Studies on Colombian Cryptogams VI.

High Andean species of Radula (Hepaticae)

by Els Jans

Institute for Systematic Botany, University of Utrecht

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ABSTRACT

This study deals with the genus Radula (Hepaticae) from the high Andean forests and paramos of Colombia, above 2500 m, and is based on the determination of Colombian collections gathered by H. Bischler and by A. M. Cleef and collaborators. A key to the 8 species known from the area is given and descriptions and ecological distribution data of R. ramulina Taylor, R. sonsonensis Stephani, R. nudicaulis Stephani, R. episcia Spruce and R. frondescens Stephani, R. ramulina Taylor var. microphylla Jans is described as new.

INTRODUCTION

The Colombian species of the large, pantropical liverwort genus Radula Dum. (Jungermanniales) are very poorly known. Although 22 species were reported from this country (Gradstein & Hekking 1979), most records were based on single specimens only. In his world monograph of the genus Radula, Castle (1937–1969) described only four species from the Colombian high Andes (above 2500 m): Radula jamesoni Tayl., Radula mollis Lindenb. & Gott., Radula ramulina Tayl. and Radula sonsonensis Steph. In addition, Winkler (1976) recorded Radula quadrata Gott. from 2900 m on the Sierra Nevada de Santa Marta. The highest record thus far of a Radula species from Colombia was of Radula jamesoni at 3700 m near Bogota.

The material of *Radula* collected in Colombia by H. Bischler (Paris) in 1956-1959 and A. M. Cleef and associates (Utrecht) in 1971-1973 and

subsequent years, formed the basis of the present study, which deals primarily with the high Andean species, occurring in the high Andean forest and the paramos. Thus, most of the material investigated originates from altitudes above 2500 m. Five species were recognised in this material: R. ramulina, R. sonsonensis, R. episcia, R. frondescens and R. nudicaulis. The latter three are apparently new to Colombia. R. ramulina is the most common species, occurring throughout the high Andean forest and the lower paramo belts from 1900–3800 m. The species are usually epiphytic on branches of trees or shrubs or terrestric on moist soil among rocks, R. episcia, however, differs from all other species by its preference for very wet localities: on very wet places in the Andean forest belt or submerged in a cold lake in the lower grassparamo. The known ecological distribution is summarized in table 1.

Table 1. Generalized ecological distribution of high Andean Radula species in Colombia.

Radula	High Andean forest (above 2500 m)	Paramo		
		terrestric	epilithic	epiphytic
episcia	×	×		
sonsonensis	×		×	
nudicaulis	×			×
ramulina	×			×
ramulina var. microphylla				×
frondescens				×

In the key given below all species of *Radula* known from above 2500 m in the Colombian Andes are included. The species descriptions mainly include vegetative characters, since reproductive structures were often lacking in the investigated material.

KEY TO THE SPECIES

- 1 Plants with discoid gemmae
- 1 Plants without discoid gemmae
- 2 Carinal portion of the leaf strongly arched and directed downward
 - 1 Radula sonsonensis Steph.

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- 2 Carinal portion of the leaf, if arched, never directed downward
- 3 Leaves densely imbricate, the free basal portion of the ventral lobe touching or overlapping the basal or carinal portion of the ventral lobe of the next alternate leaf
- 3 Leaves loosely imbricate, the free basal portion of the ventral lobe not overlapping, sometimes touching the ventral lobe of the next alternate leaf
 - 2 Radula nudicaulis Steph.

- 4 Lateral margin of the ventral lobe of the stem and branch leaves incurved and narrowly reflexed 3 Radula quadrata G.
- 4 Lateral margin of the ventral lobe of the stem and branch leaves with a slight outward curve and not narrowly reflexed

 4 Radula mollis L & G.
- 5 Auricle of the ventral lobe large, extended beyond the stem and voluted 5 Radula ramulina Tayl.
- 5 Auricle not voluted
- 6 Carinal portion of the leaf strongly arched and directed downward
 1 Radula sonsonensis Steph.
- 6 Carinal portion of the leaf, if arched, never directed downward
- 7 Vegetative branching more or less dichotomous, base of the dorsal lobe not extending beyond the stem 6 Radula episcia Spruce
- 7 Branching pinnate
- 8 The base of the ventral lobe fused to the axis more than one half its length
 2 Radula nudicaulis Steph.
- 8 The base of the ventral lobe fused to the axis less than half its length
- $\boldsymbol{9}\,$ Keel not decurrent, dorsal lobe extending across and beyond the stem

7 Radula frondescens Steph.

9 Keel decurrent, dorsal lobe usually not extending across the stem

8 Radula jamesoni Tayl.

6

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1. Radula sonsonensis Stephani, Spec. Hep. 4: 201. 1910; Castle (1963) 7-9. Fig. 1c-d.

