

LEPTODONTIUM STELLATIFOLIUM (POTTIACEAE, BRYOPHYTA) IN LA RÉUNION ISLAND, A MAJOR RANGE DISJUNCTION

RICHARD H. ZANDER¹ and TERRY A. HEDDERSON²

Summary: A species of mountainous regions of Latin America, *Leptodontium stellatifolium*, is reported from La Réunion Island in the Indian Ocean. This is a major geographic range disjunction. The species is illustrated and described from La Réunion material, and its considerable variation across its range and within La Réunion is discussed. Explanations of its distribution are suggested in terms of both ancient sky and ocean island spore dispersal, and recent, human-mediated introduction. We provide a key for species of *Leptodontium* occurring on La Réunion.

Key words: Andes, Indian Ocean, La Réunion, *Leptodontium stellatifolium*, pseudoparaphyllia.

Resumen: *Leptodontium stellatifolium* (Pottiaceae, Bryophyta) en la Isla Réunion, un rango de disyunción significativo. *Leptodontium stellatifolium*, una especie de las regiones montañosas de América Latina, es registrada para La Réunion en el Océano Índico. Esta es una disyunción geográfica significativa. La especie es descrita e ilustrada y se discute su variación a lo largo del rango de distribución y dentro de la isla. Se sugiere que su distribución puede deberse a una dispersión antigua por aire y a través de las islas o bien fue recientemente introducida por el hombre. Se incluye una clave de las especies de *Leptodontium* en La Réunion.

Palabras clave: Andes, La Réunion, *Leptodontium stellatifolium*, Océano Índico, pseudoparafilía.

INTRODUCTION

Leptodontium stellatifolium (Hampe) Broth. is unusual in the genus in its highly crowded, entire leaves, much broadened costal base; leaf basal cells and costa with deep orange or red coloration. The entire leaves are uncommon among species of *Leptodontium* (Müll. Hal.) Hampe ex Lindb. Collections of this species from La Réunion Island in the South Indian Ocean, where it was previously unknown, are particularly interesting because of the great disjunction between this mountainous ocean island and its known range in high elevation areas of Central America and South America.

Taxonomic treatment

Leptodontium stellatifolium (Hampe) Broth., Nat. Pflanzenfam. 1(3): 400. 1902. **Fig. 1.**

Anacalypta stellatifolia Hampe, Vidensk. Meddel. Dansk. Naturhist. Foren. Kjøbenhavn 34: 37. 1872. *Pottia stellatifolia* (Hampe) A. Jaeger, Ber. Thatigk. St. Gallischen Naturwiss. Ges. 1871–1872: 345. 1873. Type: Brazil, Rio de Janeiro, Glaziou, s.n., sub num. 5205 (*Holotypus* BM!; *Isotypus* S-PA!).

Leptodontium anoectangiaceum (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 400. 1902. *Trichostomum anoectangiaceum* Müll. Hal., Bull. Herb. Boissier 6(2): 91. 1898. Type: Brazil, Serra Itatiaia, Ule, 1894 (Ule, Bryoth. Brasil. 1811) (not seen).

Leptodontium chrysobaseum (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 400. 1902. *Trichostomum chrysobaseum* Müll. Hal., Bull. Herb. Boissier 6(2): 89. 1898. Type: Brazil, Serra

¹Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri, 63166. U.S.A. Email: richard.zander@mobot.org

²Bolus Herbarium, University of Cape Town, Private Bag, 7701, Rondebosch, South Africa. Email: terry.hedderson@uct.ac.za



Fig. 1. A. Habit, wet. B. Habit, dry. C. Capsule. D. Calyptra. E. Calyptra adherent to operculate capsule. F. Peristome, with prostome. G. Stem section. H–I. Pseudoparaphyllia on stem. J. Pseudoparaphyllum. K–N. Cauline leaves. O. Perichaetial leaves and archegonia. P. Leaf apex cells. Q. Basal laminal cells. R. Leaf section near apex. S. Leaf section at base. T. Gemmae. Scale bars: A = 1 mm, A–E; B = 0.5 mm, K–O; C = 50 μm, F–G, J, P–T.

Itatiaia, Ule, 1894 (Ule, Bryoth. Brasil. 1824) (*Lectotypus* designated by Zander, 1972, H!).

Leptodontium squamifolium (Müll. Hal.) Broth., Nat. Pflanzenfam. 1(3): 401. 1902. *Trichostomum squamifolium* Müll. Hal., Bull. Herb. Boissier 6(2): 90. 1898. Type: Brazil, Serra Itatiaia, Ule, 1894 (Ule, Bryoth. Brasil. 1827) (*Isotypus* H!).

