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# On *Plagiochila longiramea* Steph. (Hepaticae), a poorly known species of Bolivia

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## RÉSUMÉ

HEINRICHS, J. & S. R. GRADSTEIN (1999). *Plagiochila longiramea* Steph. (Hepaticae), une espèce peu connue de Bolivie. *Candollea* 54: 73-81. En anglais, résumés français et anglais.

*Plagiochila longiramea* Steph., une hépatique peu connue de Bolivie est redécrite grâce à du matériel frais et abondant comportant les sporophytes. Cette espèce appartient à la section *Fuscoluteae* Carl (= section *Caversii* Carl), un petit groupe d'espèces présentes à de hautes altitudes dans les Andes tropicales. Elle se caractérise par sa croissance retombante, ses feuilles à marge ventrale longuement décurrenente et des spores inhabituellement grands (jusqu'à 60 µm de diamètre). *Plagiochila caversii* Steph., *P. jensenii* Steph., *P. miyakei* Steph. et *P. nudicauda* Steph. décrits de Bolivie, sont autant de nouveaux synonymes de *P. longiramea*.

## ABSTRACT

HEINRICHS, J. & S. R. GRADSTEIN (1999). On *Plagiochila longiramea* Steph. (Hepaticae), a poorly known species of Bolivia. *Candollea* 54: 73-81. In English, French and English abstracts.

The poorly known Bolivian hepatic *Plagiochila longiramea* Steph. is redescribed based on copious fresh material with sporophytes. The species belongs in the section *Fuscoluteae* Carl (= section *Caversii* Carl), a small group of species occurring at high elevations in the tropical Andes, and stands out by its pendent growth, leaves with long decurrent ventral margin, and unusually large spores (up to 60 µm in diameter). *Plagiochila caversii* Steph., *P. jensenii* Steph., *P. miyakei* Steph. and *P. nudicauda* Steph., all described from Bolivia, are new synonyms of *P. longiramea*.

**KEY-WORDS:** *PLAGIOCHILACEAE* – *Plagiochila longiramea* – *Plagiochila* section *Caversii* – *Plagiochila* section *Fuscoluteae* – Distribution – Morphology – Systematics – Taxonomy – Neotropics – Bolivia.

Identification of neotropical *Plagiochilae* is at present very difficult. More than 500 species have been recognized in the region, often based on scanty or heterogeneous type material and incomplete descriptions. Sporophytes and oil bodies of most species are unknown and in many taxa even perianths have not yet been described.

A classification of the neotropical species into 19 sections, based mostly on leaf shape and leaf areolation, was attempted by CARL (1931). This system is now obsolete and needs to be revised taking into account important features such as perianth shape, sporophytes, oil bodies and branching type, in addition to leaf areolation. In our experience, leaf shape is of minor value in defining the sections within the genus *Plagiochila*. A first attempt towards a modern infragene-

ric classification, taking full account of the important features mentioned above, is the treatment of the species of New Zealand and Tasmania by INOUE & SCHUSTER (1971).

During field studies of the first author in Bolivia in 1997, a conspicuous, robust species of *Plagiochila* was collected in the cloud forests near Comarapa, a locality from which Stephani described several species of *Plagiochila* based on the collections of Theodor Herzog (HERZOG, 1916). Our examination of the type materials of the Stephani species in the herbarium of Geneva (G) revealed that our gatherings belong to *Plagiochila longiramea* Steph., a species until now known only from the type. Besides *P. longiramea*, four further names for the species are available: *P. caversii* Steph., *P. jensenii* Steph., *P. miyakei* Steph. and *P. nudicauda* Steph., all described in the same paper as *P. longiramea* (HERZOG, 1916) and based on plants showing only minor differences in leaf shape and areolation. The type of *P. longiramea* bears one perianth whereas types of the latter taxa are sterile or male. Therefore the name *P. longiramea* Steph. is accepted here and *P. caversii*, *P. jensenii*, *P. miyakei* and *P. nudicauda* are treated as synonyms.

A redescription of *Plagiochila longiramea*, including hitherto unknown information on sporophytic features and oil bodies, is given below.