Typus: Nova Granada, Páramo de Sonson, G. Wallis s.n., 1872 (G 19753, holo).

Plants in dried condition dull light brown, stems 0,08-0,2 mm in width, in transverse section with the cortex consisting of one cell layer, differentiated from the medulla by its darker pigmentation and by its thickened cell walls, the medullary cells colourless, slightly thinwalled, $20-32 \times 12-22$ µm; branching somewhat regularly pinnate, branches 1-6 mm in length. Dorsal leaf-lobe $0,2-1,9\times0,5-1,9$ mm, ovate, sometimes falcate, imbricate, spreading out, caducous, sometimes with discoid gemmae, apex rounded, the free portion of the base extended across the stem, the line of attachment slightly curved, the carinal region strongly inflated and directed downward. Ventral leaf-lobe 0,2-0,7 × 0,15-0,6 mm, rectangular-quadrate, not imbricate, the apex narrowly rounded or bluntly angled, the base attached to the axis over almost its entire length, very little extending across the stem, auricle 0,08-0,17 × 0,03-0,07 mm; cells of the dorsal leaf-lobe thinwalled with conspicuous trigones, or with small trigones, at the margin $10-15 \times 15-17 \mu m$, quadrate-rectangular, in the median portion 12–25 \times 10–22 μ m, rounded-hexagonal, at the base 17–48 \times 12-30 μ m, rectangular.

Distribution: Known only from Colombia: Antioquia, Boyaca, Meta, Nova Granada, Tolima. A widely distributed liverwort species in the Colombian Eastern and Central Cordillera, altitudinally ranging from 3200 up to 4170 m.

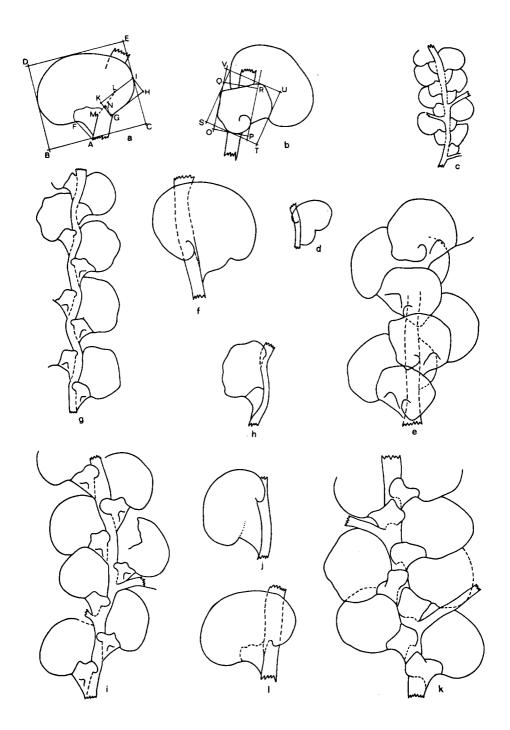


Fig. 1. Radula species of high Andean Colombia. a. R. ramulina, leaf in dorsal view. EC: length dorsal lobe; BC: width dorsal lobe; GH: width auricle dorsal lobe; HI: length auricle dorsal lobe; AF: length keel. b. Id., leaf in ventral view. ST: width ventral lobe; TU: length ventral lobe; PR: length auricle ventral lobe; RQ: width auricle ventral lobe. c. R. sonsonensis, ventral view. d. Id., leaf in dorsal view. e. R. ramulina, ventral view. f. Id., leaf in dorsal view. g. R. episcia, ventral view. h. Id., leaf in dorsal view. i. R. nudicaulis, ventral view. j. Id., leaf in dorsal view. k. R. frondescens, ventral view. l. Id., leaf in dorsal view. All drawn from Colombian specimens gathered by A. M. Cleef.

