K* (NY); West Lake: Bukoba [01°19'S, 31°49'E], *Möller s.n.* (S); Kilimanjaro: Tyska, Kibosho [03°15'S, 37°19'E], 1000-2000 m, *Daubenberger s.n.* (S); Tanga: Usambara [05°00'S, 38°40'E], Kiva Uschuscho, 1600 m, *Holst 9200* (BM, S).

UGANDA. West Mengo: Kampala [00°19'N, 32°25'E], *Rojkowski 418* (NY).

ZIMBABWE. [20°00'S, 30°00'E] 3000 ft, *Sim 8776* (NY).

7. ***Erythrodontium engleri*** (Broth.) Paris

Index Bryol. 436. 1896; *Entodon engleri* Broth., Bot. Jahrb. Syst. 20: 204. 1895. Type: Tanzania, Usambara: Kiva Ushuscho, trockene Hochwälder bei Usingo, 1600 m, *Holst 9202*, Aug. 1893, (lectotype H-BR!, isotypes BM!, S!; syntype: Tanzania, Usambara: Kiva Ushuscho, trockene Hochwälder, *Holst 9054* (S!)).

Plants medium to large, yellow-green to golden brown, in dense mats, corticolous, autocious. Stems subjulaceous, densely foliate, pinnately branched; in cross section 2-4 layers of small, yellow incrassate cells surrounding a cortex of 9-14 layers of larger thin-walled gray cells; rhizoids light orange, smooth, in clusters on ventral surface; pseudoparaphyllia foliose. Branches julaceous, straight, densely foliate, 6-10 mm long. Axillary hairs composed of a small,

yellow basal cell and 2-3 larger rectangular-elliptical hyaline apical cells. Stem leaves 1-1.35 × 0.7-0.85 mm, broadly oblong-elliptical to obvate-lanceolate, cuspidate, decurrent; margins entire; costa short, double or absent; upper laminal cells linear, 31-45 × 5.5-7.4 μm, median cells linear, 77-125 × 7.4-9.25 μm; alar cells oblate to quadrate, extending 1/5 to 1/4 the leaf length, 10-26 × 17-21 μm. Branch leaves 1.15-1.45 × 0.6-0.95 mm, broadly obvate to oblong-lanceolate, cuspidate apex, concave, decurrent, entire; costa short, double, very pale, yellow; cells as in stem leaves. Perigonial leaves broadly oblong-lanceolate, entire, ecostate; basal cells bulging rectangular; median-upper cells linear; antheridia light brown, slightly curved, 290-350 × 55-65 μm, cells rectangular, bulging; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, inner leaves oblong-long lanceolate (2.4-3.6 mm long post-fertilization), entire to slightly serrulate at apex, ecostate; basal cells long-rectangular; median to upper cells linear; archegonia 300-350 μm long, orange; paraphyses numerous, composed of a mixture of rectangular and extremely narrow linear cells. Setae yellow, smooth, 1.5-2 cm long; capsules erect, cylindric, exserted, 2.5-3.35 × 0.8-1.25 mm, brown, smooth; operculum not seen; exostome teeth 230-290 × 80-110 μm, yellow, smooth; endostome segments rudimentary, yellow, smooth, attached to back of exostome, frequently discontinuous; cilia absent. Spores spherical, yellow-brown, papillose, 19-32 μm. Calyptra smooth, naked, yellow, 3-4 mm long.

Etymology. The specific epithet engleri honors Heinrich Gustav Adolf Engler (1844-1930), leader of the Berlin school of plant taxonomy and plant geography.

Distribution. Tanzania, Figure 16.

Illustrations. Figure 17.

Ecology. Only known collections from trees in the Usambara mountains in Tanzania.

Morphologically *E. engleri* is very similar to *E. longisetum*. Both taxa have very similar leaf shapes, yellow setae and smooth, yellow peristome teeth. Molecular data suggests that *E. longisetum* may well be better placed within *Mesonodon.* If that transfer is made I believe that moving *E. engleri,* the only other member of the genus with yellow peristome teeth, into *Mesonodon* would be a logical conclusion based on morphological similarities.

Representative specimens examined.

TANZANIA. Tanga: Usambara [05°00'S, 38°40'E], Kiva Uschuscho, 1600 m, *Holst 9054* (S), *9202* (BM, S).

8. ***Erythrodontium barteri*** (Mitten) Broth. in A. Engl. & K. Prantl Nat. Pfl. 1(3): 888. 1907; *Stereodon barteri* Mitt., Trans. Linn. Soc. London 23: 51. 1860. Type: Hab. on trees in deep ravines. Nigeria, Nupe, River Niger, *Barter 1422* (lectotype NY!).

Pterigynandrum schweinfurthii Müll. Hal., Linnaea 39: 451. 1875; *Erythrodontium schweinfurthii* (Müll. Hal.) Paris, Index Bryol. 437. 1896. Type: [Sudan] Niam-niam-regiones, ad rivulum Boddo in cortice arborum, 13 Febr. 1870, *Schweinfurth s.n.* (lectotype NY!).

Pilotrichella subbiformis Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 39(2): 110. 1900; *Erythrodontium subbiforme* (Renauld & Cardot) Broth. *in* A. Engl. & K. Prantl, Nat. Pfl. 1(3): 888. 1907. Type: Rég. Congo belge: Kisantu, *J. Gillet 712* (H-BR!).

Entodon pobeguinii Broth. & Paris, Rev. Bryol. 30: 103. 1903. *Erythrodontium pobeguinii* (Broth. & Paris) Broth. *in* A. Engl. & K. Prantl, Nat. Pfl. 1(3): 888. 1907. Type: Province of Sankaran? [probably Guinea] between January and February, *H. Pobeguin s.n.* [lectotype S!]

Erythodontium vanderystii Cardot, Rev. Bryol. 36: 46. 1909, Type: Congo belge: Kisantu, *Vanderyst s.n.* (lectotype H-BR!).

Plants small to medium, mostly yellow-green, in dense mats, corticolous or more rarely saxicolous, autoicous. Stems subjulaceous to julaceous, densely foliate; in cross section 2-4 layers of small yellow, incrassate cells surrounding a cortex of 9-12 layers of larger thin-walled gray cells; pseudoparaphyllia foliose. Branches julaceous, straight to slightly curved, ascending, densely foliate, irregularly spaced, 4.5-9 mm long. Axillary hairs composed of a small yellow basal cell and 2-3 larger rectangular apical cells. Stem leaves 0.9-1.3 × 0.6-0.8 mm, broadly oblong-elliptical to ovate-lanceolate, cuspidate, decurrent; margins entire; costa short, double, very faint, yellow, extending to 1/4 the leaf length; upper laminal cells linear-rhomboidal, 31-56 × 5.5-7.5 μm; median to upper laminal cells linear, 46-100 × 5.5-7.5 μm; alar cells oblate to rectangular, extending 1/4 to 1/3 the leaf length, 9-23 × 16-22 μm. Branch leaves 0.95-1.25

× 0.4-0.67 mm, ovate to oblong-lanceolate, cuspidate, concave, recurved at apex, decurrent, entire; costa short, double or absent, very pale, yellow, extending to 1/4 the leaf length; cells as in stem leaves. Perigonial leaves 0.5-1 × 0.22-0.32 mm, ovate-oblong lanceolate, entire, ecostate; basal cells rectangular; median to upper laminal cells linear-rhomboidal; antheridia light brown, slightly curved, 235-275 × 62-74 μm, cells rectangular, bulging; paraphyses numerous. Perichaetial leaves convolute, outer leaves shorter, oblong-ovate lanceolate, inner leaves oblong-long lanceolate (2.5-3 mm long post-fertilization), entire to slightly serrulate at the apex, ecostate; basal cells short rectangular; median to upper cells linear; archegonia190-340 μm long, orange; paraphyses numerous, composed of a mixture of rectangular and extremely narrow linear cells. Setae dark yellow-brown, smooth, slightly twisted, 4.5-8 mm long; capsules erect, cylindric, exserted, 1.5-2.2 × 0.6-1.1 mm, brown, smooth to plicate; operculum brown, 1-1.4 mm long, conic, long-rostrate, slightly curved; exostome teeth 230-280 × 75-115 μm, orange, striate to middle, variously striate to reticulate in upper half, sometimes splitting along medial line to near base; endostome segments rudimentary, yellow, smooth, composed of rectangular cells, approaching length of exostome teeth but frequently discontinous; cilia absent. Spores spherical, yellow-golden brown, papillose, 19-28 μm. Calyptra, hairy, pale yellow, 2.25-2.75 mm long.

Etymology. The specific epithet barteri honors Charles Barter, collector of the type specimen and one of the earliest collectors of bryophytes in Nigeria.

Distribution. Cameroon, Central African Republic, Guinea, Liberia, Nigeria, Sudan, Figure 18.

Illustrations. Mitten (1860, Table 5, Fig. 2, 1-3); Figure 19.

Ecology. Corticolous or rarely saxicolous, all examined collections below 500 m.

The distinctive hairy calyptra easily separates *E. barteri* from other members of the genus. In many respects *E. barteri,* with its short seta, plicate capsules and similar looking leaves, resembles *E. warmingii.* The many morphological resemblances combined with the geographic localities of the two, *E. barteri* on the central west coast of Africa and *E. warmingii* on the eastern edge of Brazil, leads me to suspect the two may be very closely related but without molecular data from *E. warmingii* this hypothesis cannot as of yet be corroborated.

Representative specimens examined.

CAMEROON. Cameroun Oriental: Ad Massakam, pagum in territorio Batangæ [04°24'N, 11°01'E], *Dusén 682* (S); Cameroun Occidental: Victoria [04°01'N, 09°11'E], *Luce s.n.* (S), Kumba [04°37'N, 09°25'E], *Argent 828* (MO).

CENTRAL AFRICAN REPUBLIC. Ouaku: Bambari [05°45'N, 20°40'E], *Tisserant 2024* (S).

GABON. Nyanga: Singa sur Lolo [03°01'S, 10°50'E], *Le Testu s.n.* (MO).

GUINEA. Faranah: Sarkaran Province, near Faranna [Faranah] [10°01'N, 10°43'W], *Chevalier s.n.* [Jan. 1909] (S); Nzérékoré: Nzérékoré [07°45'N, 08°49'W], *Baldwin 13163* (NY);

LIBERIA. Central Province? [06°00'N, 10°00'W], Sarokwele district, *Baldwin 13196b* (FH).

NIGERIA. Benin: Bendel, Okomu Forest Reserve, near Nikrowa, 06°15'N, 05°20'E, *Richards 5066* (MO); North Eastern: Kurmi Katara, 4 mi NE of Dogon Kurmi saw mill, Sanga River Forest Reserve, Jemaa [10°10'N, 09°25'E], Kafanchan District, *Jones 953* (NY); Ondo: between Ilesha and Effon, 07°40'N, 04°50'E, *Richards 5103b* (MO); West Central: Nupe (07°55'N, 7°25'E), River Niger, *Barter 1422* (NY).

SUDAN. Al-istiwâ' Îyah: Mudiryat el Istwaya District near Li Yuba [05°22'N, 27°15'E], *Rojkowski 436* (FH, NY).

Molecular and morphological analyses of *Erythrodontium*

In the process of revising *Erythrodontium*, one of four genera currently recognized within the Entodontaceae, molecular data were obtained and analyzed from two non-coding regions from the chloroplast (*trnL-F*) and nuclear (ITS) genomes. These regions were selected due to previous usage in other phylogenetic studies at the intrageneric level in a wide variety of plants (Baldwin et al., 1995; Geilly & Taberlet, 1994, 1996; Groth et al., 2002; Potter et al., 2000; Schilling et al., 1998). Additionally, morphological characters were analysed in combination with the molecular data. The sequence data generated in this study were used to evaluate: 1) the monophyly of the *Erythrodontium*, 2) phylogenetic relationships between genera in the Entodontaceae, and 3) species relationships within *Erythrodontium*.

MATERIALS AND METHODS

DNA sequence data from the nuclear ribosomal internal transcribed spacers 1 and 2, and the chloroplast *trnL-F* region (*trnL* intron and *trnL-F* spacer) were collected for six species of *Erythrodontium*, three species of *Entodon*, one species of *Mesonodon*, one species each of *Isopterygium*, *Leucodon* and *Pylaisiella* as putative outgroup taxa. Other sequence data were obtained from GenBank for the following taxa: *Entodon seductrix*, *Neckera douglasii*, *Neckera pennata* and *Platygyrium repens*. Of these, five had only partial or no sequence data for one or the other (Table 1). DNA extractions were accomplished using a

modified CTAB method (Struwe et al., 1998) from herbarium specimens at MO and NY. DNA amplifications utilized standard PCR procedures and products were purified, cycle sequenced and run through a sephadex column. Sequences were run on an automated sequencer (ABI 377), and were aligned and edited using the program Sequencher. The aligned sequences were analyzed using the parsimony criterion (Farris, 1983) and the software package PAUP 4.0 (Swofford, 1998).

Morphological data were gathered from light microscopy as well as literature references. The morphological matrix consists of 19 characters obtained for 13 members of the Entodontaceae and eight outgroup taxa.

RESULTS AND DISCUSSIONS

Sequences of the *trnL-F* for 11 members of the Entodontaceae were almost alike. The sequences for the six outgroups were also very similar to the members of the Entodontaceae. The length of the *trnL-F* for all taxa was 409 nucleotides after editing. Of these, 357 characters were constant, 23 variable characters were parsimony uninformative and 29 were parsimony informative characters. Variation between members of Entodontaceae as well as the outgroup taxa was minimal

Sequences of the ITS region for ten members of the Entodontaceae and the three outgroups were a maximum of 788 base pairs long after editing. Of these, 463 characters were constant, 224 variable characters were parsimony uninformative and 101 were parsimony informative characters. Sequences for the

members within Entodontaceae were fairly similar whereas the sequences for the outgroups, two species of *Neckera* and *Leucodon brachypus*, were noticeably different in many regions. The sequences between the two species of *Neckera* were very similar whereas they differed noticeably from *L. brachypus*. The inclusion of only three outgroups for the ITS analysis was due to the ambiguous alignment of ITS data between ingroup and outgroup taxa.

A comparison of general features found with "bootstrap" searches is summarized in Table 2. Parsimony analysis of 11 members of the Entodontaceae and six outgroup taxa for the *trnL-F* non-coding region yielded 82 trees of 92 steps (CI = 0.6522; RI = 0.5, Figures 20, 21). The analysis of *trnL-F* resolved all members of the Entodontaceae within the same clade but the bootstrap value in this branch was low (56%). Resolution within the Entodontaceae clade was non-existent.