Plants forming a low, dense turf, brown above, reddish to yellowish below. **Stem** length 2–3 cm, section rounded-pentagonal, central strand absent, sclerodermis present in 1 layer, hyalodermis absent; often with chaffy epipillose entire or dentate pseudoparaphyllia at base of branches and stem. **Axillary hairs** with basal 1–2 cells brown, ca. 8 cells in length. **Tomentum** thin or absent, all terminal cells elongate or occasionally with series of 3–4 short cells ending the thicker rhizoids. **Leaves** usually very crowded, appressed-incurved and imbricate when dry, spreading-recurved when wet, ligulate to ovate, 1.2–1.5 mm in length, distal lamina weakly carinate but deeply channeled along costa, leaves at base of stem ovate-lanceolate, with ca. 2 bifid papillae per lumen, acuminate to a long sharp single-celled apiculus; **leaf margins** reflexed in proximal 1/2, edentate but minutely crenulate in distal 1/2 by projecting cell walls and papillae; **leaf apex** acute to obtuse and apiculate, apiculus short, broad and flat or occasionally absent, occasionally 1–2 small marginal teeth near apiculus, apex keeled or occasionally weakly cucullate; **leaf base** ovate, differentiated across leaf, no stripes, 2–4 rows marginal cells shorter and less colored, basal cells filling only 1/4–1/3 of leaf, not porose, no miniwindows, basal cells 9–11 μm , 4–5:1; **costa** when mature green with orange to reddish basal cells, costa ending (2–)4–6 cells before apex, much wider at insertion than at midleaf, occasionally spurred, adaxial costal cells elongate, rows of cells across costa at midleaf viewed in section 3–4, width at base 50–80 μm , section flattened-elliptic in shape, adaxial stereid band in 1–2 layers, abaxial band in 1 layer, 2–4 fully included guide cells; **medial laminal cells** subquadrate, leaf border not differentiated, marginal cell thickness in section about same compared to medial cells, medial cell width 9–11 μm , 1:1, cell walls moderately thickened, superficial cells walls bulging; medial laminal papillae flattened,

simple to 2- or 3-fid, 2–3 per lumen, or multifid and somewhat fused. **Specialized asexual reproduction** by gemmae, obovoid, 35–45 \times 75–90 μm , with 2–4 transverse and 1 longitudinal septa, borne on stem. **Sexual condition** dioicous. **Perigonia** terminal or subterminal by innovation. **Perichaetial leaf length** 2–2.5 mm. **Seta** 8–10 mm in length. **Capsule** cylindric, 1.25–1.5 mm, exothecial cells short-rectangular, 1–1.5:1, stomates present or apparently absent, annulus 2–4 rows of reddish brown cells; **peristome** linear, 400–450 μm , indistinctly striate, 5–7 articulations, preperistome occasionally present, short, basal membrane absent, **operculum** short-conic, ca. 0.4 mm, cells straight. **Calyptra** cucullate, smooth, calyptra length 2–2.5 mm, clasping the seta. **Spores** round, 15–18 μm in diameter, colorless, weakly papillose. **KOH laminal color reaction** distally yellow to red-orange, basal cells and costa strongly colored red-orange.

DISCUSSION

Leptodontium stellatifolium occurs in Costa Rica, as reported by Allen (2002), as well as in Colombia and southeastern Brazil. The Costa Rican material entirely lacks the clear, one-celled apiculus, whilst plants from Brazil only occasionally lack this feature. The Costa Rican plants also have more flattened distal superficial laminal cell walls, giving the appearance of that of *Leptodontium luteum* (Taylor) Mitt. A herbarium specimen from Colombia (Churchill *et al.* 14095, MO) is also *L. stellatifolium*, differing as an extreme form with strongly rounded apex, no apiculus and costa ending ca. 6 cells before the apex. A specimen from Réunion (Hedderson 16643, BOL, MO) is intermediate, with rounded, cucullate apex, costa ending 2–3 cells before the apex, but with the apiculus present though reduced to 2–4 cells.