***Plagiochila longiramea* Steph.**, in Herzog, Biblioth. Bot. 87 (2): 204. 1916. Type: Bolivia, Rio Tocarani, 2100-2400 m, *Herzog 4095* (holotype, G [c.per.]).

- = *Plagiochila caversii* Steph., in Herzog, Biblioth. Bot. 87(2): 194. 1916, **syn. nov.** Type: Bolivia, San Mateo-Sunchal, above 2000 m, *Herzog 4467* (p.p.) (holotype, G [male, scanty, together with other *Plagiochila* species]).
- = *Plagiochila jensenii* Steph., in Herzog, Biblioth. Bot. 87 (2): 201. 1916, **syn. nov.** Type: Bolivia, Corani, 2600 m, *Herzog 5059* (holotype, G [ster.]).
- = *Plagiochila miyakei* Steph., in Herzog, Biblioth. Bot. 87 (2): 206. 1916, **syn. nov.** (syn. of *Plagiochila jensenii* fide Herzog (1955: 200)). Type: Bolivia, Corani, 1500-1900 m, *Herzog 4704* (holotype, G [ster.]).
- = *Plagiochila nudicauda* Steph., in Herzog, Biblioth. Bot. 87 (2): 207. 1916, **syn. nov.** Type: Bolivia, sine loc., *Herzog 4466* (holotype, G [male]).

*Plants* large in size, (3-)6-18(-32) cm long and 5.0-9.0 mm broad (flattened), yellowish green, brownish green or green, growing in diffuse patches, differentiated into short creeping stoloniform shoots and pendent aerial leafy stems. Leafy stems about 500-620  $\mu\text{m}$  in diameter, deep brown to blackish brown, moderately to almost completely concealed by leaves both dorsally and ventrally, in cross section about 24-32 cells across, the cortical cells in 4-6 layers, very thick-walled, ca. 18-27  $\times$  12-22  $\mu\text{m}$  with lumina 5-17  $\times$  2-12  $\mu\text{m}$ , the medullary cells slightly thick-walled to thin-walled (especially in the center of weaker stems), ca. (25-)30-40(-43)  $\times$  19-27  $\mu\text{m}$ , without trigones or with minute, rarely medium sized triangular ones; branches few in number, occasionally lacking, of the lateral-intercalary type.

*Leaves* moderately to densely imbricate, sometimes remote, moderately, occasionally distinctly bent to the ventral side, not ampliate to distinctly ampliate, ventral margin moderately to long decurrent with a narrow, sometimes  $\pm$  broad strip, dorsal margin moderately to long decurrent along dorsal midline of stem, decurrent part  $\pm$  channelled, broad and more or less triangular or narrowed in the middle, lobe-like, edentate paraphyllia sometimes present beside or below the decurrent dorsal part of leaf; leaves oblong, oblong-ovate or ovate-oblong, with subtruncate to truncate, occasionally (irregularly) rounded apex; ventral margin above the leaf base straight or weakly, in individual leaves distinctly convex, dorsal margin weakly concave, occasionally straight, weakly to distinctly recurved, occasionally flat, leaves 2.5-4.3  $\times$  1.4-3.0 mm, 1.3-1.9 times as long as wide; teeth present on apical and often upper two thirds of ventral leaf margin, occasionally on upper half of dorsal leaf margin, teeth of dorsal and ventral margin triangular, sometimes elongated triangular, (2-)3-6(-10) cells long and (1-)2-4(-7) cells wide, teeth of apex often larger, coarser, sometimes lobe-like and with 0-2 accessory teeth, teeth straight or curved,

perpendicular to leaf margin or somewhat directed forward, individual teeth occasionally pointed backwards, number of teeth (0-)1-7(-9) on ventral leaf margin, (1-)2-6(-7) on apex and 0-2(-3) on dorsal leaf margin. *Leaf areolation* variable, cells of upper leaf half composed of slightly elongated cells with scattered strongly elongated or isodiametric cells, cells of leaf base above the stem mainly strongly elongated, forming a broad inconspicuous vitta, cells in the center of upper leaf half (20-)32-42(-55) × (15-)19-30(-35) μm, (1.0-)1.3-1.7(-2.2) times as long as wide, cells above the stem (40-)60-85(-115) × 18-32 μm, (1.7-)2.8-3.4(-4.6) times as long as wide, walls thin except those along leaf margins, trigones large, subnodulose to nodulose, often subconfluent to confluent on long walls (especially in the vitta area), intermediate thickenings moderately to frequently present especially on long walls of stronger elongated cells, cuticle smooth. Oil bodies opaque, colourless, (4-)5-9(-14) per median leaf cell, ca. 5-12 × 4-6 μm, broadly to narrowly ellipsoid, sometimes round, formed of many protruding oil-globules. *Underleaves* small, ca. 150-250 μm long and up to ca. 300 μm broad, composed of up to ca. 20 short cilia often terminated by slime papillae. Asexual reproduction not observed.