Phylogenetic analysis of the ITS characters for ten members of the Entodontaceae and three outgroup taxa yielded 388 trees of 400 steps (CI = 0.9350; RI = 0.8267, Figures 22, 23). There was support for one clade within the Entodontaceae but with *Entodon seductrix* as a sister group to the rest of the members. The family had strong support (bootstrap = 99%) but like the *trnL-F* analysis, resolution within the clade was minimal with the exception of *Erythrodontium barteri* and *E. julaceum* (bootstrap = 100%).

Analysis of the combined molecular data set for ten members of the Entodontaceae and three outgroup taxa resulted in 460 trees of 450 steps (CI =

0.9222; RI = 0.8177, Figures 24, 25). The consensus is consistent with the ITS data set alone but slightly less resolved.

Analysis of the combined molecular and morphological data set for 13 members of Entodontaceae and 8 outgroup taxa resulted in 767 trees of 697 steps (CI = 0.7805; RI = 0.5678, Figure 26). The addition of morphological data did little to increase resolution within the family although all members were part of the same clade (bootstrap = 77%). The characters used in the morphology matrix are denoted (0), (1), (2), etc. The character matrix used for the analyses is presented in Table 3.

Character states used in morphological analyses

1. Seta brown (0), yellow (1) or orange/red (2). 2. Seta short (< 10 mm long) (0) or long (> 10 mm long) (1) 3. Spores with moderate/large papillae (0) or spores with small papillae or smooth (1). 4. Outer peristome smooth with light striations at the bottom (0), striate to mid-tooth and papillose in upper portion (1), striate to near top (2), papillose (3), striate/reticulate (4) or smooth to ± lightly papillose (5). 5. Peristome teeth hyaline/yellow (0) or orange/red (1). 6. Capsule short-cylindric (< 2.5 mm long) (0) or long-cylindric (> 2.5 mm) (1). 7. Calyptra hairy (0) or naked (1). 8. Capsule orientation erect (0) or curved/inclined (1). 9. Peristome attachment deep below mouth (0) or near mouth (1). 10. Sexuality autoicous (0) or dioicous (1). 11. Basal membrane low/absent (0) or medium/high (1). 12. Exostome width at base narrow (< 90 μm) (0) or broad (> 90 μm) (1). 13. Endostome smooth (0), papillose (1) or exhibits both smooth and papillose forms (2). 14. Median laminal cell length linear (> 70 μm) (0) or short/rhombic

(< 70 μm) (1). 15. Pseudoparaphyllia foliose (0) or filamentous (1). 16. Alar cell shape quadrate to longer than wide (0), alar cells oblate (1). 17. Leaf plication absent (0) or present (1). 18. Branch leaf shape oblong- to ovate-lanceolate (0), suborbicular to very short ovate-lanceolate (1) or lanceolate (2). 19. Branch leaf length (< 1.0 mm) (0) or (> 1.0 mm) (1).

The close relationship between *E. julaceum* and *E. barteri* that was suggested by molecular data alone was still evident with the addition of morphological data. *Erythrodontium warmingii*, for which no molecular data exist, was also shown to be more closely related to the previous two than to other members of the genus. The only other members to show a closer relationship to each other than to other members of the family were *E. squarrosum* and *E. subjulaceum*. Morphologically these two members are separated from the other members of the genus by a dark red seta and suborbicular leaves. The close relationship between *Entodon beyrichii, E. longisetum* and *Mesonodon flavescens* that was suggested by molecular data alone was not evident when morphological characters were incorporated in the analysis.

The nuclear and chloroplast DNA sequence data exhibited low levels of variability within members of the Entodontaceae. Variability in the *trnL-F* region is lower than in the nuclear genome ITS. The low resolution provided scant information with regard to interspecific relationships within the family although it does suggest that some rearrangements of generic concepts may be necessary upon further analysis of additional molecular data.

The relatively low levels of variation may be due to the autoicous conditions of the plants. This would presumably allow for higher levels of self fertilization thus decreasing the amount of variation that would be seen compared to groups of plants that are obligate outcrossers over the same time period. Another possibility is that divergence within the family may be a relatively recent evolutionary event.

The apparently close relationship between *Erythrodontium barteri* and *E. julaceum* was not expected. Geographically *Erythrodontium julaceum* is the widest occurring species within the genus, stretching from Sudan eastward to Papua New Guinea. *Erythrodontium barteri* is largely confined to west central Africa although collections have been made in the Central African Republic and Sudan as well. Morphologically the two are quite distinct from each other. *Erythrodontium julaceum* is one of the larger members of the genus whereas *E. barteri* is generally noticeably smaller than *E. julaceum*. *Erythrodontium barteri* has a very short, stout seta while *E. julaceum* has a relatively long seta. *Erythrodontium barteri* is also the only member of the genus to exhibit a hairy calyptra.

The presence of *Erythrodontium longisetum* allied with *Mesonodon flavescens* although weakly supported in the combined molecular data set is not totally unexpected as they both share several morphological features. Overall leaf morphology between the two is similar although *Mesonodon* generally exhibits some degree of plication. The two also have relatively long, yellow setae and yellow peristome teeth. The only other member of *Erythrodontium* exhibiting

these last two characters is *E. engleri* from which DNA was unobtainable due to the age of the collections.

From the molecular data obtained and from additional morphological data there is support for E*rythrodontium* being polyphyletic. *Erythrodontium longisetum* and *E. engleri* may be better encompassed under the generic concept of *Mesonodon* but that decision will have to await further molecular evidence. The phylogenetic relationships among the genera of Entodontaceae and among the species in the family are unclear. Additional molecular data from a more encompassing group of the family will be necessary to better understand the relationships for both.

Non-coding regions have been presumed to be more useful at low taxonomic ranks because they are less functionally constrained and are therefore free to vary, thereby potentially providing more phylogenetically informative characters per unit of sequencing effort (Clegg et al. 1994; Small et al. 1998). However, the ITS and the *trnL-F* non-coding regions within the Entodontaceae exhibited less phylogenetically informative characters than do most other plant species assayed with comparable methods (Baldwin et al. 1995).

Doubtful or invalid names associated with *Erythrodontium*

Erythrodontium bicolor Gepp *in* Hiern, *hom. illeg. non* Lindb. & Ångstr. = I have not seen the specimen to which this name is attached.

Erythrodontium fluminense M. Fleisch., *nom. nud.*, = I have not seen the specimen to which this name is attached.

Excluded taxa of *Erythrodontium* Hampe

Erythrodontium densum (Hook. *in* Kunth) Paris = *Platygyriella densa* (Hook. *in* Kunth) W. R. Buck

Erythrodontium densum var. *brevifolium* Cardot = *Platygyriella pringlei* (Cardot) W. R. Buck

Erythrodontium felicis (Renauld & Cardot) Broth. *ex* Paris = *Entodon felicis* Renauld & Cardot

Erythrodontium imbricatifolium Williams *ex* Cardot = *Platygyriella pringlei* (Cardot) W. R. Buck

Erythrodontium orientale (Mitt.) Müll. Hal., *nom. inval. in synon.* = *Pterobryopsis orientalis* (Mitt.) M. Fleisch.

Erythrodontium pallidissimum (Müll. Hal.) Paris = *Platygyriella densa* (Hook.) W. R. Buck

Erythrodontium platygyrioides (Müll. Hal.) M. Fleisch., *syn. nov.* = *Platygyriella densa* (Hook.) W. R. Buck

Table 1. Geographic origins, voucher numbers, and GenBank accession numbers of the investigated taxa. Details of each sample are provided in the following order: species name, locality, voucher, GenBank Acc. # ITS, trnL-F. If not indicated otherwise, vouchers are deposited at NY. Molecular information for taxa without locality and voucher data were obtained directly from GenBank.

Entodon beyrichii, Colombia, *Churchill et al. 14611*, AY255494, AY255481; *E. brevisetus*, Georgia, *Buck 21705*, AY256514(*trnL-F*); *E. jamesonii*, Colombia, *Churchill et al. 16255*, AY255495, AY255490; *E. seductrix*, AJ288358 (ITS 1), AJ288572 (ITS 2); *Erythrodontium barteri*, Sudan, *Rojkowski 436*, AY255496, AY255479; *E. julaceum*, Bali, *Hegewald E. & P. 9984* (MO), AY255498, AY255493; *E. longisetum*, Costa Rica, *Granum 9594* (MO), AY255497, AY255484; *E. squarrosulum*, Papua New Guinea, *Bellamy 1503* (MO), AY255500, AY255487; *E. squarrosum*, Colombia, *Callejas 8490* (MO), AY255499, AY255492; *E. subjulaceum*, Malawi, *Magill 10875* (MO), AY255501; AY255491; *Leucodon brachypus*, Georgia, *Reese 18415*, AY256515; AY255488; *Mesonodon flavecens*, Colombia, *Churchill et al. 15016*, AY255502, AY255483; *Neckera douglasii*, AY009808, AF315070; *N. pennata*, AY009809, AF315072; *Platygyrium repens*, AY009798, AF161131

Table 2. Comparisons of results with three sequence data sets. Analysis 1 includes 11 taxa from the Entodontaceae. Analysis 2 and 3 are for 10 taxa from the Entodontaceae. Other columns are: number of trees found in strict consensus analyses, length, consistency index (CI), retention index (RI).

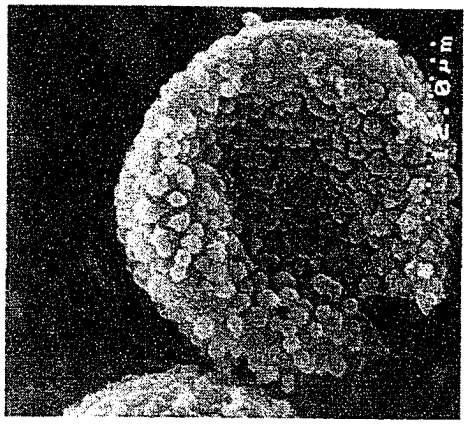
Analyses	# characters	Informative	%	# trees	Length	CI	RI
1) *trnL-F* + 6 outgroups	409	29	7.09	82	101	0.6522	0.5000
2) ITS + 3 outgroups	788	101	12.82	388	400	0.9350	0.8267
3) ITS + *trnL-F* + 3 outgroups	1197	123	10.28	460	450	0.9222	0.8177
4) molecular + morphological data + 8 outgroups	1216	131	10.77	767	697	0.7805	0.5678

Table 3. Morphological character matrix. The character states are further discussed in the text.

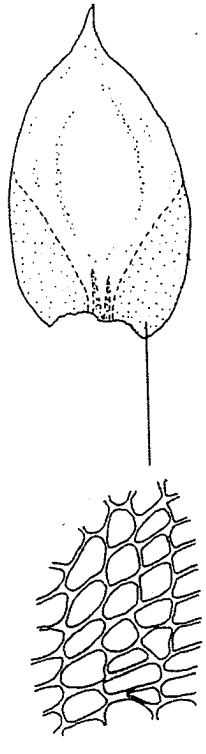
Character number	00000 12345	00001 67890	11111 12345	1111 6789
Entodon beyrichii	21130	11000	00200	0001
E. brevisetus	10031	01000	00110	0001
E. jamesonii	11021	11000	01000	0001
E. seductrix	20051	01000	00000	0001
Erythrodontium barteri	00141	00000	00000	1001
E. engleri	11000	11000	01000	1001
E. julaceum	01021	11000	00010	1001
E. longisetum	11000	11000	00000	1001
E. squarrosulum	01021	01000	00010	1000
E. squarrosum	21021	01000	01010	1010
E. subjulaceum	21021	11000	00010	1010
E. warmingii	00121	01000	00010	1000
Isopterygium tenerum	21111	01110	10211	0000
Leucodon brachypus	20030	01010	00110	0101
Mesonodon flavescens	11011	01000	01000	0101
Neckera douglasii	10150	01011	00010	0001
N. pennata	10000	01010	00010	0001
Platygyrium repens	21110	01011	00011	0100
Pylaisiadelpha tenuirostris	20110	01011	10111	0000
Pylaisia selwynii	21050	01010	10110	0000
Sematophyllum demissum	20110	01110	10110	0021

Figure 1. Some morphological characteristics of *Erythrodontium*. A. Peristome showing rudimentary endostome. B. Papillose spore. C. Oblate alar cells in branch leaf (from Enroth (1991), with permission. D. Upper portion of capsule showing deeply inserted peristome (from Brotherus, 1925).