Ecology: Radula sonsonensis is a characteristic epilithic liverwort occurring on volcanic rocks and outcrops of sandstone and limestone on the atmospherically humid side of the mountains.

This species has been found in the upper Andean Weinmannia cloud forest belt; on rock surfaces covered by Arcytophyllum caracasanum (Rub.) in the bambooparamo; and up into the upper condensation zone of the lower superparamo of the Nevado de Sumapaz. Here, at 4000–4200 m, R. sonsonensis was gathered on limestone outcrops covered by composite (dwarf) shrubs, e.g. Loricaria complanata and Diplostephium rupestre.

Colombian specimens seen: Boyaca: Páramo N.W. de Belen, Cleef 2137, 2141 (COL, U); Cauca: Bischler 982,1060 (COL, PC, U); Meta: Páramo de Sumapaz, Cleef 7750, 8150 (COL, U); Tolima: Nevado de Tolima, Van der Hammen and Jaramillo 3347 (COL, U).

Note: The specimens seen differ from typical R. sonsonensis in the leaves not being falcate. Among the Bischler collections studied, one specimen might also be placed here, although it differs by the leaves not being caducous: Cauca, Macizo Colombiano, Valle de las Papas, epiphytic, Bischler 1060, 11.IX.1958 (COL, PC, U). This specimen differs further in the base of the ventral lobe extending slightly further across the stem: $\frac{1}{4}$ or more.

2. Radula nudicaulis Stephani, Spec. Hep. 4: 174. 1910; Castle (1967) 33-35. Fig. 1i-j.

Typus: Brazil, Serra Itatiaia, in woods, 2100 m, E. Ule, 1894 (not seen, cf. Castle 1967).

Plants yellow-brown in dried condition, stems 0,12-0,45 mm in width, often deeply pigmented, in transverse section with the medulla colourless, the cortical cells differentiated from the medullary by their pigmentation and by their thickened cell walls, especially the outside walls, the cortex existing of one layer, the medullary cells $12-27 \times 12-27 \mu m$, slightly thinwalled; branching pinnate, leaves of the stem contiguous, subimbricate. Dorsal leaf-lobe $1,25-2,1\times0,5-2,5$ mm, caducous, ovate concave, the apex rounded, sometimes with discoid gemmae, the free portion of the base rounded and extended usually the entire distance across the stem, often beyond the stem, auricle $0.02-0.5\times0.7-0.5$ mm, the line of attachment curved, the keel usually slightly arched, up to 0.8 mm. Ventral leaf-lobe $0.4-0.9 \times 0.4-1.0$ mm, clearly visible, quadrate, the apex bluntly angled, the base free about one-third its length, the free portion rounded and extended one half the distance across the axis, or less, the auricle $0.05-0.3\times0.05-0.3$ mm, the line of attachment straight, usually with a prominent outpocket in the lower midcarinal area; cells of the dorsal

leaf-lobe with trigones, at the margin 7-18 \times 10-15 μ m, quadrate-rectangular, in the median portion 10-24 \times 7-28 μ m, rounded-hexagonal, and at the base 20-50 \times 17-30 μ m, elliptical-rectangular.

Distribution: This is the first report of Radula nudicaulis for Colombia (see Gradstein & Hekking 1979). This species was previously known from Brazil, Bolivia and Madeira. The material studied came from the Central and Eastern Cordillera of Colombia ranging between 3000 and 3600 m elevation.

Ecology: Radula nudicaulis apparently is a species of the high Andean cloud forest. In Colombia it has only been found so far in the Weinmannia timberline condensationzone on the atmospherically humid side of the mountains.

It is a typical epiphyte, gathered only occasionally terrestric in roadside habitats together with Marchantia, Symphyogyna brasiliensis, some mosses and lichens. In the Weinmannia rollotii timberline cloud forest at about 3000 m on the Casanare slope of the Sierra Nevada del Cocuy R. nudicaulis was collected on a trunk together with species of Adelanthus, Herbertus, Hygrolejeunea, Plagiochila and Trichocolea. Further were associated Lepicolea pruinosa, Riccardia cf. fucoides and the moss Chorisodontium setaceum. In the Weinmannia cloud forest at about 3200 m in the Páramo de Guasca near Bogota epiphytic liverwort communities consist of Radula nudicaulis, R. ramulina, Brachiolejeunea laxifolia, Harpalejeunea ancistrodes, Microlejeunea colombiana, Bazzania longistipula and Plagiochila spp.