*Male plants* as large as female plants or somewhat smaller. Androecia intercalary on main stems and on branches, bracts in 4-16 pairs, closely imbricate, the basal ones sometimes moderately imbricate or remote, basal part strongly inflated, distal part obliquely spreading, margin with 0-4 teeth, basal bracts occasionally with somewhat elongated, more leaflike distal half. *Gynoecea* terminal on shoot, subgynoeceal innovations frequent in absence of fertilization, 1-2(-3) in number, bracts ovate with rounded to truncate apex, ca. 4.2-5.3 × 3.8-4.8 mm, dorsal margin strongly recurved, ventral margin, apex and sometimes upper half of dorsal margin beset with 17-29 coarse, (elongated-)triangular teeth, cells of bracts similar to those of leaf cells but vitta broader; perianths campanulate, 5.2-7.3 × 4.5-6.2 mm, ca. 1.1-1.3 times as long as wide, wingless or basal half of dorsal keel with a low, occasionally high, 0-1 toothed wing, perianth mouth weakly arched upwards, densely toothed by triangular to elongated triangular teeth; cells of perianth similar to leaf cells but trigones sometimes stronger confluent. *Capsule* round, on a short seta, exceeding the perianth only little, occasionally partly remaining in the perianth, capsule valves brown, epidermal cells in surface view often somewhat elongated, with nodulose thickenings on the longitudinal, occasionally on the transverse walls (especially in shorter cells at the valve apex), innermost cells irregular to elongated, with mostly complete semiannular thickenings, valves in cross section ca. 140-170 μm, 7-9 stratose, epidermal cells ca. 20-30 μm thick, inner cells 12-20 μm thick, inner cells with thickenings on the walls. Spores trilete, globose, ca. (32-)36-50(-60) μm in diameter, sporoderm with granulate basal surface and ± densely spaced pila or somewhat tooth-like bacula sensu BOROS & JÁRAI-KOMLÓDI (1975: 16). Elaters ca. 9-14 μm in diameter, with two spiral bands, in the middle occasionally trispiral.

*Additional specimens examined.* – **BOLIVIA. Dept. Cochabamba:** Prov. Carrasco: San Mateo-Sunchal, ca. 2680 m, *Herzog 4466* (JE, sub *Plagiochila caversii*); road Cochabamba-Comarapa between Pojo and La Siberia, 64°50'W, 17°45'S, 2600-2700 m, grazed cloud forest; 14 October 1997, *Heinrichs, Anton & Müller 4061, 4071, 4074, 4088* (GOET, LPB). **Dept. La Paz:** Cejagürtel von Sillutimara, *Troll 107* (JE, 2 specimens, sub *P. sparsifolia*). **Dept. Santa Cruz:** Prov. Caballero: Nebelwald über Comarapa, *Herzog 3940a p.p.* (JE, sub *P. sparsifolia*) & *Herzog 3802 p.p.* (G, intermingled with the holotype of *P. sparsifolia*); road Cochabamba-Comarapa between La Siberia and Torrecillas, 64° 43'W, 17°51'S, 2800 m, steep slope with grazed cloud forest, 16 October 1997, *Heinrichs, Anton & Müller 4084-4087, 4089-4091* (GOET, LPB); *ibid.*, 64°41'W, 17°51'S, 2650 m, grazed cloud forest, partly damaged by fire, 15 October 1997, *Heinrichs, Anton & Müller 4062* (GOET, LPB). Duplicates of selected specimens gathered by Heinrichs & al. are deposited in the following herbaria: B, G, JE, MANCH, MO, NICH and STU.