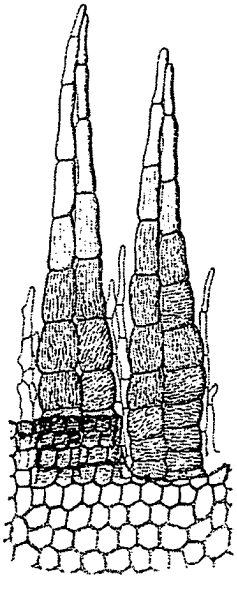
A



B



C



D

Figure 2. Distribution of New World species of *Erythrodontium* (*E. longisetum*, *E. squarrosum* and *E. warmingii*)

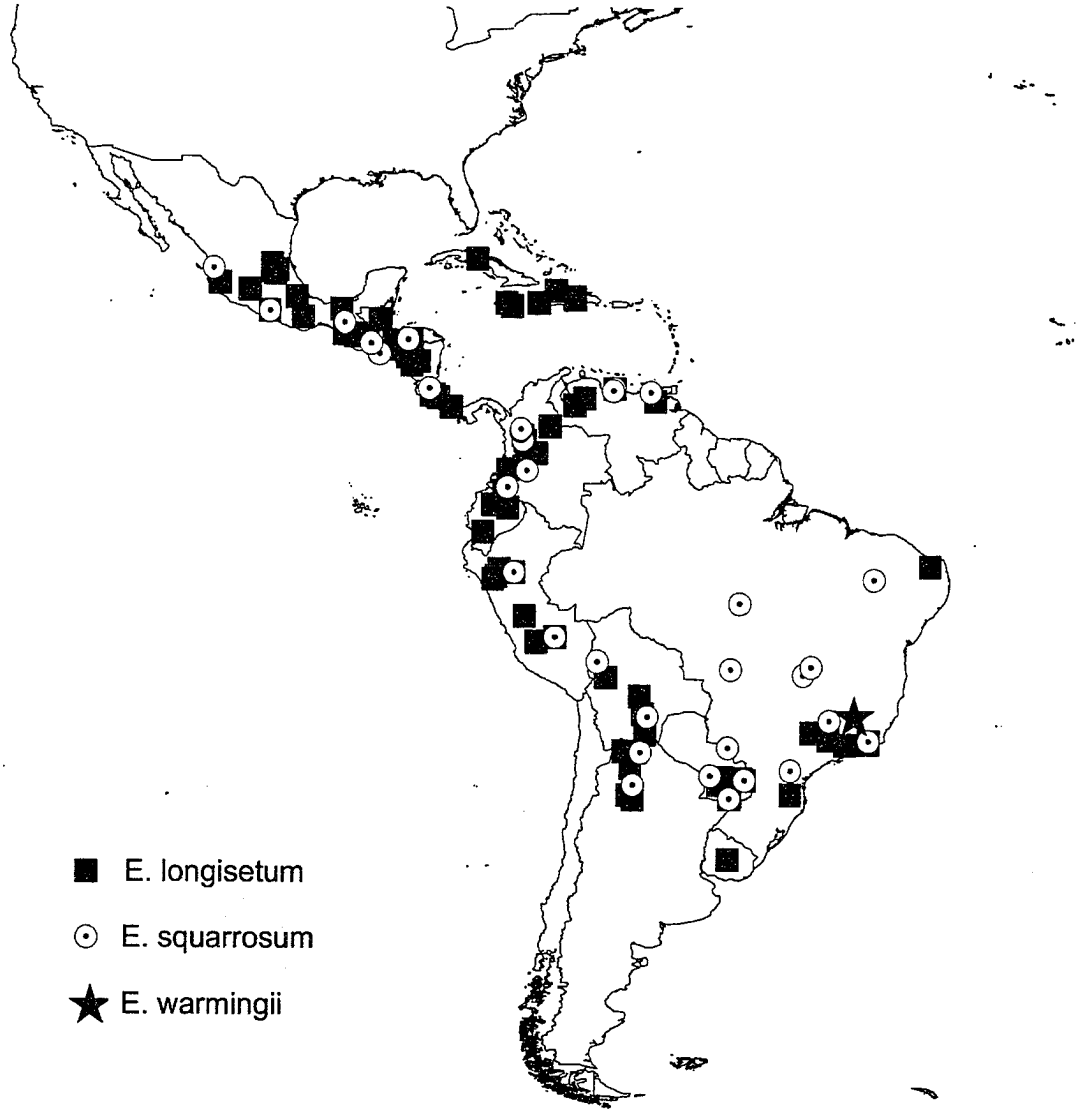


Figure 3. Distribution of Old World species of *Erythrodontium* (*E. barteri, E. engleri, E. julaceum, E. squarrosulum* and *E. subjulaceum*)

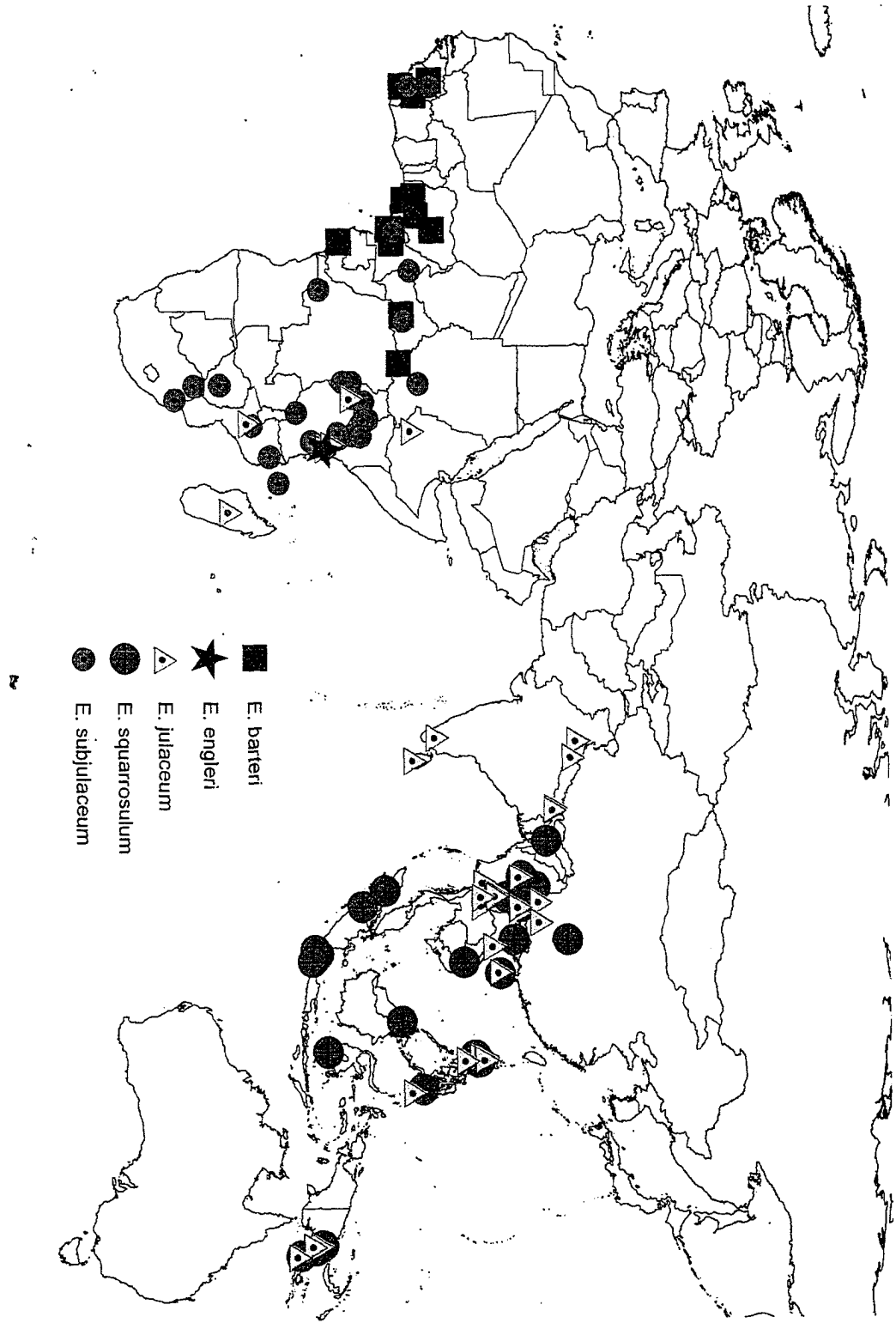


Figure 4. Distribution of *Erythrodontium longisetum*

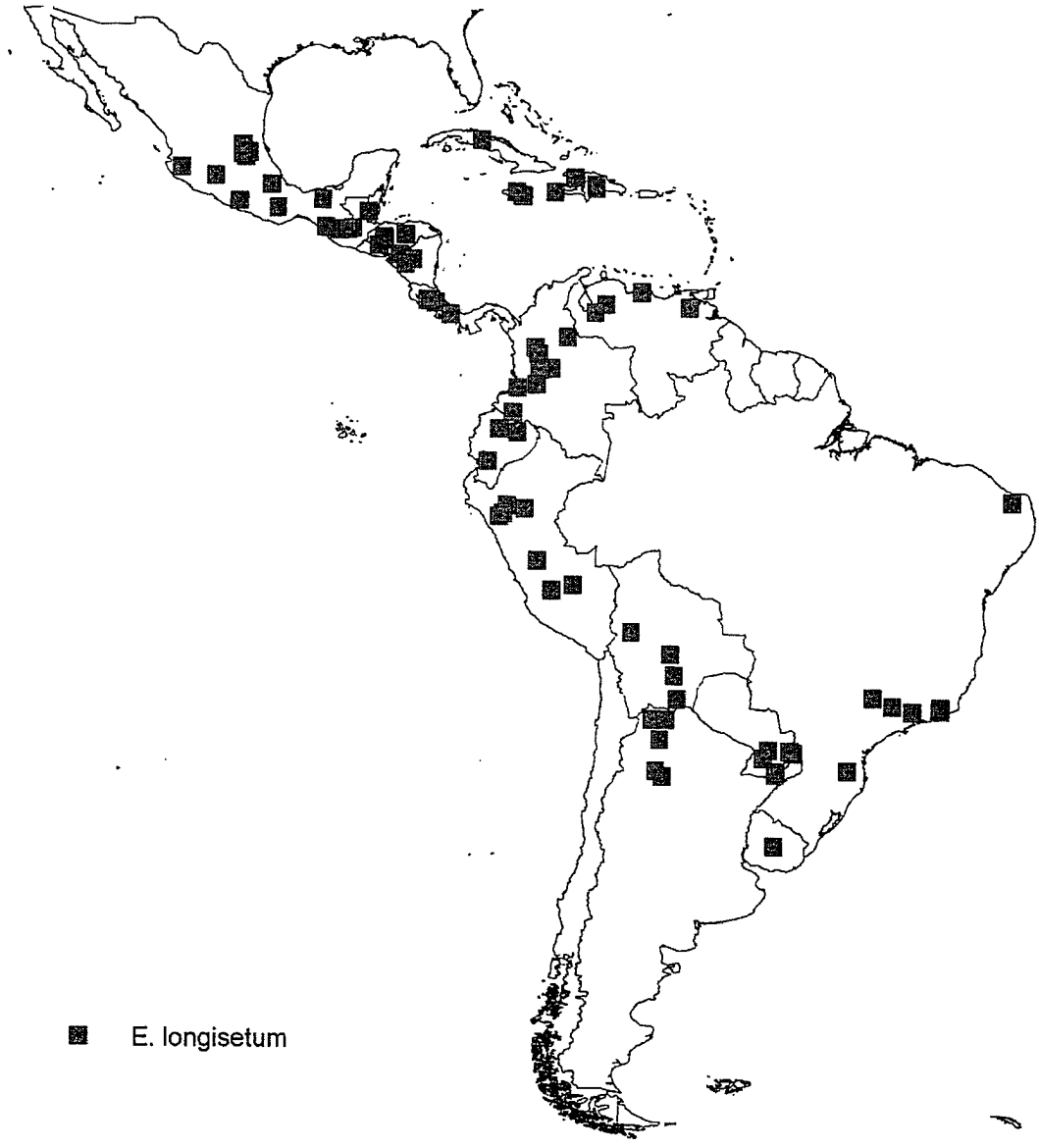


Figure 5. *Erythrodontium longisetum*. A-E. Branch leaves showing variation (A-B: type *Neckera longiseta*, C: type *Leptohymenium affine*, D: type *Erythrodontium macrocarpum*, E: *Buck 12149A*). F. Stem leaf. G. Capsule, from Buck (1998), with permission. H. Median laminal cells. I. Alar cells. Left scale bar = 0.5 mm (A-F), right scale bar = 100 μm (H, I). H-I from type of *Neckera longiseta*.

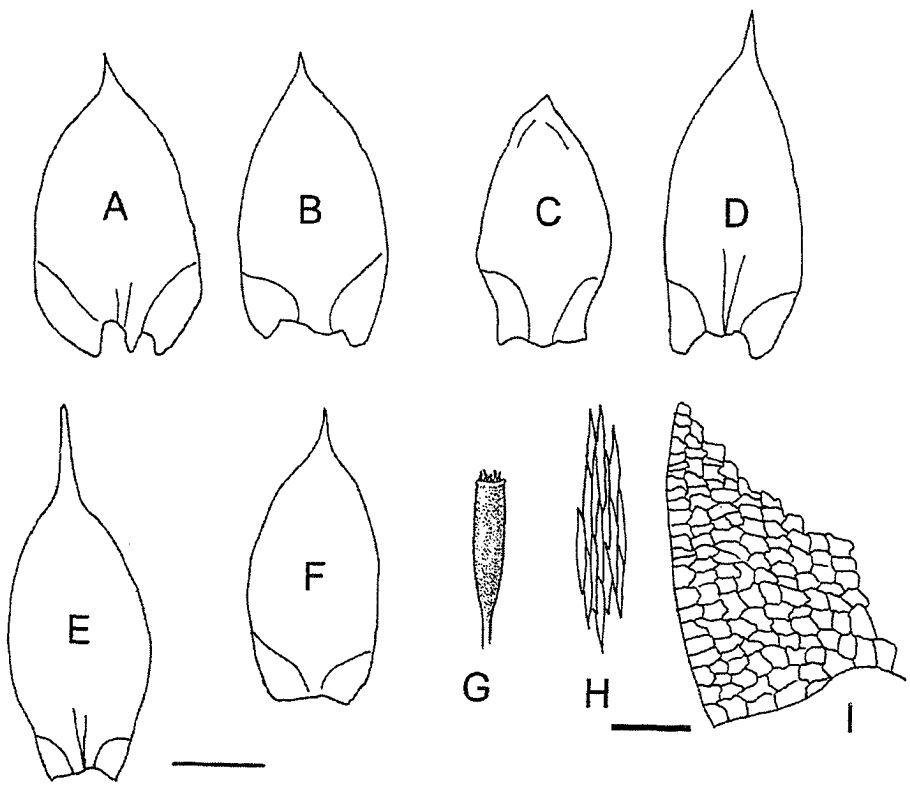


Figure 6. Distribution of *Erythrodontium squarrosum*

Figure 7. *Erythrodontium squarrosum*. A. Branch, × 14. B. Branch leaves. C. Stem leaf. D. Median laminal cells. E. Alar cells. F. Portion of peristome, × 200. Upper scale bar = 0.5 mm (B, C), lower scale bar = 50 μm (D, E). A, F from Sharp et al. (1994), with permission, B-C type *Neckera squarrosa*, D-E *Churchill et al. 14600.*

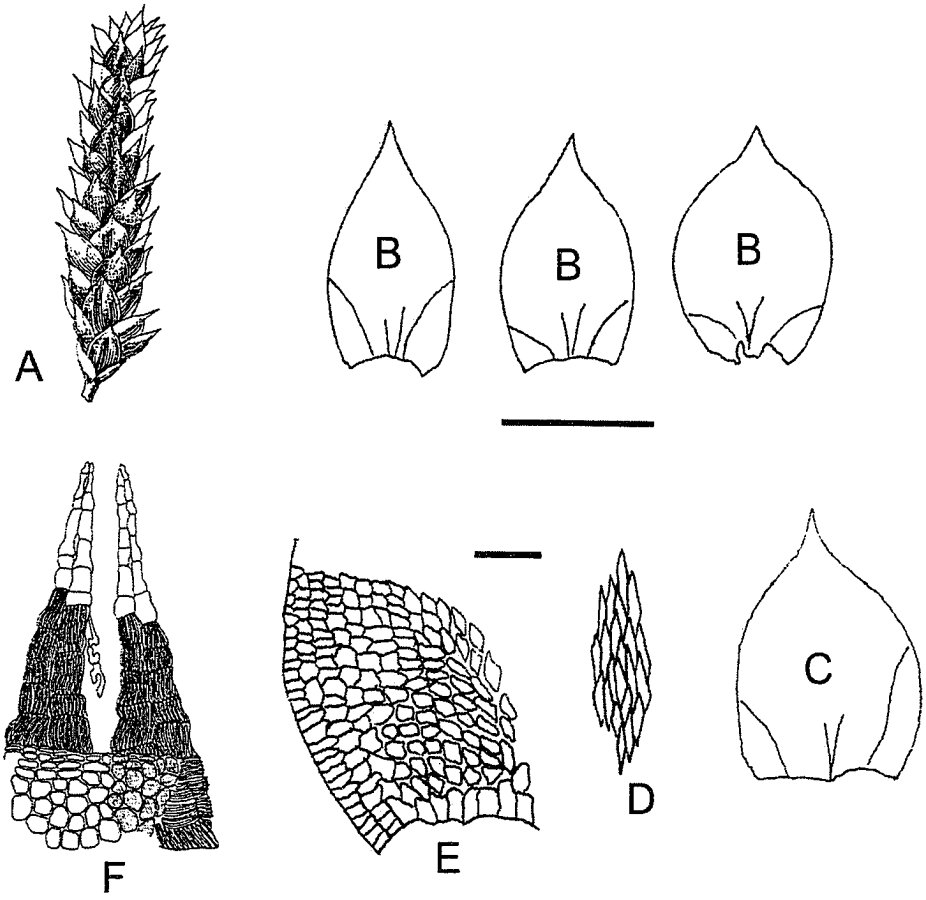


Figure 8. Distribution of *Erythrodontium warmingii*

Figure 9. *Erythrodontium warmingii*. A. Alar cells. B. Branch leaves. C. Stem leaves. D. Median laminal cells. (All drawn from type). Left scale bar = 50 μm (A, D), Right scale bar = 0.5 mm (B, C).