The scattered distribution in South America disjunctive to Réunion Island in the Indian Ocean suggests a complex biogeographic history. One possible explanation for the presence of this Andean species in the Old World is human introduction, as apparently is the case with similar gemmiferous Andean species of relatively small

plants for the genus. These include *Leptodontium proliferum* Herz., which occurs in Colombia, Bolivia, Peru (Churchill *et al.*, 2000), Gt. Britain (Porley & Edwards, 2010) and Africa (Lesotho, J. G. Duckett & H. W. Matcham s.n., April 14, 1994, MO); *L. gemmascens* (Mitt.) Braithw., which is known from Europe, Marion and Prince Edward islands and Kerguelen; and *L. stellaticuspis* E. B. Bartram, which is found in Colombia, Ecuador, Venezuela and Kerguelen (Terre Grande, Port Couvreur, R. Ochyra 378/06, November 19, 2006, MO). On the other hand, Réunion also hosts the non-gemmiferous *Hymenostylium xanthocarpum* (Hook.) Brid., otherwise known only from the Himalayas of Nepal and India, and Cameroon (Zander & Hedderson, 2016). On Réunion *L. stellatifolium* is mostly associated with indigenous *Erica*-dominated vegetation and is not at all associated with anthropogenic habitats, suggesting that human introduction is not likely for this species.

La Réunion is a young (2–3 mya), isolated, oceanic volcano, and all of its biota must be the result of chance long-distance dispersal. An extreme example of this is the endemic mid-altitude forest tree *Acacia heterophylla*, which originated from direct dispersal to Réunion of its nearest relative in Hawaii ca. 1.4 mya (Le Roux *et al.*, 2014). It is quite possible that these Réunion species and other uncommon species survive as scattered relicts across the tropics and subtropics, in both sky and ocean islands, perhaps human dispersed in some cases and not in others. Further study using molecular data may clarify this.

A further possibility is that *L. stellatifolium* is actually more widespread than current records indicate. Although *L. stellatifolium* has been collected frequently over a long time period on Réunion, specimens have previously all been identified as *L. flexifolium* (Dicks.) Hampe. It is possible that “high-altitude” forms of *L. flexifolium* reported from various high-elevation localities across continental Africa (e.g., De Sloover, 1987) actually represent *L. stellatifolium*; these need to be examined.

Leptodontium stellatifolium is easily distinguished by the crowded leaves, bright green distal laminal cells contrasting with the red-orange costa and basal cells, and, except for the clear conical apical cell (which may be

lacking), entire but minutely crenulate leaves. The stem sclerodermis has no trace of thin outer cell walls while more robust plants of the somewhat related *Leptodontium flexifolium* have a weakly distinguishable hyalodermis. *Leptodontium flexifolium*, doubtfully present on Réunion, is quickly distinguishable by more distantly inserted leaves, presence of marginal teeth in larger plants, usual presence of a marginal border of 2–4 rows of cells with thickened and less papillose walls, lack of differentially colored basal leaf cells, and larger distal laminal cells 11–15 µm in width. Flagellate forms of *L. stellatifolium* with smaller, distant leaves (e.g. Hedderson 15805) may morphologically phenocopy *L. flexifolium* in lacking the red-orange basal cells and distal laminal cells enlarged and bifid-papillose, but are distinguishable by completely lacking any marginal laminal teeth or enlarged pseudoparaphyllia. The abaxial surface of the costa is also more strongly simply papillose in *L. stellatifolium* than in *L. flexifolium*.

Hyophila nymaniana (M. Fleisch.) M. Menzel (= *H. rosea* R.S. Williams) of tropical and subtropical regions may be confused with this species, especially by its similar leaf shape and red basal cells, but that species has stellate gemmae and the costa in section shows a clearly differentiated adaxial epidermal layer in addition to the adaxial stereid band. The genus *Zygodon* Hook. & Taylor (Orthotrichaceae) may be similar in aspect but is distinguished by the ribbed capsule, perichaetial leaves similar to the cauline leaves, and usually homogeneous costal section.

Dentate epapillose pseudoparaphyllia occur at bases of stems or buds as, but are also occasionally found isolated as phylloids on the stem or below the perichaetium. They are nearly matched by those of *Leptodontium araucarieti* (Müll. Hal.) Paris (Zander, 1972). Although similar though smaller pseudoparaphyllia may occur at the base of branches of other *Leptodontium* species, e.g. *L. excelsum* (Sull.) E. Britton, and the similar *L. flexifolium*, the sometimes scattered position of those of *L. stellatifolium* and the common narrowing of the base to a single stalk cell is unique. The sharp contrast between the dentate epapillose pseudoparaphyllia and the entire, papillose cauline leaves is distinctive, and compared to the size of the plants the former are

rather large. The chaffy phylloids are similar to but not as simple as the elongate bi-(tri-)seriate axillary hairs of *Tortella humilis* (Hedw.) Jenn. (Pottiaceae).