*Plagiochila longiramea* is a robust species with pendent, aerial leafy stems producing few lateral-intercalary branches. Particularly characteristic are the big campanulate perianths, the elongated-triangular, toothed leaves with an often long decurrent ventral margin, leaf cells with large trigones, and the extremely large spores measuring up to 60 μm in diameter.

Until now, *Plagiochila longiramea* is known only from a few localities in the Bolivian Andes, where it grows pendent from trunks and branches in montane cloud forest between 1500 and 2800 m elevation. Most likely the taxon has a larger geographical range and older names possibly exist. However, our examination of the vast *Plagiochila* collections in the herbarium of Geneva remained unsuccessful in finding an older name for the species.

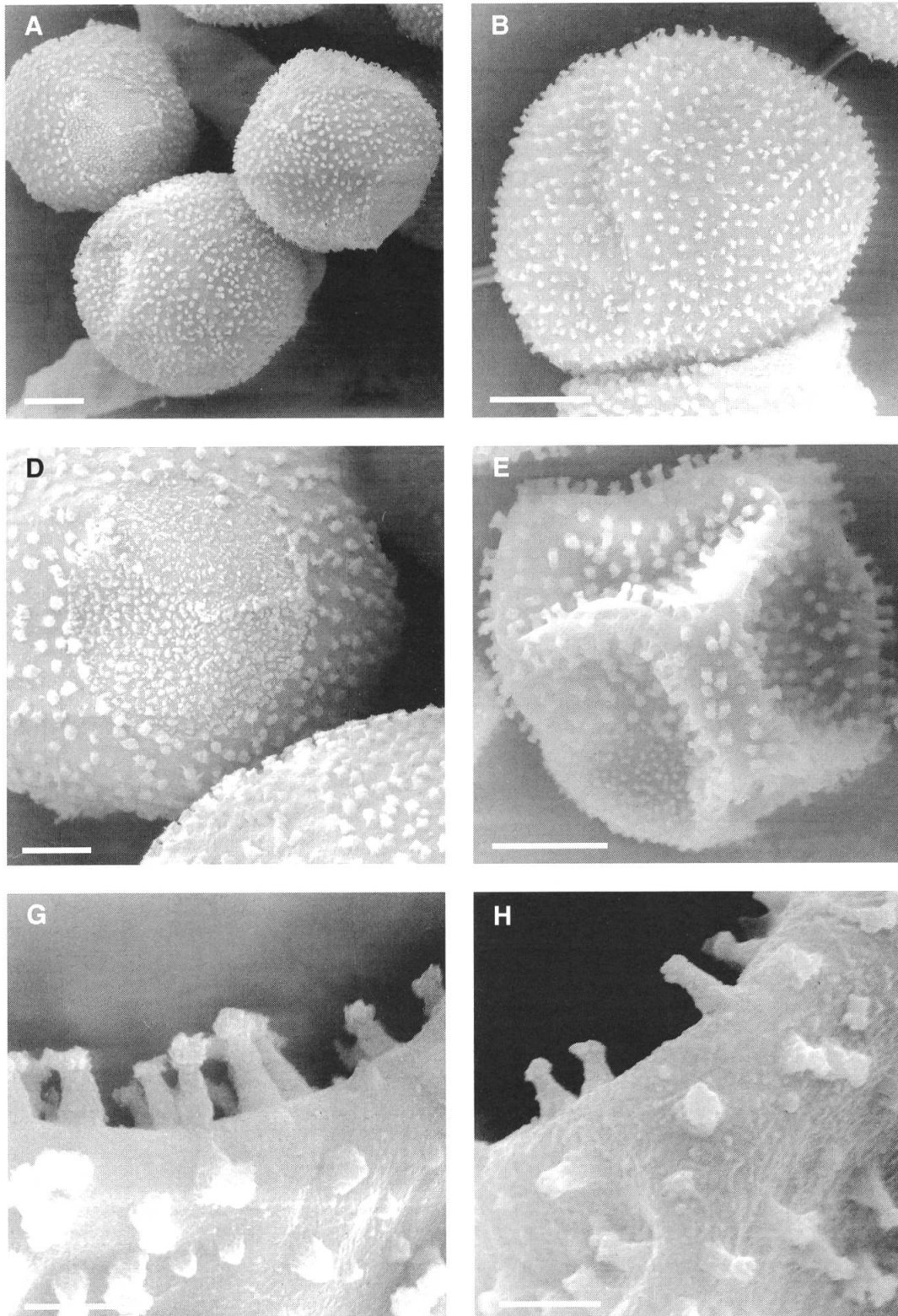
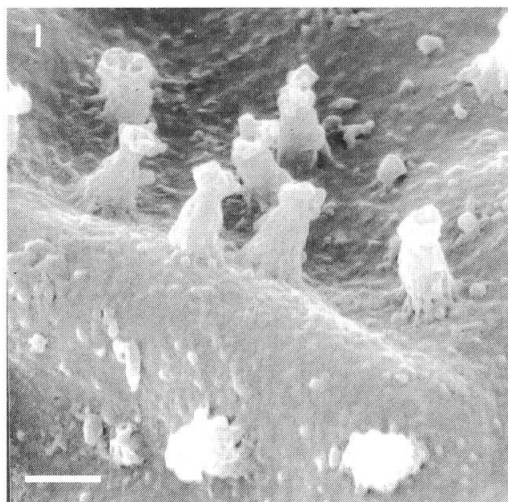
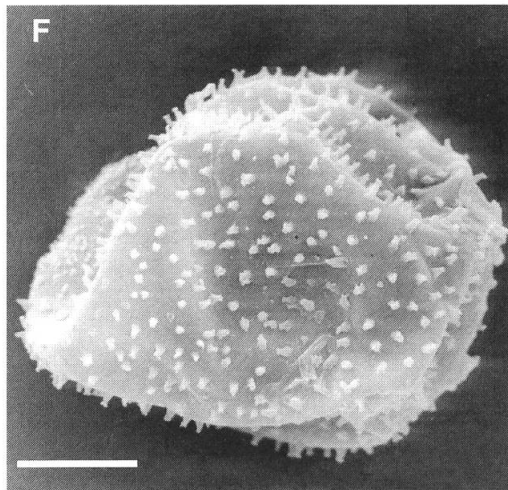
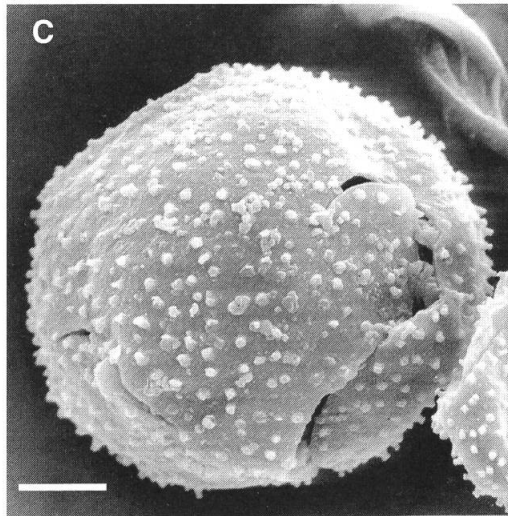