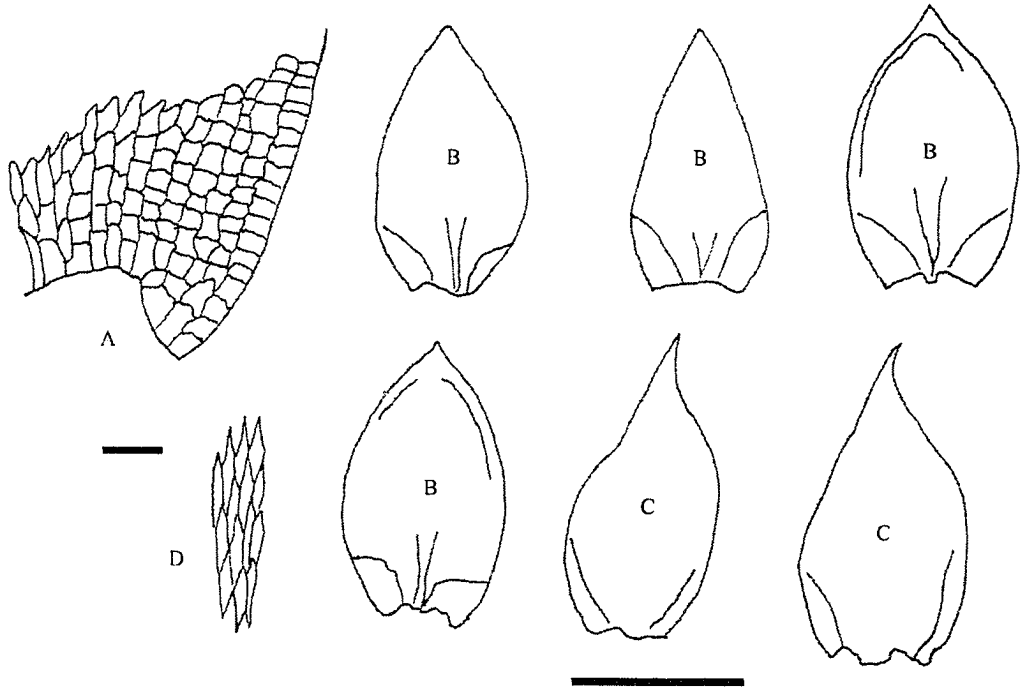


Figure 10. Distribution of *Erythrodontium julaceum.*

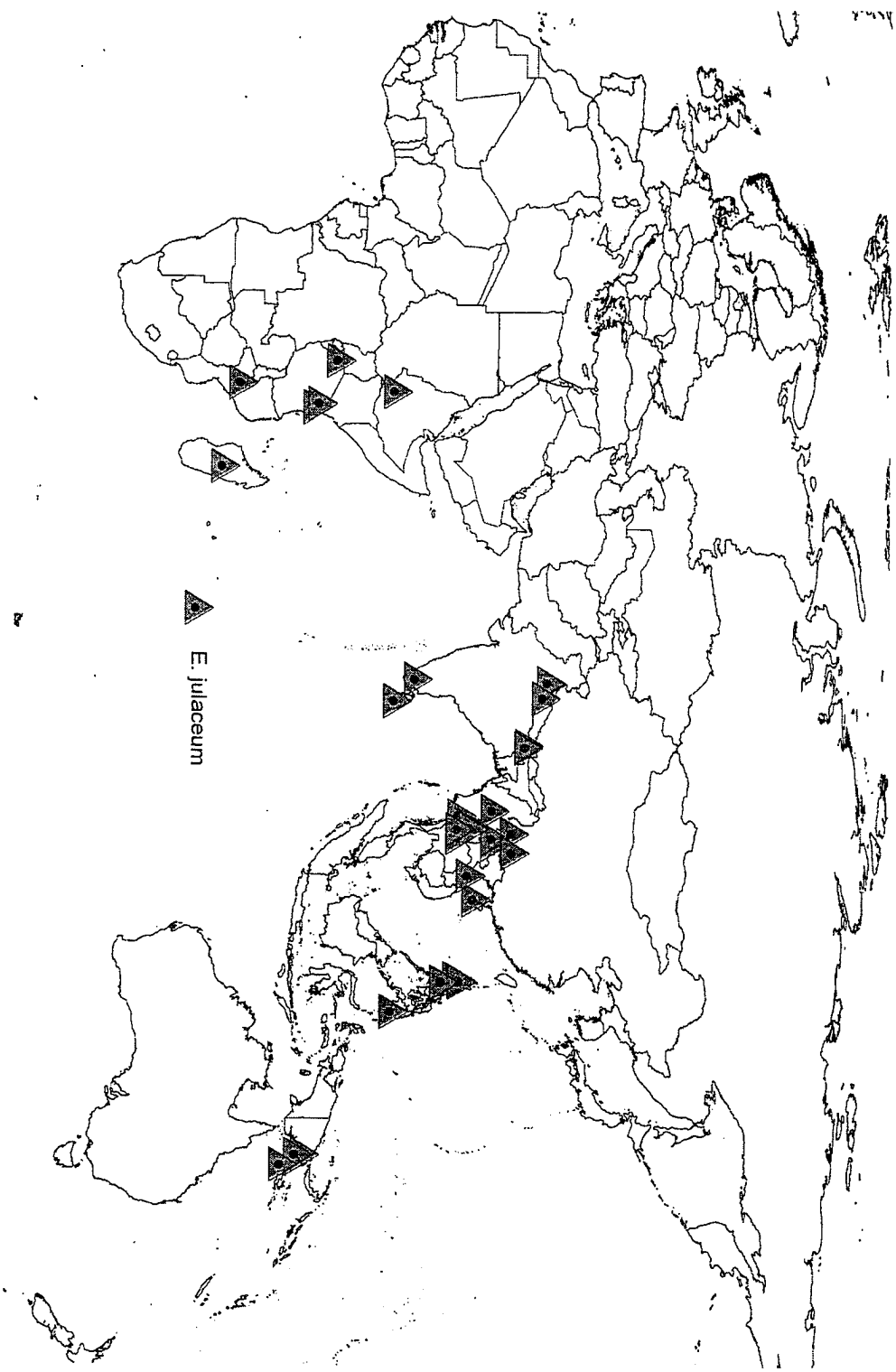


Figure 11. *Erythrodontium julaceum* and *E. squarrosulum* (A-E. *E. julaceum*; F. *E. squarrosulum*). A. Branch leaves. B. Stem leaf. C. Median laminal cells. D. Alar cells. E. Marginal cells above alar region for *E.* julaceum. F. Marginal cells above alar region for *E. squarrosulum*. Upper scale bar = 0.5 mm (A, B), Lower scale bar = 50 μm (C-F). A-E. All drawn from type of *Neckera julacea*. F. Drawn from type of *Pterogonium squarrosulum*.

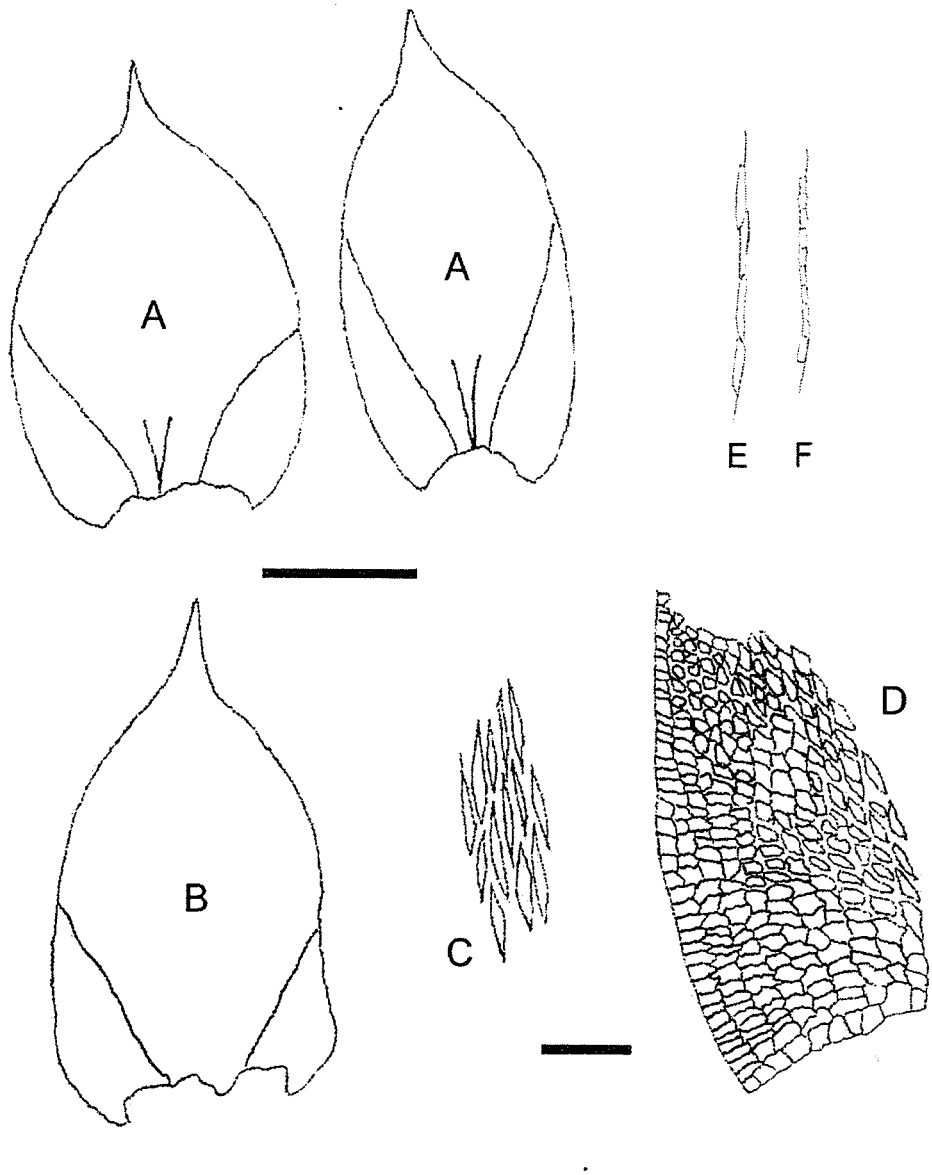


Figure 12. Distribution of *Erythrodontium squarrosulum*

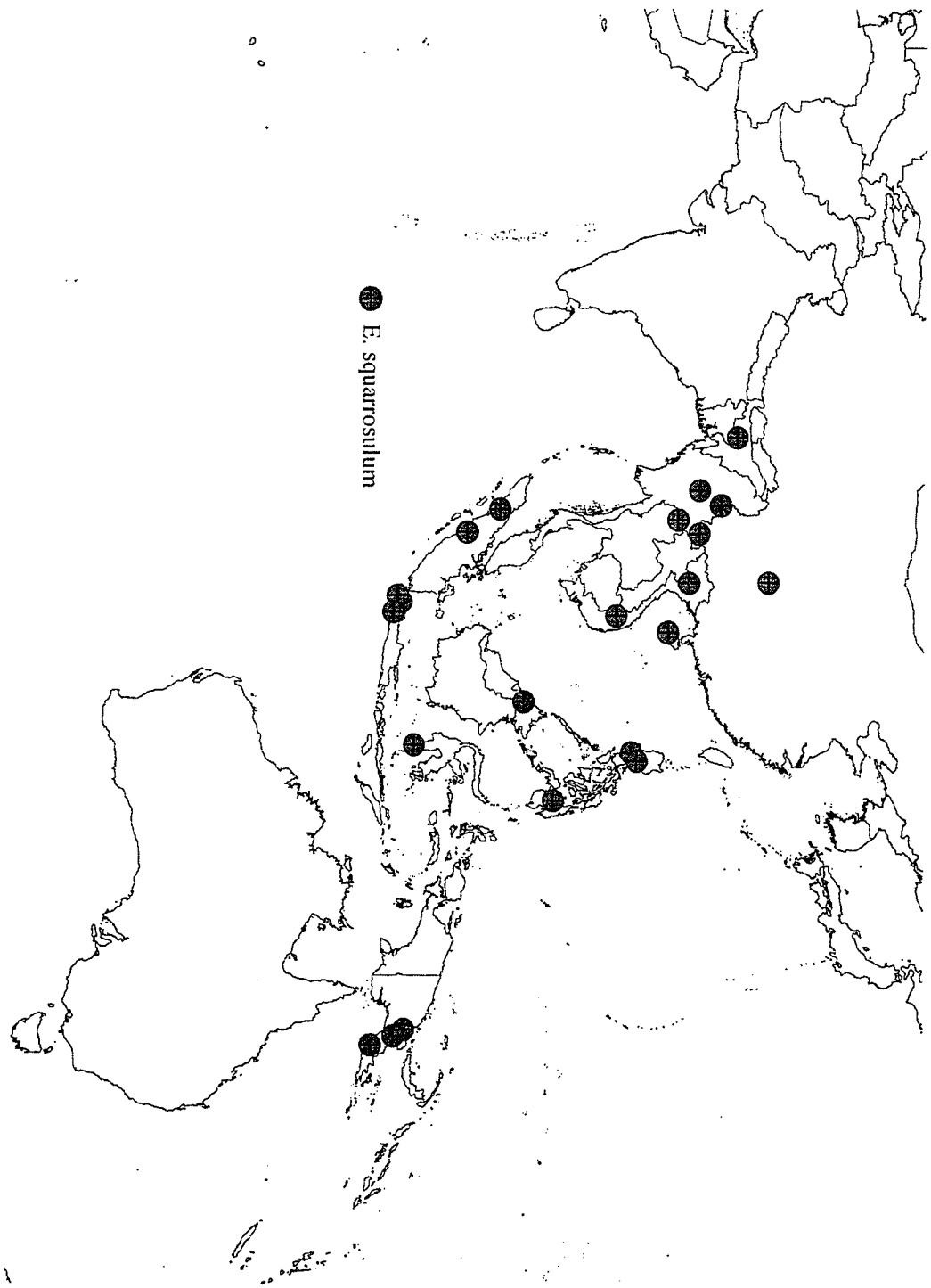


Figure 13. *Erythrodontium squarrosulum*. A. Tip of plant dry. B. Capsule. C. Branch leaves. D. Stem leaf. E. Median laminal cells. F. Alar cells. A,B from Enroth (1991), with permission, C-F from type *Pterogonium squarrosulum*. Upper scale bar = 5.0 mm (A, B), lower left scale bar = 50 μm (E, F), lower right scale bar = 0.5 mm (C, D).