Colombian specimens seen: Arauca: Sierra Nevada del Cocuy, Cleef 10167 (COL, U); Caldas: Florschütz 4319, 4352 (COL, U); Cundinamarca: Páramo de Cruz Verde, Cleef 3380 (COL, U); Páramo de Guasca, Cleef 397, 3430 (COL, U).

Note: Among the Colombian material two further specimens with discoid gemmae were detected: Cundinamarca, Cruz Verde, alt. 2715 m, Van der Hammen 2136 (COL, U), and Cundinamarca, alt. 2700 m, Bischler 235 (PC, U). These specimens differ from R. nudicaulis by the base of the ventral lobe being fused along a shorter distance to the stem (half the length of the base or less). Differences are also in the extension of the dorsal lobe across the stem.

At present it is difficult to determine the taxonomic position of these specimens with certainty.

3. Radula quadrata Gottsche, Syn. Hep.: 255. 1844; Castle (1965) 332-334.

Recorded from high Andean Colombia by Winkler (1976).

Distribution: Mexico, Central America and Colombia: Cesar, Magdalena; known alt.: 1900–2900 m.

4. Radula mollis Lindenberg & Gottsche, Syn. Hep.: 725. 1847; Castle (1965) 334-338.

Recorded from high Andean Colombia by Castle (l.c.).

Distribution: Southeastern United States, Mexico and Central America, West-Indies, Venezuela, Brazil, Ecuador, Peru and Colombia: Cundinamarca; known alt.: 2700 m.

5. Radula ramulina Taylor, Lond. Jour. Bot. 5: 374. 1846; Castle (1965) 339-343. Fig. 1 a-b.

Typus: Jameson s.n. ex hb. Pearson (MANCH iso).

Plants in dried condition brown-yellow, occasionally yellow-green; stem 0,1-0,6 mm in average diameter, in transverse section with the cortex consisting of 1-2 cell layers, differentiated from the medulla by its darker pigmentation and by its thickened cell walls, the medullary cells colourless, thin-walled, with small trigones, $18-38 \times 12-25 \mu m$, rounded hexagonal; branching pinnate, the branches 2-30 mm in length, sometimes a few microphyllous branches. Dorsal leaf-lobe 1,3-2,6 ×1,4-2,7 mm, imbricate, slightly falcate, often caducous, the base free about one half its length, the free portion auriculate and extended across and beyond the stem, auricle 0,15-0,19 ×0,2-1,2 mm, the line of attachment curved, the keel slightly incurved, up to 1,2 mm long. Ventral leaf-lobe $0.5-1.8 \times 0.8-2.8$ mm, imbricate, ovate to orbicular, the apex often slightly extended into a blunt tip, the free portion extended across and beyond the stem, auriculate, auricle $0,1-1,8\times0,2-1,5$ mm, voluted and extended over and beyond the line of fusion and frequently beyond the stem, frequently with a mammilliform outpocket in the keel-area, rhizoids infrequent, the line of attachment curved; cells of the dorsal leaf-lobe usually uniformely thinwalled with small trigones, at the margin $7-23 \times 5-20 \mu m$, rectangular, in the median portion $8-33 \times 12-28 \,\mu\text{m}$, rounded-hexagonal, at the base $12-56 \times 12-28 \,\mu\text{m}$, elliptical-rectangular.

Distribution: West Indies, Venezuela, Brazil, Mexico and southward through the Andean region to Argentina; Colombia: Boyaca, Caldas Cauca, Cundinamarca, Meta, Tolima. This species is widely distributed in the Colombian Cordillera Oriental and Central between 3200 and about 3800 m.

Ecology: Radula ramulina is a common epiphytic species confined to the upper Andean cloud forest and the lower part of the paramo belt. In the upper Weinmannia cloud forest R. ramulina occurs in epiphytic bryophyte communities with such liverworts as Bazzania longistipula, Brachiolejeunea laxifolia, Frullania sp., Harpalejeunea ancistrodes, Leptoscyphus fragilis, Microlejeunea colombiana, Plagiochila spp., Radula nudicaulis and the characteristic moss Prionodon fusco-lutescens. In the paramos R. ramulina mainly occurs epiphytically in the shelter of dwarfed forests and zonal subparamo thickets and dwarfshrubs both at the climatologically dry and humid side of the mountains. It is especially common on stems of the endemic paramo shrub Aragoa abietina (Scroph.) where this Radula species grows associated with liverworts e.g.: Brachiolejeunea laxifolia, Drepanolejeunea sp., Frullania sp., Harpalejeunea sp., Metzgeria sp. and species of lichens Leptogium and Oropogon.