The closely crowded leaves of *Leptodontium stellatifolium* are unique in the genus, and show up commonly as two sectioned leaf bases when sectioning the stem. This, plus the character states of small size and orange basal laminal cells, indicates a derived status for this species. The widely disjunctive distribution and isolated combination of morphological traits imply that this is a fairly successful remnant of a larger, ancient assemblage of similar species.

Distribution. Central America (Costa Rica); South America (Colombia, southeastern Brazil); Indian Ocean Islands (Réunion); soil, at high elevations.

Representative specimens examined (see also Zander 1972 for additional Brazil collections).

BRAZIL. *Rio de Janeiro*, Parque Nacional Itatiaia, from Agulhas Negras to Brejo da Lapa, 2000–2300 m, 25–VII-1977, J. P. Frahm 1182 (MO). COSTA RICA. San José, M. R. Crosby 3900B (MO). COLOMBIA. *Antioquia*, Santa Rosa de Osos, soil, 2500 m, July 6, 1986, S. P. Churchill 14095 (MO). LA RÉUNION. N

sloping plateau of la Roche Ecrite, S of St. Denis, terricolous, subalpine ericaceous bush, 2100 m, 23-VIII-1994, G. Kis 9420/CB (EGR); *Commune St. Benoit*, Piton des Neiges, Along trail from Caverne Dufour to Hell-Bourg, on soil banks, 2370 m, 26-III-2008, T. A. Hedderson 16643 (BOL, MO); *Commune Sainte Rose*, Piton de la Fournaise, Cratere Commerson, trail to Caverne des Lataniers, Erica-dominated vegetation, on basalt, 2370 m, 1-XII-2004, T. A. Hedderson 15805 (BOL, MO); *Commune Le Tampon*, Plaine de Caffres, walk from Mare á Boue to Piton des Neiges, Erica-dominated vegetation, on volcanics, 1730 m, 26-VI-2016, T. A. Hedderson 18941 (BOL); *Commune St. Denis*, Sentier du Roche Ecrit, from les Haute du Brûlé, rain forest with *Cyathea*, over volcanic rock, 1400 m, 11-XII-2007, T. A. Hedderson 16579 (BOL, MO); *Commune Saint Joseph*, Route to Piton de la Fournaise, Puy la Pas de Sables, Ericaceous vegetation in dried out lake bed, 2370 m, 27-V-2015, T. A. Hedderson 18897 (BOL, MO); *Commune Saint Louis*, Forêt des Makes, along trail to summit, in ericaceous vegetation, 2150 m, 26-XI-2014, T.A. Hedderson 18760 (BOL).

The species of *Leptodontium* occurring on La Réunion may be distinguished by the following key. We provisionally exclude *L. flexifolium* (Dicks.) Hampe from the flora of La Réunion.

Key for species of Leptodontium occurring on La Réunion

1. Stem in section with outer cells thick-walled, not collapsing in older portions, stem outline smooth. 2
 2. Small plants, usually < 3 cm tall, leaves to ca. 3mm, ligulate to oblong. *L. stellatifolium* (Hampe) Broth.
 - 2'. Larger plants, mostly > 4 cm tall, leaves larger, lanceolate to ovoid-lanceolate. *L. viticulosoides* (P. Beauv.) Wijk. & Marg.
- 1'. Stem in section with thin-walled outer cells, these collapsed in older portions, making the stem fluted. ... 3
 3. Lamina with sharp teeth on both surfaces, forming bi- to tri-stratose patches in section, leaves longitudinally wrinkled. *L. longicaule* ssp. *stellatum* (Brid.) De Sloover
 - 3'. Lamina lacking teeth, but sometimes with scattered mammillose cells, unistratose in section, longitudinal wrinkles absent. 4
 4. Plants stiff, rigid, forming dense, yellow-brown tufts, leaves arched when moist, sheath relatively weakly differentiated, apex with elongate non-papillose cells, a patch of median basal cells usually strongly orange or yellow-orange. *L. pungens* (Mitt.) Kindb.
 - 4'. Plants soft, often elongate and flexuose, yellow to yellow green or brownish, leaves squarrose when moist, sheaths sharply distinct, apical cells not or scarcely differentiated, papillose, patch of orange median basal cells absent. *L. longicaule* ssp. *longicaule* Mitt.

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