Fig. 1. – *Plagiochila longiramea* Steph. (C, F, H, I) and *Plagiochila fuscolutea* Taylor (A, B, D, E, G). A, B, C, E, F, spores (bar 10  $\mu\text{m}$ ); D, detail of laesurae (bar 5  $\mu\text{m}$ ); G, H, I, sporoderm with granulate basal surface and pila or somewhat tooth-like bacula (G, H, bar 2  $\mu\text{m}$ , I, bar 1  $\mu\text{m}$ ) [A-D, critical point drying; E-I, direct mounting from dry capsules, sporoderm with stronger protruding pila].





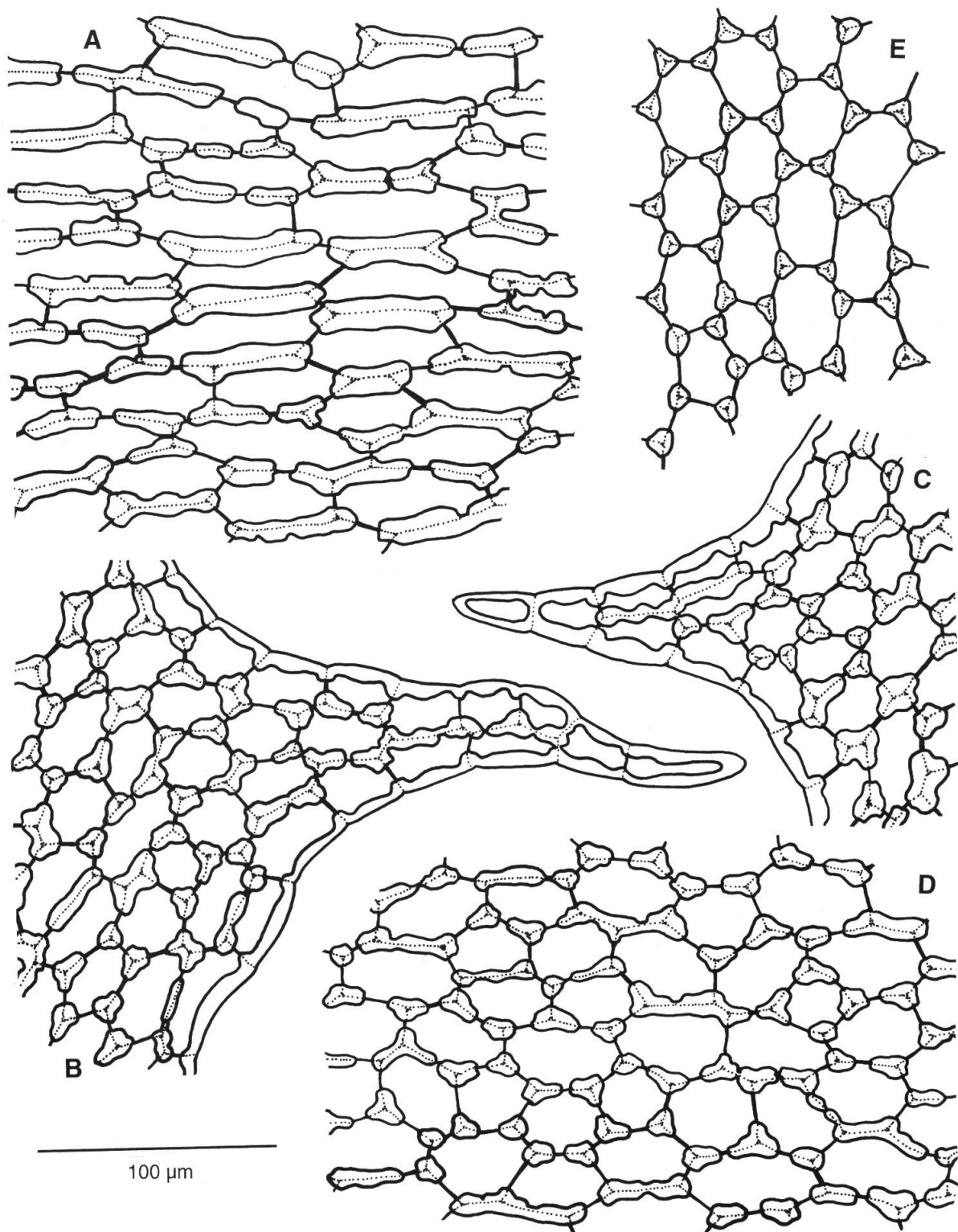


Fig. 2. – *Plagiochila longiramea* Steph. A, basal leaf cells; B, C, teeth of ventral leaf margin; D, E, cells of upper leaf half [A–D from Heinrichs & al. 4062, E from type of *P. miyakei*].