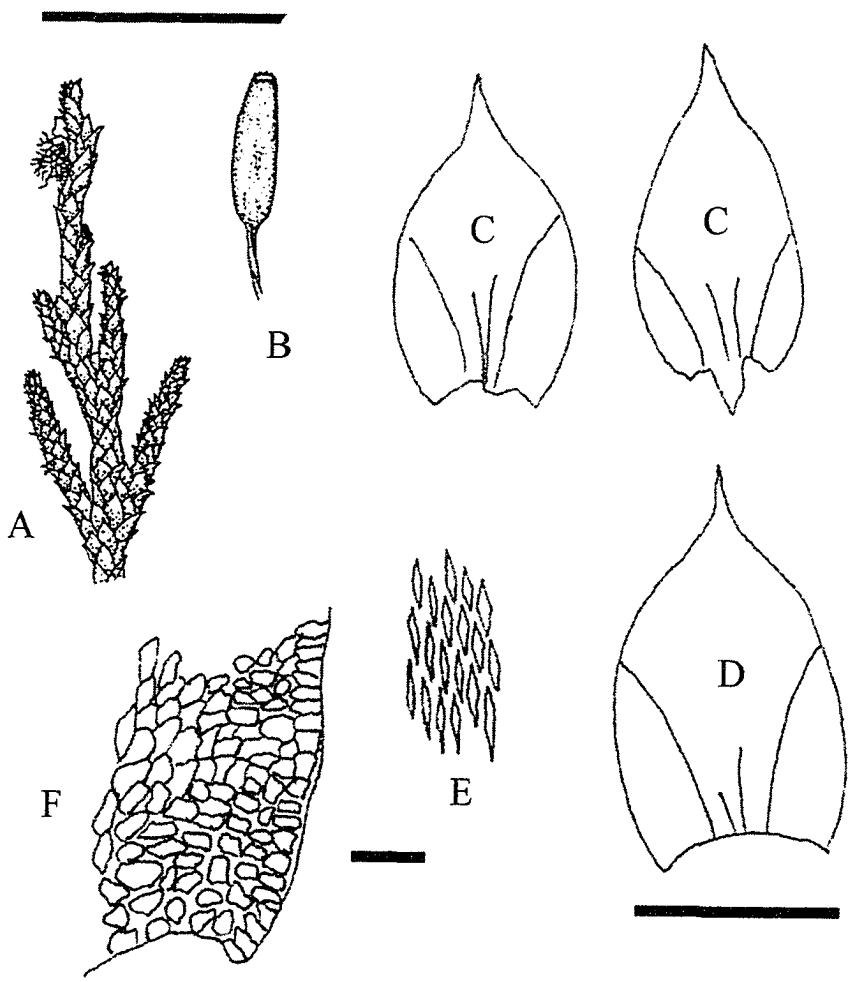


Figure 14. Distribution of *Erythrodontium subjulaceum*

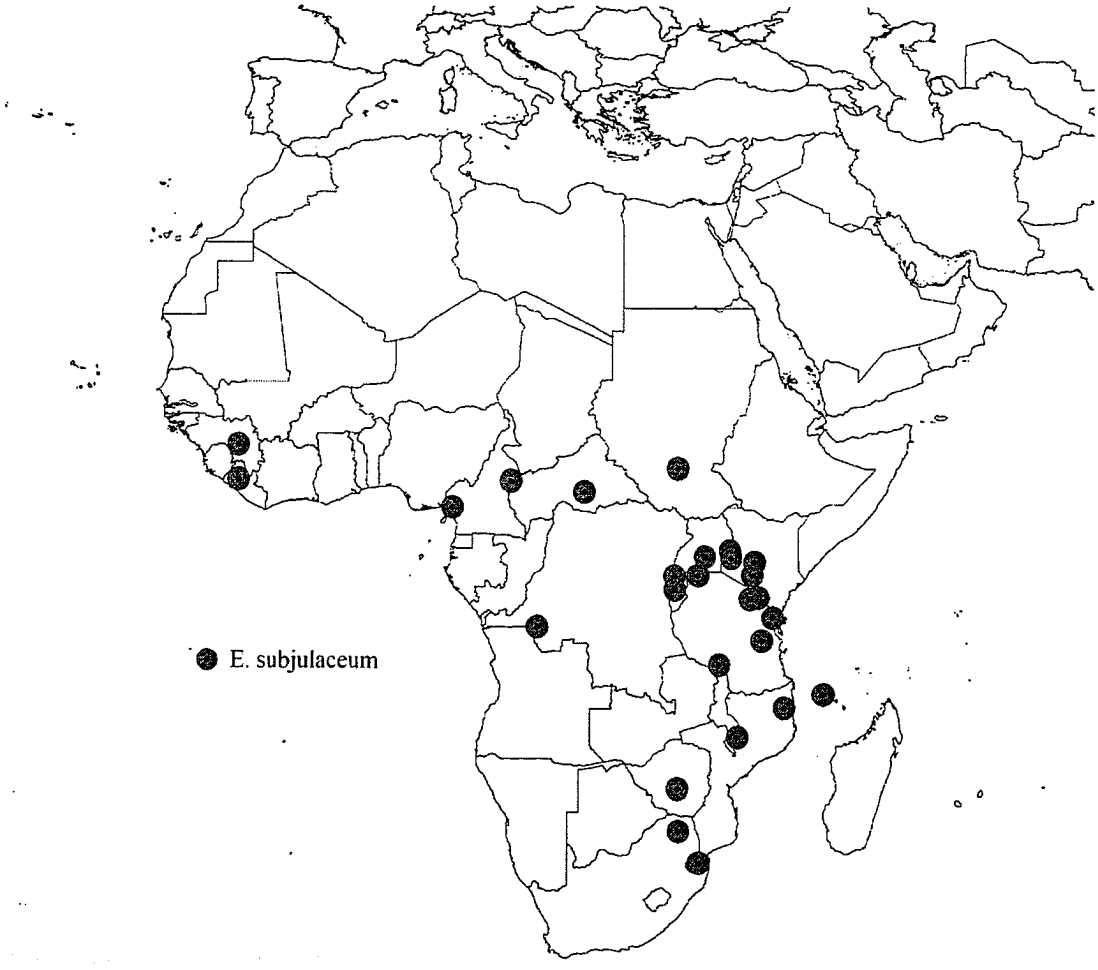


Figure 15. *Erythrodontium subjulaceum*. A. Branch leaves. B. Branch leaf from type of *Entodon rotundifolius*. C. Stem leaf. D. Median laminal cells. E. Alar cells. F. Peristome × 250 (from Brotherus, 1925). (A, C-E, drawn from type of *Pterigynandrum subjulaceum*). Left scale bar = 0.5 mm (A-C), Right scale bar = 50 μm (D, E).

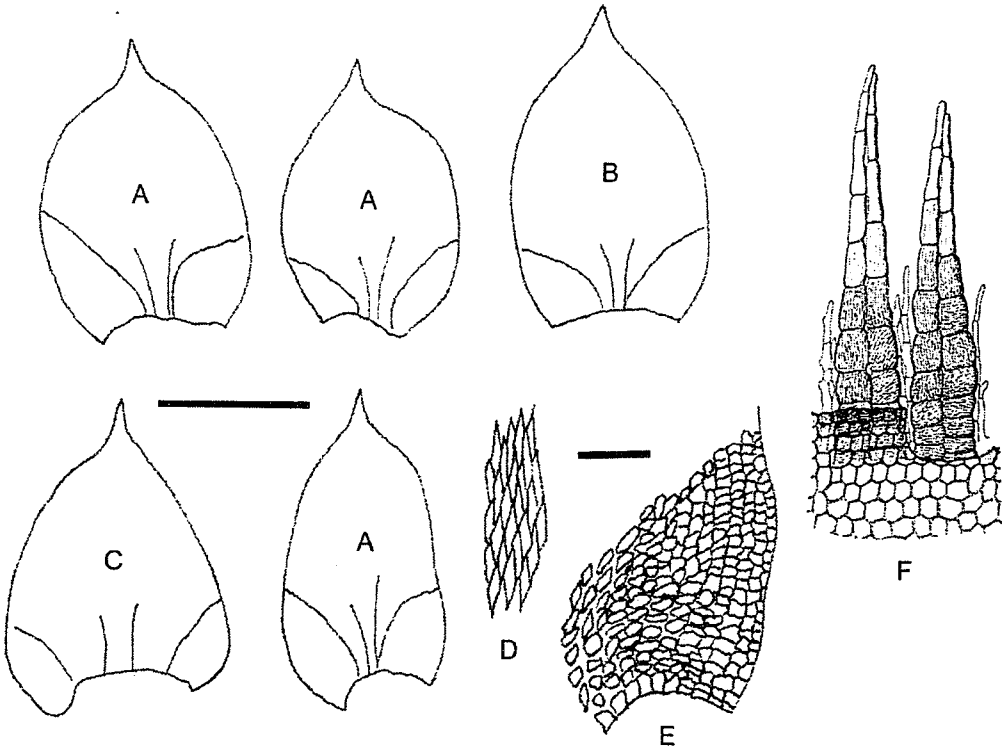


Figure 16. Distribution of *Erythrodontium engleri*

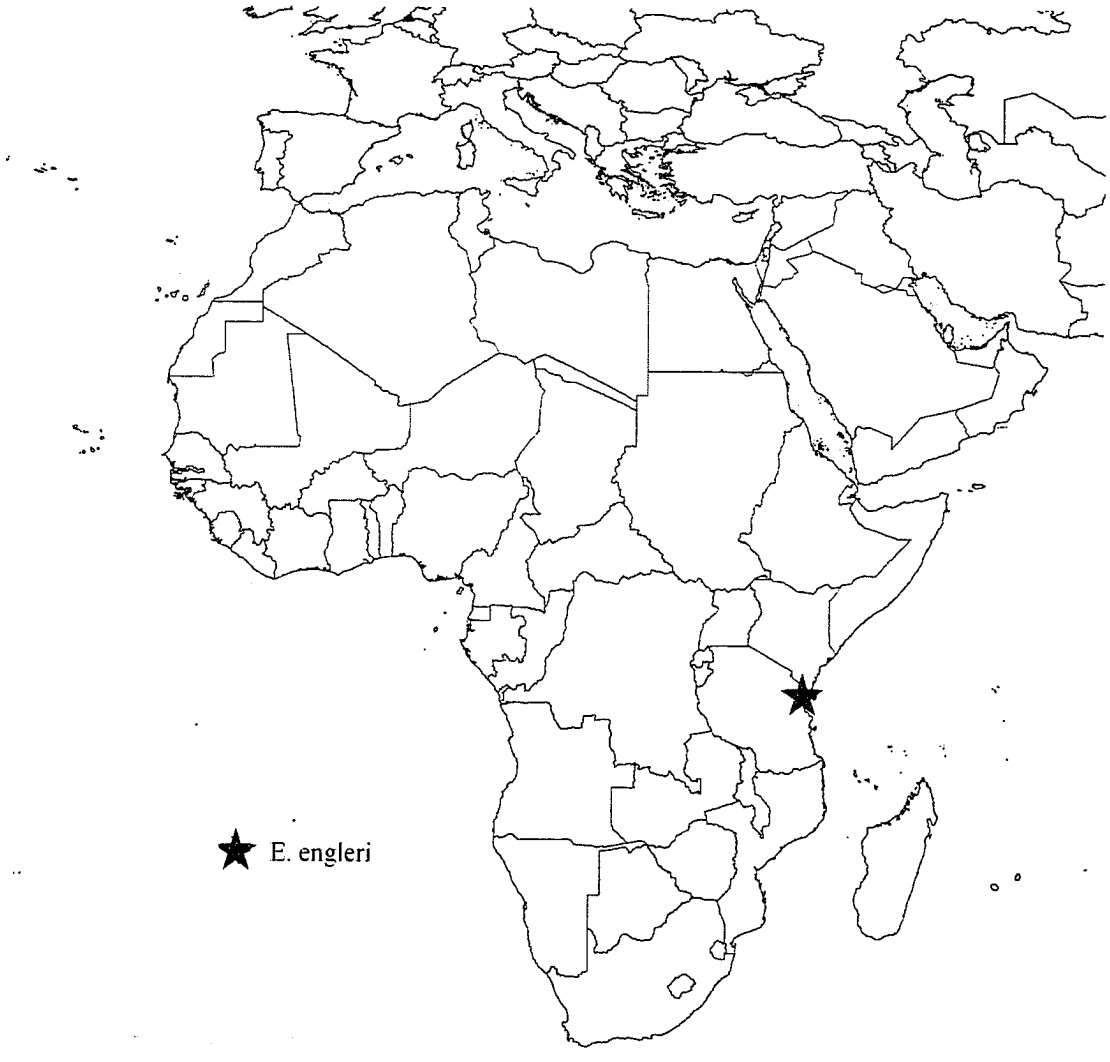


Figure 17. *Erythrodontium engleri*. A. Branch leaves. B. Stem leaf. C. Median laminal cells. D. Alar cells (all drawn from type). Left scale bar = 0.5 mm (A, B), right scale bar = 100 μm (C, D)