In the grassparamo this species only occurs as stem epiphyte in the shelter of patches of azonal woody vegetation-types up to about 3800 m: e.g. dwarf forests of Gynoxys, Acnistus quitoensis, Polylepis quadrijuga, Aragoa perez-arbelaeziana, Gaultheria ramosissima, and Hypericum laricifolium subsp. laricifolium thickets with some dwarfed trees.

In Polylepis quadrijuga dwarf forests R. ramulina was found growing over boulders together with Thuidium sp., Lepyrodon tomentosus, Campylopus concolor, C. pittieri, Barbula sp. and Zygodon sp. Occasionally this Radula species was found terrestric; it is possible, though, that these terrestric samples originally were attached epiphytically.

Colombian specimens seen: Boyaca: Páramos al N.W. de Belen, Cleef 1973 (COL, U); Páramo de La Rusia, Cleef 6930, 7097 (COL, U); Bischler 2914 (COL, PC, U); Caldas: Nevado del Ruiz, Cleef 2482 (COL, U); Cauca: Bischler 950, 964, 981 (COL, PC, U); Cundinamarca: Páramo de Cruz Verde, Cleef 59, 692, 2776, 2849 (COL, U); Páramo de Guasca, Cleef 3429, 3447 (COL, U); Páramo de Palacio, Cleef 3964, 5146, 5150 (COL, U); Páramo de Sumapaz, Cleef 8379 (COL, U); Bischler 226, 2277, 2331 (COL, PC, U).

5a. Radula ramulina var. microphylla Jans var. nov. Fig. 2.

Typus: Páramo de Sumapaz, Hoya Sitiales, Laguna La Primavera, alt. 3580 m, A. M. Cleef 969 (COL holo, U iso).

Radula ramulina var. microphylla differt a var. ramulina fere omnis ramulis microphyllis.

Distribution: Only known from the lower paramos between about 3400 and 3600 m in the surroundings of Bogota, Colombian Cordillera Oriental.

Ecology: An epiphytic liverwort occurring in the zonal lower subparamo thickets with e.g. Ageratina (Eupatorium) tinifolia, Hypericum goyanesii

and Rapanea dependens, up to patches with azonal Hypericum laricifolium groves in the lower grassparamo.

Colombian specimens seen: Cundinamarca: Páramo de Cruz Verde, Cleef 3185 (COL, U); Páramo between Cogua and S. Cayetano, Florschütz 3603 (COL, U); Meta: Páramo de Sumapaz, Cleef 969 (COL holo, U iso).

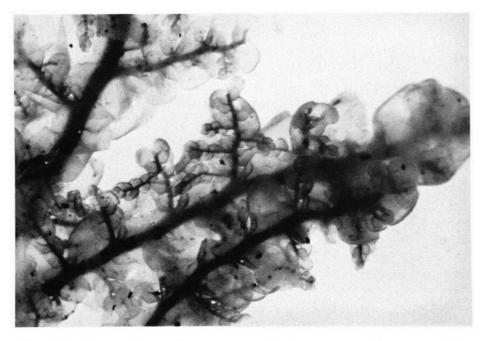


Fig. 2. Radula ramulina Tayl. var. microphylla Jans var. nov. Fragment of the plant in ventral view, showing the microphyllous branches. From the type.

Note: The variety microphylla strikingly differs from R. ramulina by the presence of numerous small, microphyllous branches, which are either branches of the first order or of the second order. Second order branches are always microphyllous, while first order branches might bear ordinary leaves as well.

It should be noted that Spruce (1885), in his description of R. ramulina, already noticed the occurrence of microphyllous branches in this species.

6. Radula episcia Spruce, Hep. Amaz. And. 318. 1885; Castle (1959) 27–29. Fig. 1 g-h.

Typus: Ecuador, Pastasa River, R. Spruce s.n. (not seen, cf. Castle 1959).