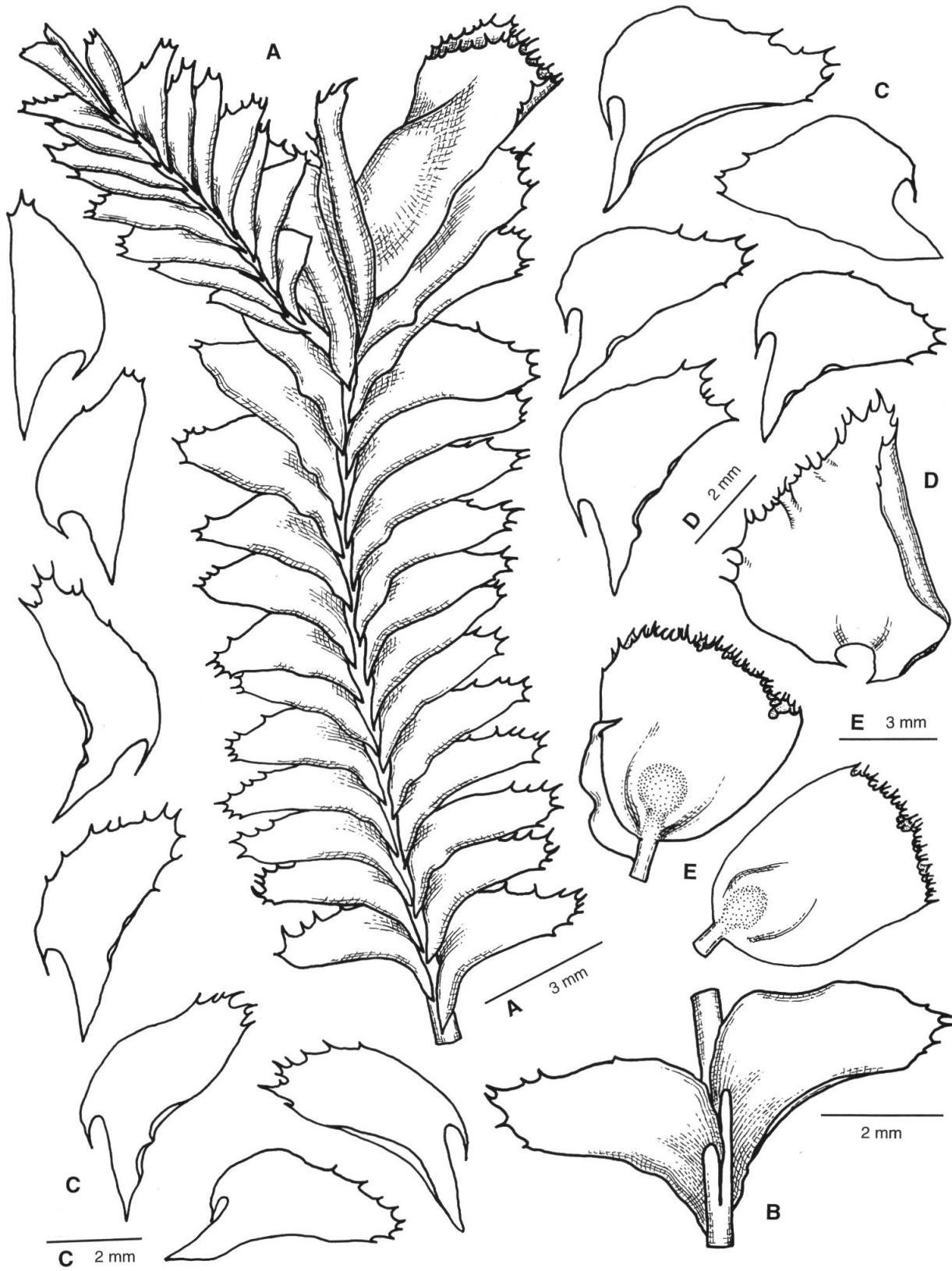


Fig. 3. – *Plagiochila longiramea* Steph. **A**, part of female shoot, dorsal view; **B**, part of shoot, ventral view; **C**, leaves; **D**, female bract; **E**, perianths, lateral view [all drawn from *Heinrichs & al.* 4091].



The type material of *P. longiramea* is from Rio Tocarani, not from Comarapa. Although Herzog spent a week collecting in the cloud forests above Comarapa (HERZOG, 1916, 1923), there are no specimens of *P. longiramea* or its synonyms from that locality in his herbarium (JE, G), unless the material of *P. nudicauda* ("sine loco natali") came from Comarapa. The only material of *P. longiramea* from Comarapa found in the Herzog-herbarium are a few plants intermingled with gatherings of *P. sparsifolia* Steph., a taxon of the section *Bursatae* Carl and synonymous to *P. beauverdii* Steph.<sup>1</sup> *Plagiochila beauverdii* is somewhat similar to forms of *P. longiramea* with slender leaves but differs e.g. in the stronger trabeculate leaf cell pattern with weaker trigones, the smaller perianths and the spores hardly reaching 35 µm in diameter.