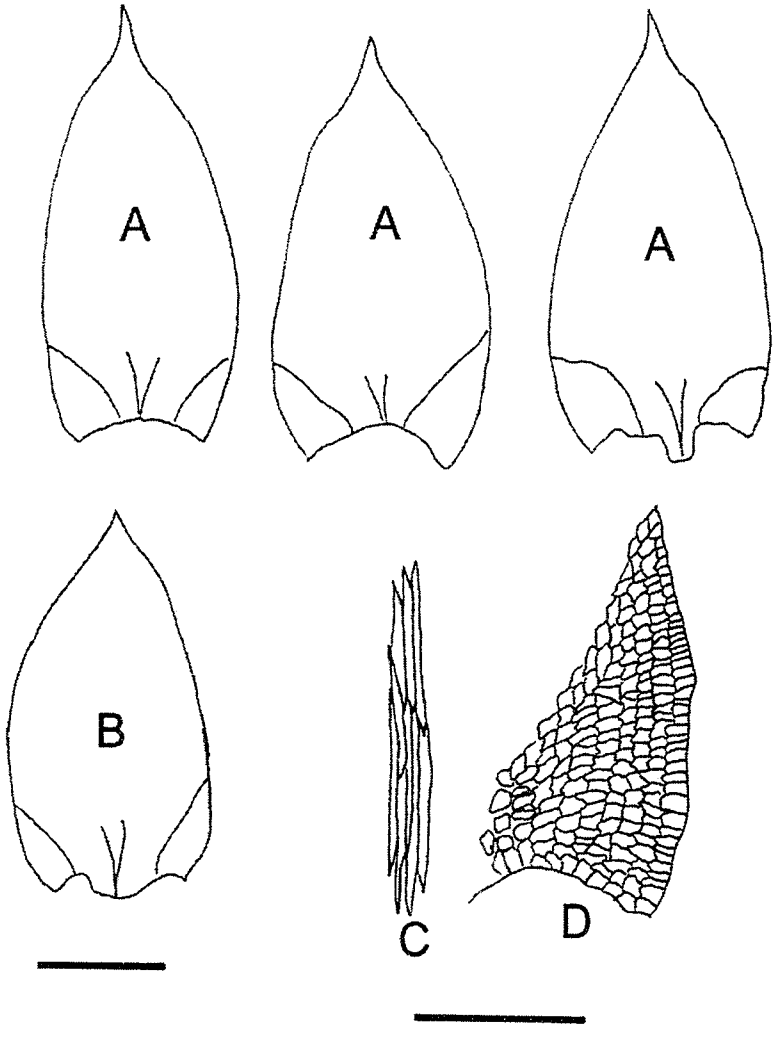


Figure 18. Distribution of *Erythrodontium barteri*

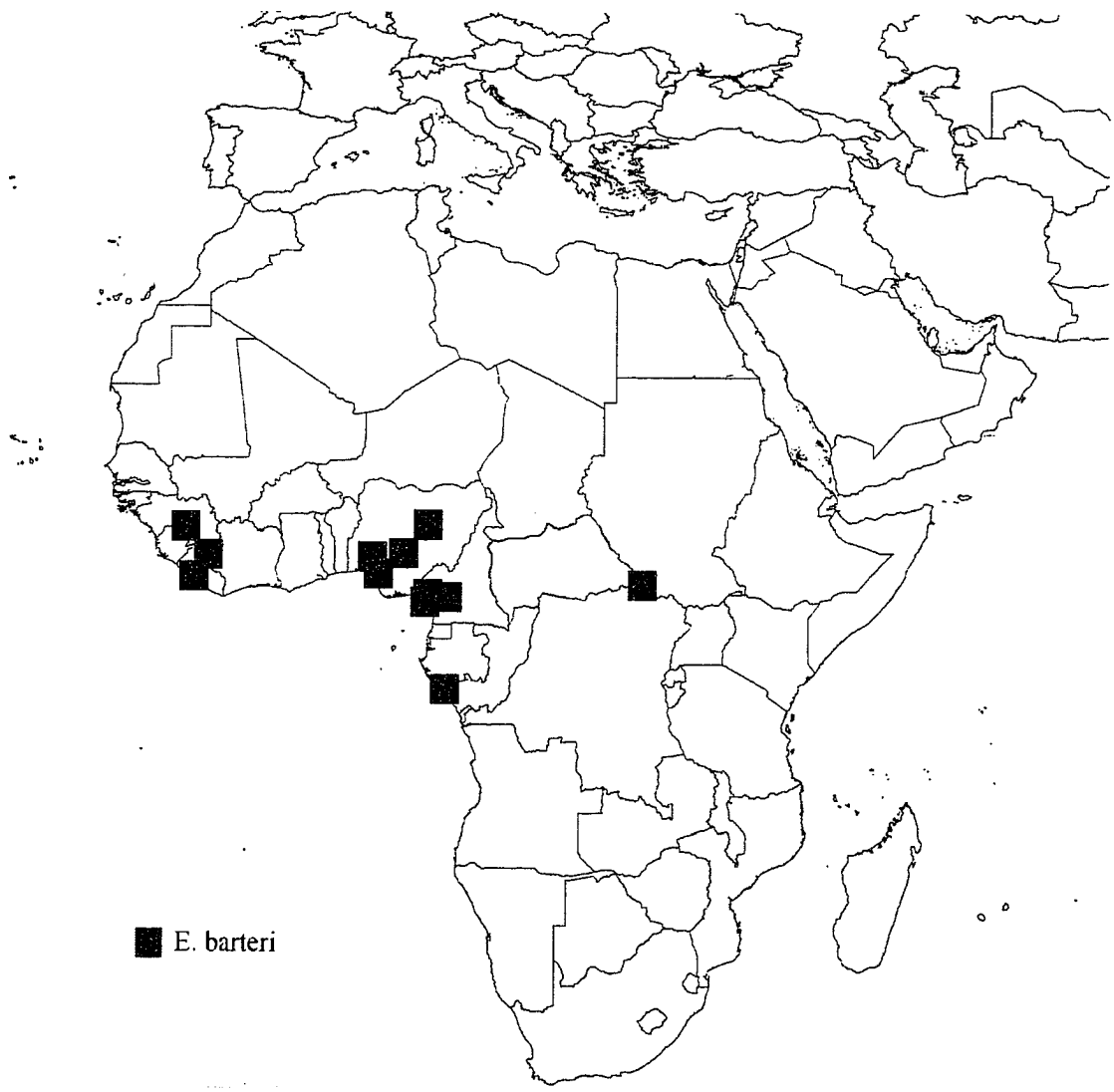


Figure 19. *Erythrodontium barteri*. A. Branch leaves. B. Stem leaves. C. Alar cells. D. Median laminal cells (all drawn from type). E. Calyptra. Upper scale bar = 50 μm (C, D), lower left scale bar = 0.5 mm (A, B), lower right scale bar = 1.0 mm (E).

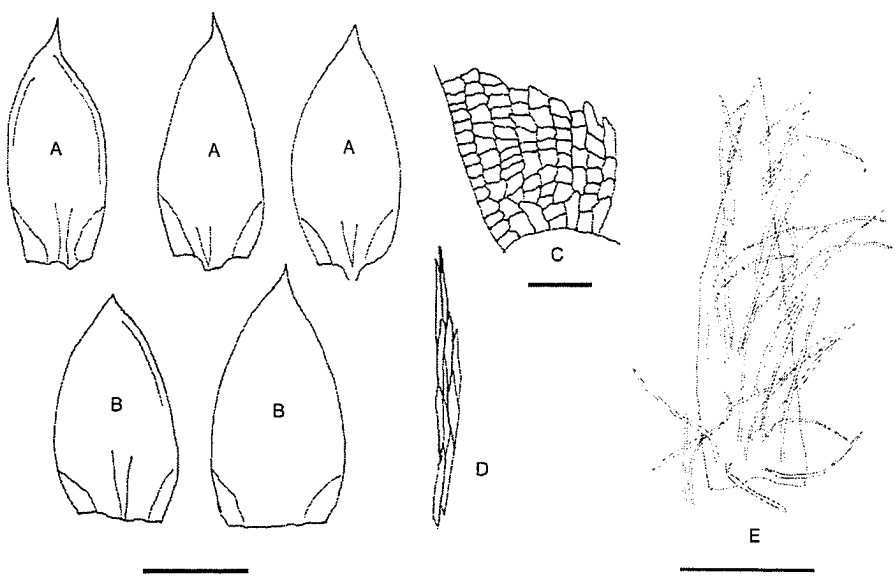


Figure 20. Phylogenetic tree showing relationships within Entodontaceae (11 taxa) derived from the *trnL-F* sequence data. Outgroups: *Isopterygium tenerum, Leucodon brachypus, Neckera douglasii, N. pennata, Platygyrium repens,* and *Pylaisia selwynii*. Strict consensus of 82 equally most parsimonious trees (length 92, CI = 0.6522, RI = 0.5000). Numbers above branches are bootstrap values for 500 replicated analyses.

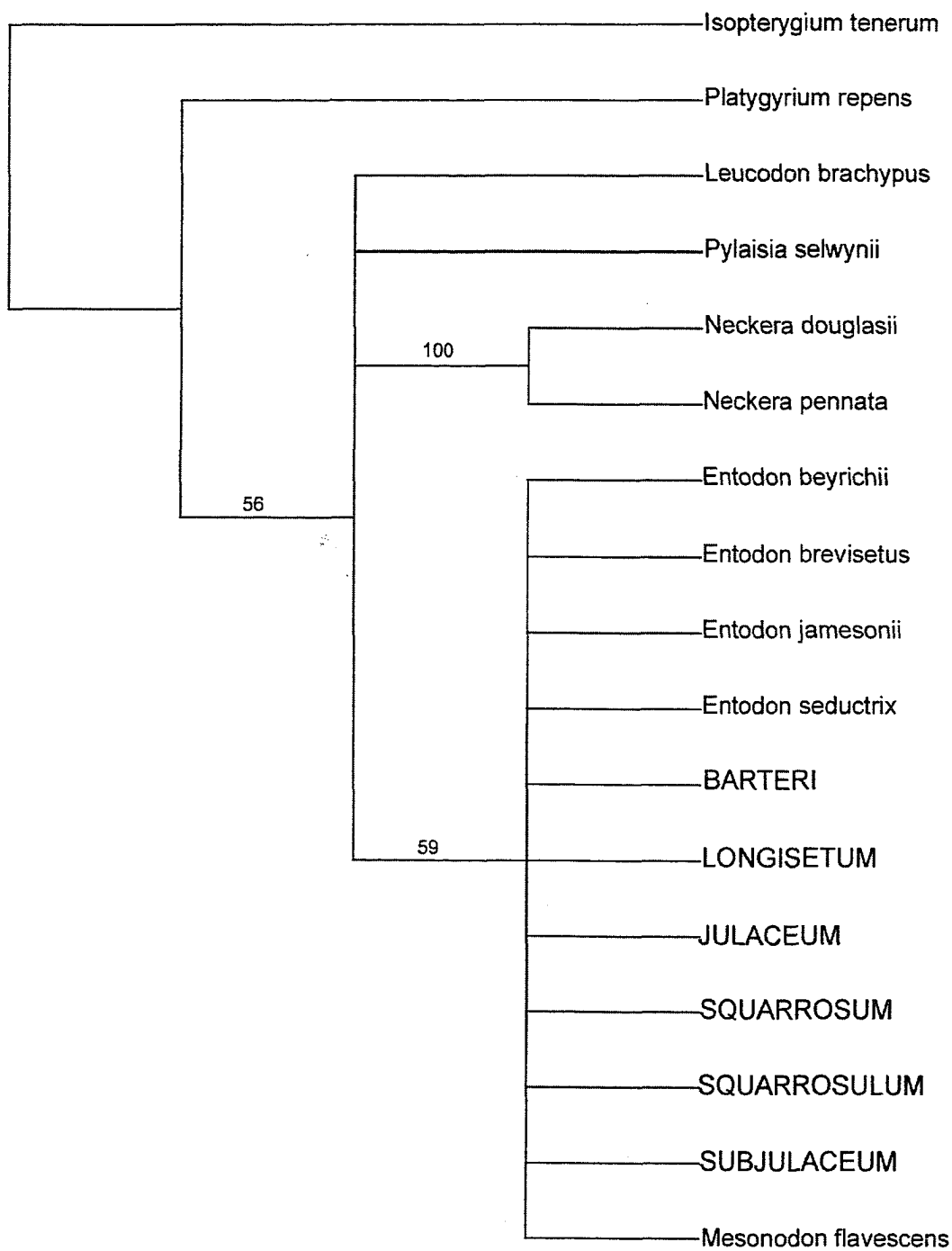


Figure 21. One randomly chosen tree derived from the *trnL-F* sequence data with branch lengths proportional to the number of changes. Number of changes shown above branches.