Plants brown-green in dried condition, stem 0,07-0,3 mm in average diameter, in transverse section with the cortex consisting of one cell layer, differentiated from the medullary cells by their darker pigmentation and

by their thickened cell walls, the medullary cells colourless, thinwalled, $27-63\times14-27~\mu m$, rounded-hexagonal; branching for the most part dichotomous, irregular and occasionally pinnate. Dorsal leaf-lobe $0.9-2.2\times0.75-1.6$ mm, ovate-orbicular, clearly visible, the free base portion rounded and extended one half the distance across the axis, the line of attachment straight, the keel incurved, usually with a small mammilliform outgrowth, the keel up to 0.6 mm long. Ventral leaf-lobe $0.6-0.8\times0.2-0.6$ mm, triangular, clearly visible, the lateral margin more or less parallel to the axis, tend to turn toward the dorsal lobe, the basal portion free less than one fourth its length, the free portion extended across the axis less than one half the distance, the line of attachment straight; cells of the dorsal leaf-lobe with small trigones, at the margin $12-20\times10-17~\mu$ m, quadrate, in the median portion $15-27\times15-27~\mu$ m, rounded-hexagonal, at the base $12-20\times10-17~\mu$ m, rectangular.

Distribution: Andes of Ecuador; Colombia: Bogota, Meta. In the Colombian Cordillera Oriental found between 2200 and about 3500 m.

Ecology: This hygrophilous species was found only twice: 1) in the Andean forest belt growing over wet stones in an open roadside seepage area; 2) submerged in a cold lake in the lower grassparamo, where it was found together with Fissidens rigidulus, Ditrichum submersum and Calliergon sp., growing over dense Isoetes brasiliensis communities.

Colombian specimens seen: Bogota, Florschütz 3729 (COL, U); Meta: Páramo de Sumapaz, Cleef 7562 (COL, U).

7. Radula frondescens Stephani, Sp. Hep. 4: 181. 1910; Castle (1966) 29-31. Fig. 1 k-l.

Typus: Peru, Sandia, alt. 3000 m, Weberbauer 807 (G 19801 holo).

Plants dark-brown in dried condition, stems 0,15–0,35 mm in width, in transverse section with the cortex consisting of one cell layer, differentiating from the medullary cells by their darker pigmentation and by their thickened cell walls, the medullary cells colourless, slightly thinwalled, with small trigones, cells $7-30\times15-28~\mu\mathrm{m}$, rounded-hexagonal; branching pinnate, the branches 5–47 mm in length. Dorsal leaf-lobe $2,0-1,3\times2,5-2,8$ mm, imbricate, ovate, more or less falcate, somewhat concave, the apex rounded, the base auriculate and extended across and somewhat beyond the stem, auricle $0,1-0,3\times0,4-0,8$ mm, the line of attachment curved, the keel incurved, up to 0,8 mm long. Ventral leaf-lobe $0,95-1,2\times0,95-1,2$ mm, clearly visible, quadrate, the apex with a rounded angle of 90° and often turned toward the dorsal lobe, the base auriculate, free more than one half its length, auricle $0,45-0,8\times0,2-0,4$ mm, extended

one half or more the distance across the stem, the line of attachment curved, rhizoids absent, mammilliform outpocket present; cells of the dorsal lobe mostly thinwalled, sometimes with small trigones, at the margin 7-18 \times 5-13 μ m, quadrate, in the median portion 15-25 \times 22-35 μ m, sub-hexagonal, at the base 20-35 \times 20-40 μ m, rectangular.

Distribution: Peru; Colombia: Cundinamarca. The single record known was gathered at 3800 m in the paramo belt of the Colombian Eastern Cordillera.

Ecology: Radula frondescens was collected once in the Páramo de Chisaca, Sumapaz, south of Bogota, at the base of a rock along a small stream.

Colombian specimens seen: Cundinamarca, Páramo de Sumapaz, Cleef 2587 (COL, U).

8. Radula jamesoni Taylor, Lond. Jour. Bot. 5: 375. 1846; Castle (1966) 27-29.

Recorded from high Andean Colombia by Castle (l.c.).

Distribution: Ecuador, Bolivia and Colombia: Caldas, Tolima; known alt.: 3700 m.

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