The cloud forests just above Comarapa are destroyed today and similar moist forests are found only in some distance to the village, most of them grazed by cattle and partly destroyed by fire clearings.

Using Carl's key and his descriptions of the sections of the genus *Plagiochila* (CARL, 1931), designation of section membership of *Plagiochila longiramea* (= *P. caversii*, see above) leads to sect. *Caversii* Carl, a section defined in terms of the ± ampliate, toothed leaves with trabeculate cell pattern and perianths with a toothed mouth (CARL 1931).

The extremely large spores of *P. longiramea*, however, would seem to lead to *P.* sect. *Fuscoluteae* Carl, too, a monotypic group containing only *Plagiochila fusco-lutea* Taylor.

*Plagiochila fusco-lutea* is a species of high-Andean cloud forests and paramo vegetation, where it builds cushions up to ca. 30 cm thick. Our study of sporophytes of *P. fusco-lutea* revealed that spores and elaters as well as capsule anatomy in this species are essentially similar to those of *P. longiramea*. Both species have very large spores, averaging 32-60 µm in diameter. Other characters shared by the two species are the very large campanulate perianth, intercalary androecia, leaf areolation, and the rigid habit with few lateral-intercalary branches.

The section *Fuscoluteae* was defined by CARL (1931) based on the supposedly entire leaf margin and perianth mouth of *P. fusco-lutea*; similarities were assumed between the *Fuscoluteae* and the section *Caversii*. However, our examination of the type of *Plagiochila fusco-lutea* (FH!) as well as many further gatherings of the species reveal the frequent presence of a few, short-triangular teeth both on leaf margins and perianth mouth in this species. Obviously, the definition of section *Fuscoluteae* needs to be revised and the differences between sect. *Fuscoluteae* and sect. *Caversii* alleged by CARL (1931) do not hold. Hence, sect. *Caversii* is treated here as synonymous to sect. *Fuscoluteae*:

***Plagiochila* sect. *Fuscoluteae*** Carl, Ann. Bryol., Suppl. 2: 46. 1931. Type species: *Plagiochila fusco-lutea* Taylor

= *Plagiochila* sect. *Caversii* Carl, Ann. Bryol., Suppl. 2: 68. 1931, **syn. nov.** Type species: *Plagiochila caversii* Steph. (= *Plagiochila longiramea* Steph., see above).

It has to be emphasized that the trabeculate leaf cell pattern given as a feature of the *Caversii* by CARL (1931) is found only in basal parts of the leaves (Fig. 2, A), whereas upper parts show at best transitional stages (Fig. 2, D, E).

Beside *P. caversii* and *P. jensenii*, both of them synonyms of *P. longiramea*, 10 further species were accommodated in the *Caversii* by CARL (1931). As sporophytes of none of these 10 taxa could be studied it is impossible to decide on their sectional membership at present.

<sup>1</sup>*Plagiochila beauverdii* Steph., in Herzog, Biblioth. Bot. 87 (2): 191. 1916. Type: Bolivia, Comarapa, 2600 m, Herzog 4262 (holotype, G [c.per.]).

= *Plagiochila sparsifolia* Steph., in Herzog, Biblioth. Bot. 87 (2): 211. 1916, **syn. nov.** Type: Bolivia, Nebelwald über Comarapa, 2600 m, Herzog 3802 p.p. (holotype, G [c.per., with *P. longiramea* [ster.]]).

The species of *Plachiochila* sect. *Fuscoluteae* resemble *Plagiochila adiantoides* (Sw.) Lindenb., type species of *Plagiochila* sect. *Adiantoideae* Lindenb. in several respects, e.g. exclusively lateral intercalary branching, leaf areolation with subnodulose to nodulose trigones and intercalary androecia. As sporophytes of *Plagiochila adiantoides* (Sw.) Lindenb. are still unknown, it is not possible to decide on the relationship of the two sections at present.

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