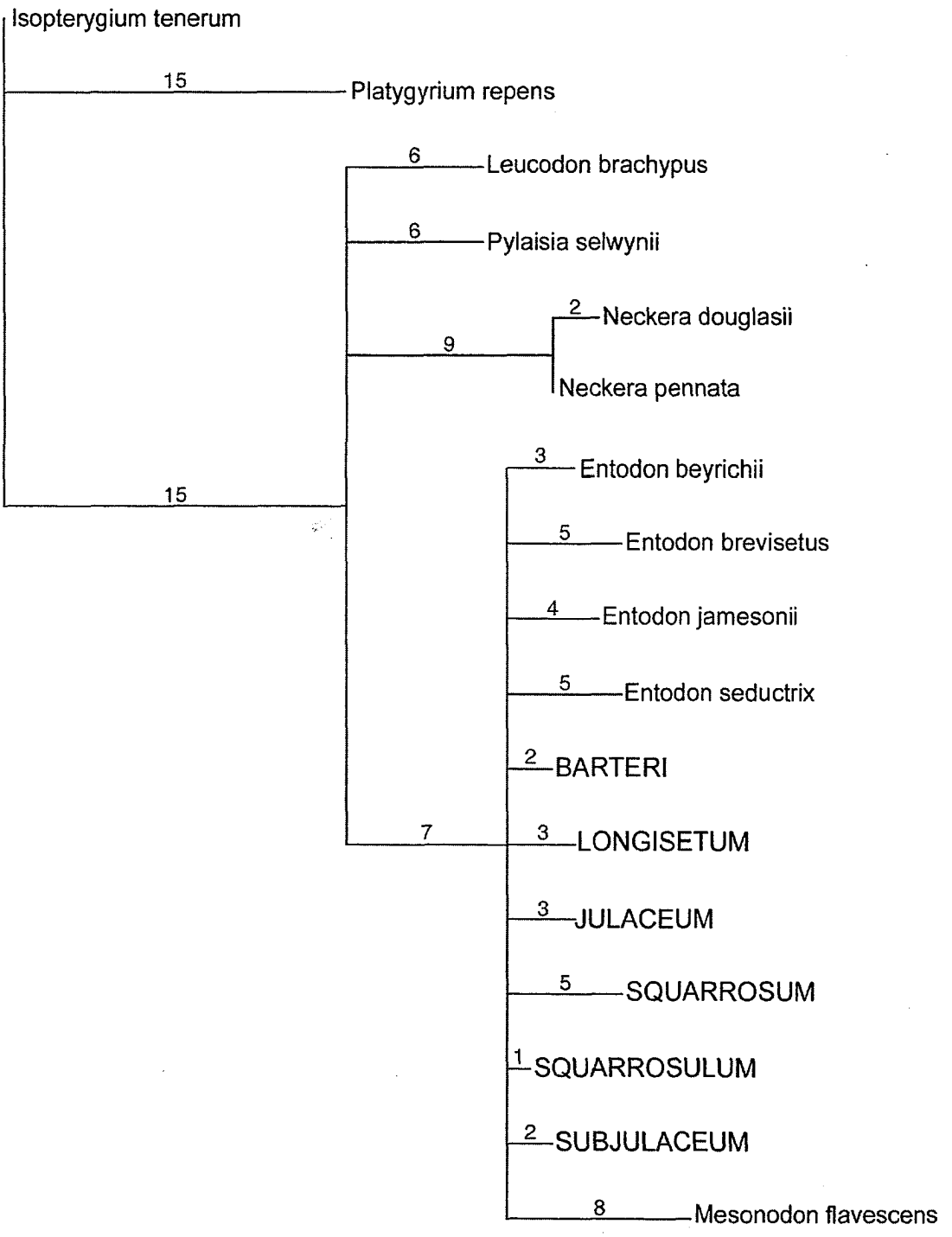


Figure 22. Phylogenetic tree showing relationships within Entodontaceae (10 taxa) derived from the ITS sequence data. Outgroups: *Leucodon brachypus, Neckera douglasii* and *Neckera pennata*. Strict consensus of 388 equally most parsimonious trees (length 400, CI = 0.9350, RI = 0.8267). Numbers above branches are bootstrap estimates for 500 replicate analyses.

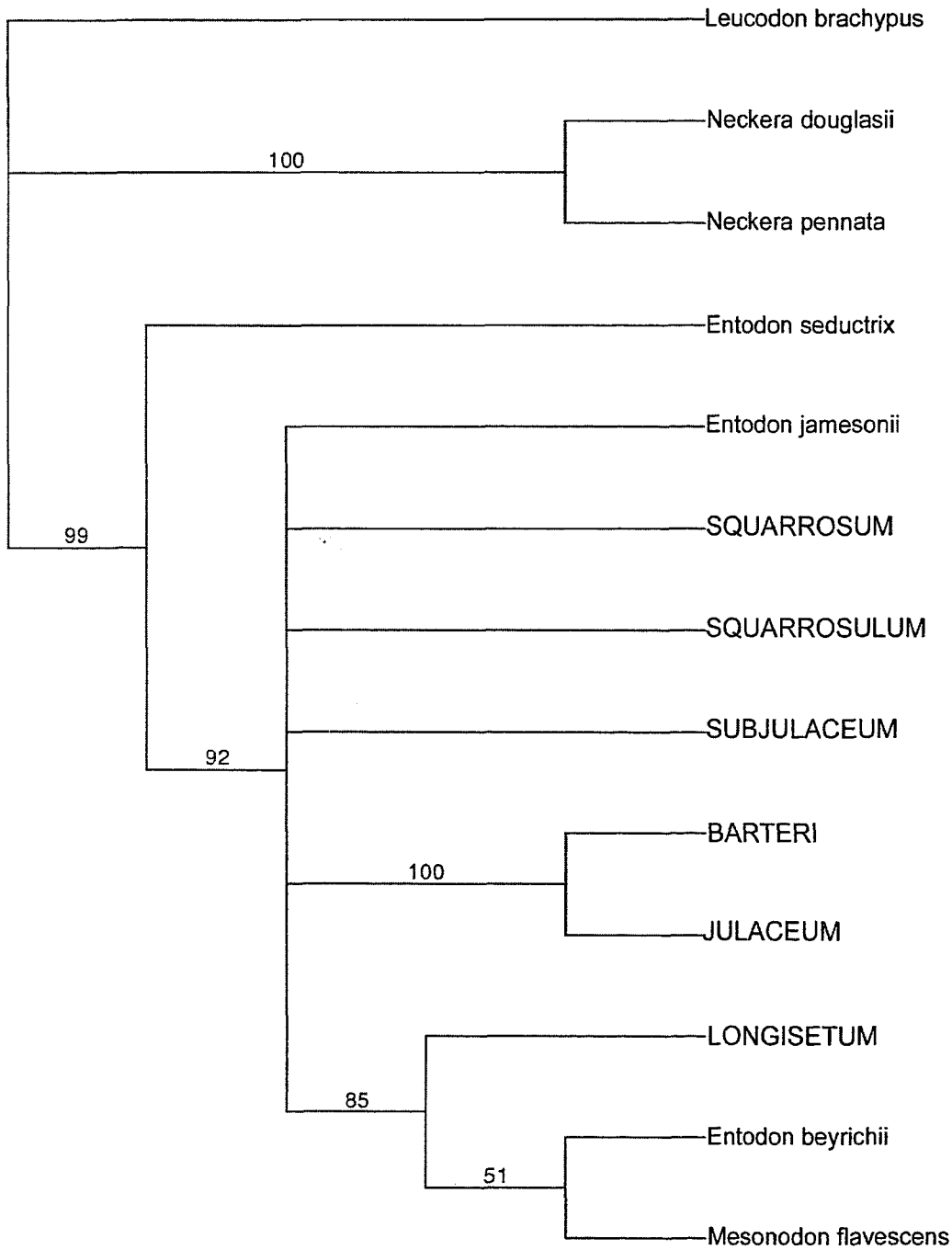


Figure 23. One randomly chosen tree derived from the ITS sequence data with branch lengths proportional to the number of changes. Number of changes shown above branches.

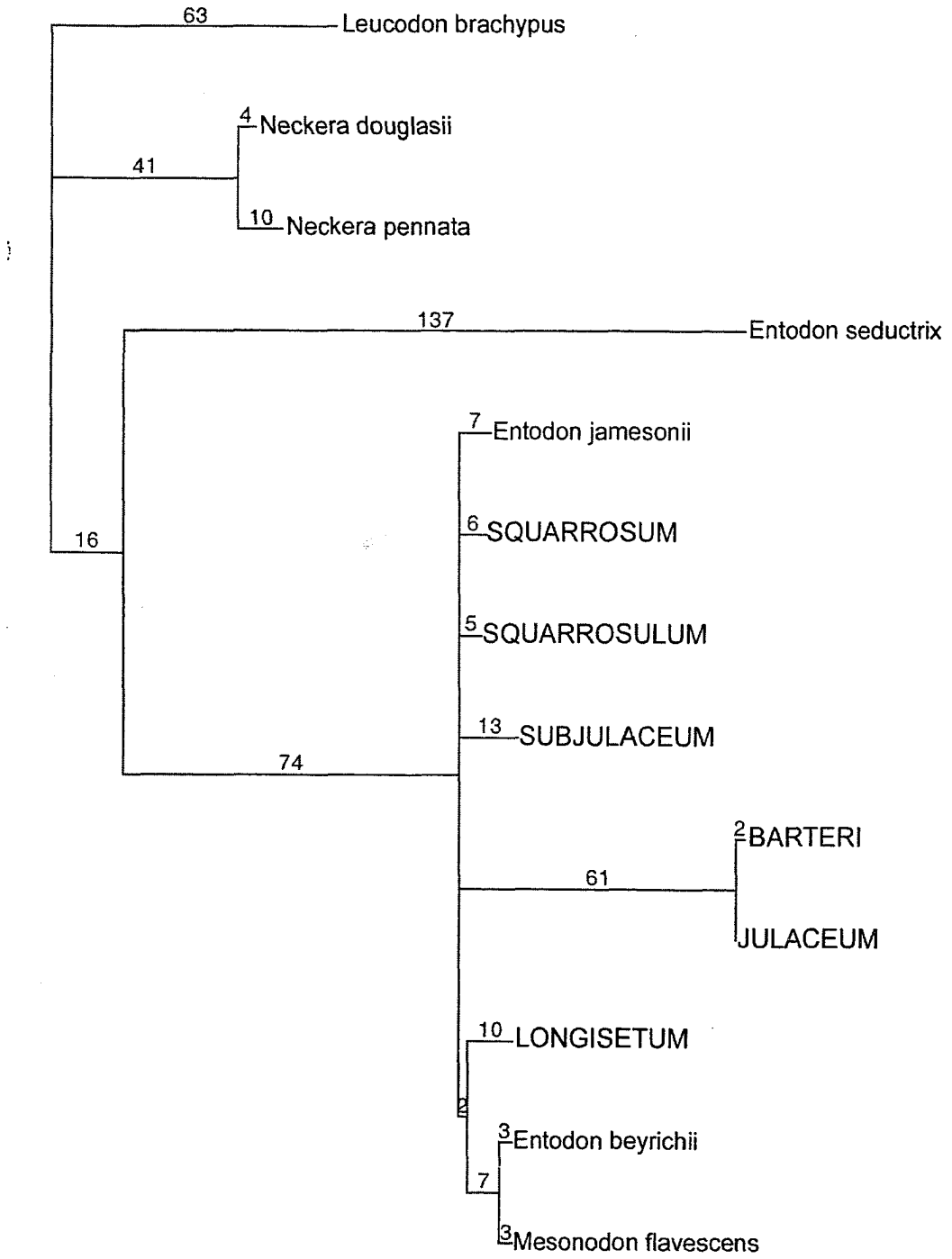


Figure 24. Phylogenetic tree showing relationships within Entodontaceae (10 taxa) based on a combined data set of ITS and *trnL-F* sequence data. Outgroups: *Leucodon brachypus, Neckera douglasii* and *Neckera pennata*. Strict consensus of 460 most parsimonious trees (length 450, CI = 0.9350, RI = 0.8267). Numbers above branches are bootstrap estimates for 500 replicate analyses.

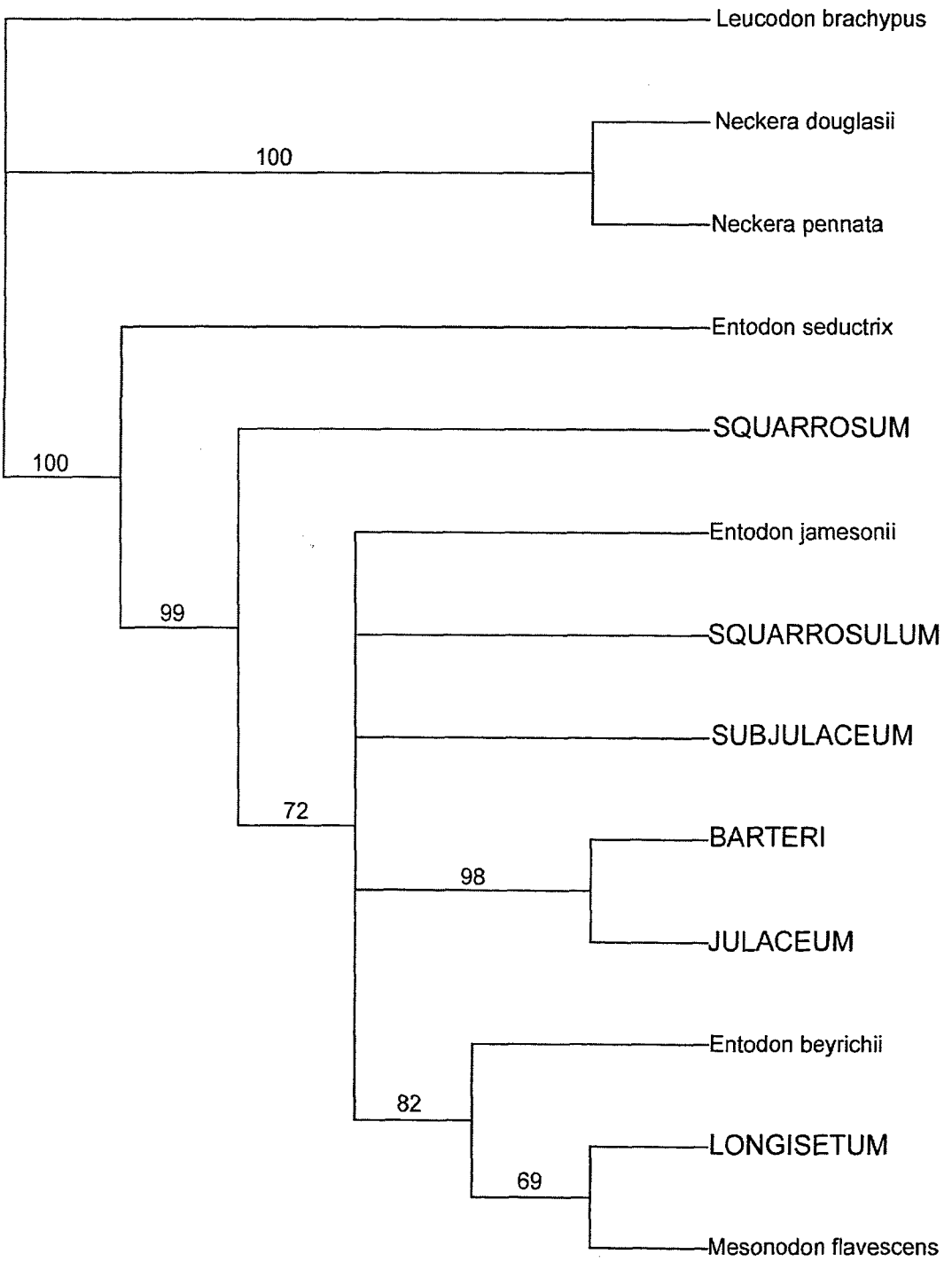


Figure 25. One randomly chosen tree derived from combined data set of ITS and *trnL-F* sequence data with branch lengths proportional to the number of changes. Number of changes shown above branches.

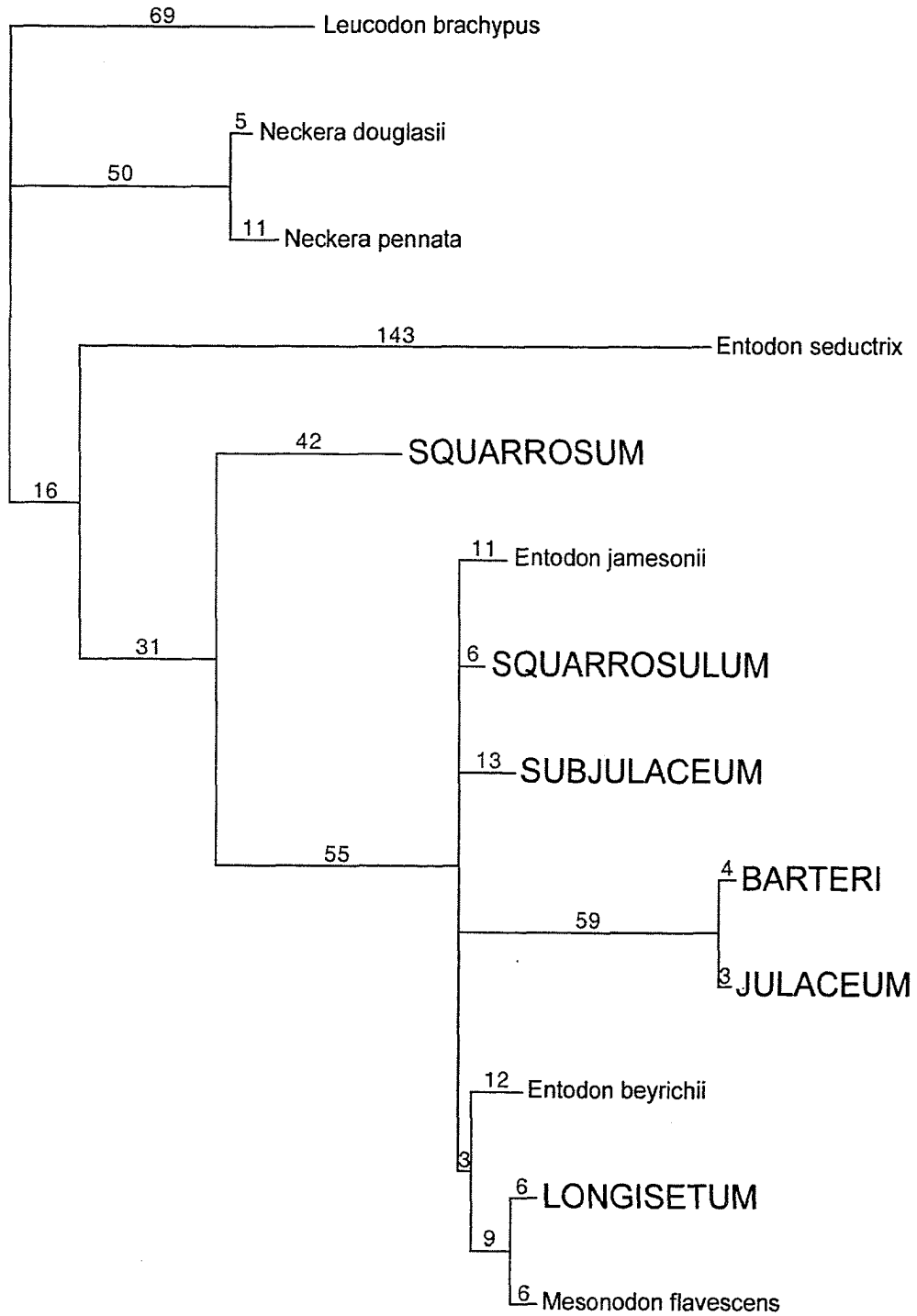
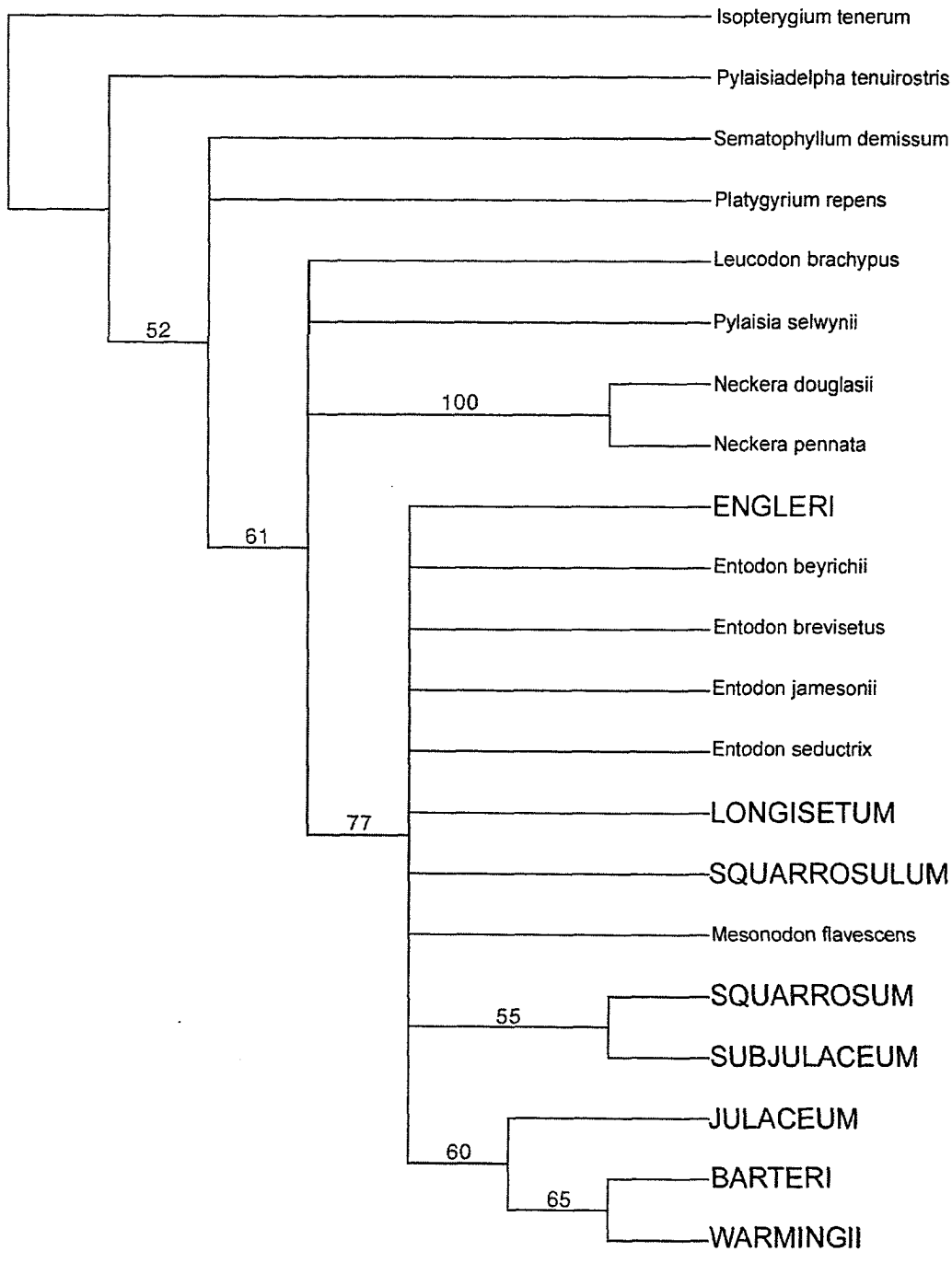


Figure 26. Phylogenetic tree showing relationships within Entodontaceae (13 taxa) based on combined data sets of ITS and *trnL-F* sequence data and morphological character set. Outgroups: *Isopterygium tenerum, Leucodon brachypus, Neckera douglasii, N. pennata, Platygyrium repens, Pylaisiadelpha tenuirostris, Pylaisia selwynii* and *Sematophyllum demissum*. Strict consensus of 767 equally most parsimonious trees (length 607, CI = 0.7805, RI = 0.5678). Numbers above branches are bootstrap estimates for 500 replicate analyses.



Literature Cited

Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell & M. J. Donoghue. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence of angiosperm phylogeny. Ann. Missouri Bot. Gard. 82: 247-277.

Bartram, E. B. 1949. Mosses of Guatamala. Fieldiana, Bot. 25: i-v, 1-442.

Brotherus, V. 1893-1909. Musci. II. Specieller Teil. *In* Engler, A. & K. Prantl (eds.), Die natürlichen Pflanzenfamilien 1(3): 277-1246. Engelmann, Leipzig.

Brotherus, V. 1924-25. Musci (Laubmoose). *In* Engler, A. (ed.), Die natürlichen Pflanzenfamilien, Ed. 2, vols. 10-11. Engelmann, Leipzig.

Buck, W. R. 1980. A generic revision of the Entodontaceae. J. Hattori Bot. Lab. 48: 71-159.

Buck, W. R. 1998. Pleurocarpous mosses of the West Indies. Mem. New York Bot. Gard. 82: 1-400.

Churchill, S. P. & E. L. Linares C. 1995. Prodromus bryologiae Nova Granatensis: introducción a la flora de musgos de Colombia. Parte 2: Grimmiacae a Trachypodaceae. Bibliot. José Jerónimo Triana 12: 455-924.

Clegg, M. T., B. S. Gaut, G. H. Learn Jr. & B. R. Morton. 1994. Rates and patterns of chloroplast DNA evolution. Proc. Natl. Acad. Sci. U. S. 91: 6795-6801.

Crosby, M. R., R. E. Magill, B. Allen & S. He. 2000. A checklist of the mosses.

320 pp. Missouri Botanical Garden, St. Louis.

Enroth, J. 1991. Bryophyte flora of the Huon peninsula, Papua New Guinea. XLII. Entodontaceae (Musci). Acta Bot. Fenn. 143: 43-55.

Farris, J. S. 1983. The logical basis of phylogenetic analysis. Advances Cladist. 2: 7-36.

Fleischer, M. 1922. Die Musci der Flora von Buitenzorg: zugleich Laubmoosflora von Java mit berücksichtigung aller Familien und Gattungen der gesamten Laubmooswelt. 4th vol: v-xxxi, 1105-1729. E. J. Brill, Leiden.

Gangulee, H. C. 1980. Mosses of Eastern India and adjacent regions. Fascicle 8 (Hypnobryales-Hypineae: Floristic trends: Index: Errata). Pp. (xlv-liii) + 1753-2145. Calcutta, India.

Gielly, L. and P. Taberlet. 1994. The use of chloroplast DNA to resolve plant phylogenies: noncoding versus *rbc*L sequences. Molec. Biol. Evol. 11: 769-777.

---------- and ----------. 1996. A phylogeny of the European gentians inferred from chloroplast *trn*L (UAA) intron sequences. Bot. J. Linn. Soc. London 120: 57-75.

Groth, H., G. Helms & J. Heinrichs. 2002. The systematic status of *Plagiochila* sects. *Bidentes* Carl and *Caducilobae* Inoue (Hepaticae) inferred from nrDNA ITS sequences. Taxon 51: 675-684.

Hampe, G. E. L. 1870. Symbolae ad floram Brasiliae centralis cognoscendam. Musci frondosi. Vid. Medd. Dansk Naturh. For. Kjöbenh. 8: 267-296.

Hooker, W. J. 1818. Musci Exotici: containing figures and descriptions of

new or little known foreign mosses and other cryptogamic subjects. 2 vols., 76 plates, text unnumbered. London.

Mitten, W. 1860. On some new species of Musci and Hepaticae in the herbarium of Sir W. J. Hooker, collected in tropical Africa, chiefly by the late Dr. Vogel and Mr. Barter. Trans. Linn. Soc. London 23: 51-58 + Tab. 5,6.

Potier de la Varde, R. 1925. Mousses nouvelles de l'Afrique tropicale français. (Diagnoses préliminaires). Bull. Soc. Bot. France 72: 351-367.

Potter, D., J. J. Luby & R. E. Harrison. 2000. Phylogenetic relationships among species of *Fragaria* (Rosaceae) inferred from non-coding nuclear and chloroplast DNA sequences. Syst. Bot. 25: 337-348.

Renauld, F. & J. Cardot. 1909. Essai sur les Leucoloma et supplément au prodrome de la flore bryologique de Madagascar et des Comores. vii-xi, 1-139. Monaco.

Schilling, E. E., C. R. Linder, R. D. Noyes & L. H. Rieseberg. 1998. Phylogenetic relationships in *Helianthus* (Asteraceae) based on nuclear ribosomal DNA internal transcribed spacer region sequence data. Syst. Bot. 23: 177-187.

Schwaegrichen, C. 1828. Species muscorum frondosorum descriptae, Suppl. 3(2), 24 pls., text unnumbered. Leipzig.

Sharp, A. J., H. Crum & P. M. Eckel, editors. 1994. The moss flora of Mexico. Part 2. Mem. New York Bot. Gard. 69(2): 581-1113.

Sim, T. R. 1926. The Bryophyta of South Africa. Trans. Roy. Soc. S. Afr. 15: 1-475.

Small, R. L., J. A. Ryburn, R. C. Cronn, T. Seelanan & J. F. Wendel. 1998. The tortoise and the hare: choosing between noncoding plastome and nuclear *Adh* sequences for phylogeny reconstruction in a recently diverged plant group. Amer. J. Bot. 85: 1301-1315.

Struwe, L., M. Thiv, J. W. Kadereit, A. S. R. Pepper, T. J. Motley, P. J. White, J. H. E. Riva, K. Potgieter & V. A. Albert. 1998. *Saccifolium* (Saccifoliaceae), an endemic of Sierra de la Neblina on the Brazilian-Venezuelan border, is related to a temperate-alpine lineage of Gentianaceae. Harvard Pap. Bot. 3: 199-214.

Swofford, D. 1998. PAUP: Phylogenetic analysis using parsimony, version 4.0. Lab. Molecular Systematics, Smithsonian Inst., Washington, D. C.