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Disjunct or Continuous? On the Distributional Pattern of *Cephaloziella hampeana* (Nees) Schiffn. *ex* Loeske (Cephaloziellaceae, Marchantiophyta) in South America

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Abstract – *Cephaloziella hampeana* (Nees) Schiffn. *ex* Loeske is recorded for the first time in South America. This record considerably extends the distributional range of *C. hampeana* and raises the question on the role that high mountain environments play in dispersing species along the continent. The morphological differences of *C. hampeana* with its purportedly allied species are discussed. Additionally, its disjunct distributional pattern is briefly compared with those of other liverworts. Photomicrographs and a distributional map are provided.

Distribution / Marchantiophyta / South America

It is widely recognised that distributional patterns of some bryophytes groups are scarcely known, owing to either bias sampling or intrinsic features (Matteri, 2000). Nevertheless, some biogeographic patterns are clearly established (Shaw, 2001; Ochyra *et al.*, 2008). Among these, Ochyra *et al.* (2008) identified the bipolar intermediate pattern as a remarkable distribution type reportedly found in only a few species. This type of distribution involves a disjunction between circumboreal and circumantarctic areas, with an intermediate location at high mountains within the tropics (Ochyra *et al.*, 2008). Typically, most of the species comprising bipolar distributions are boreal species with strict environmental requirements (Shaw, 2001). Thus, ecological conditions found at high altitudinal habitats might have allowed the displacement of several boreal species.

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Cephaloziella (Spruce) Schiffn., a leafy liverwort genus with about 40 species worldwide, includes several species within the tropics (Fulford, 1976) and is mainly distributed in grassland or open habitats (Fulford, 1976; Gradstein & Costa, 2003). Although *Cephaloziella* has been recorded for a few localities of tropical South America (Fulford, 1976; Gradstein & Costa, 2003), it is commonly found in Central-North America (Fulford, 1976; Fulford & Sharp, 1990), southern South America (Hässel de Menéndez & Rubies, 2009) and in the Antarctic islands as well (Bednarek-Ochyra *et al.*, 2000). Only four species have been recorded for the southern Neotropics, including *Cephaloziella fragillima* (Spruce) Fulford from Bolivia, and *Cephaloziella divaricata* (Sm.) Schiffn., *Cephaloziella granatensis* (J. B. Jack *ex* Steph.) Fulford and *Cephaloziella stellulifera* (Taylor *ex* Carrington & Pearson) Croz. from Brazil. The identity of the reported material of *Cephaloziella exiliflora* (Tayl.) Douin and *Cephaloziella serrata* Steph. remains dubious (Gradstein & Costa, 2003).

Recently, during a field trip carried out at “La Cienaga” (northwest Argentina), several bryophytes were collected (Suárez *et al.*, 2010; Suárez *et al.*, 2013). Among this material, a specimen of *Cephaloziella hampeana* (Nees) Schiffn. was identified for the first time for South America and is the first record of the genus in subtropical Argentina. According to Fulford (1976), Fulford & Sharp (1990) and Pérez (2009), *C. hampeana* is a species widely distributed in the Northern Hemisphere and its most southern localities are Veracruz (Mexico) and El Quiche (Guatemala). The present new record for South America depicts a potential disjunct distribution of *C. hampeana* involving the Nearctic-austral Neotropics, a striking distribution type that has been found before for several liverworts (Hässel de Menéndez & Rubies, 2009).

The purpose of the present paper is to i) provide a brief description of the collected material of *Cephaloziella hampeana*, ii) compare its differences with morphologically allied species and iii) discuss its disjunct distributional pattern. A key with the subtropical species and a distribution map are provided.

Key to the subtropical species of *Cephaloziella*

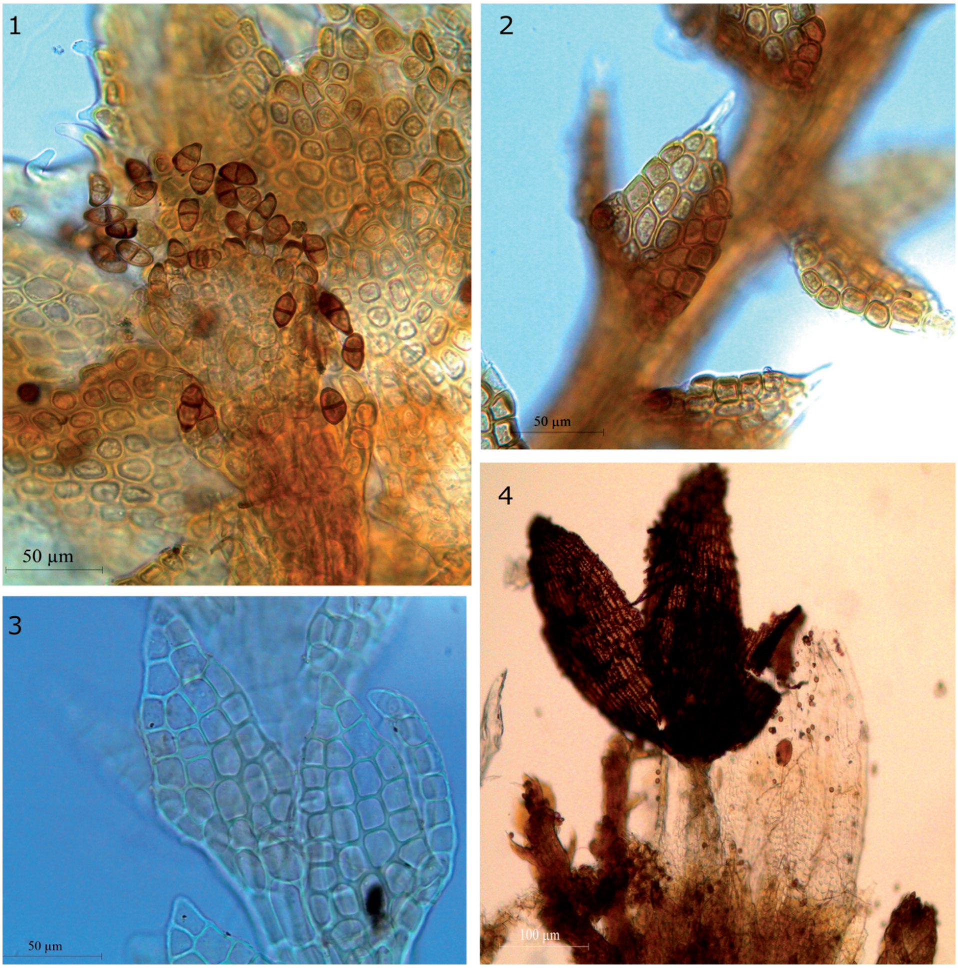
1. Underleaves present in sterile axis 2
   2. Male and female bracts found on the same axis. Plants green, never blackish .... *Cephaloziella stellulifera* (Taylor) Schiffn.
   2’. Male and female bracts found on separate axes. Plants blackish .... *Cephaloziella divaricata* (Sm.) Schiffn.

1’. Underleaves absent in sterile axis 3
   3. Perianth margins with rounded teeth; Leaves laminal cells 10 × 8 µm......... ....*Cephaloziella fragillima* (Spruce) Fulford
   3’. Perianth margins with acute teeth; Leaves laminal cells 105-13.5 × 7.5-9 µm 4
      4. Lobe laminal cells with thin walls, 13.5 × 8 (9) µm; Gemmae somewhat rectangular, with four acute projections at angles ....*Cephaloziella granatensis* (J.B. Jack) Fulford
      4’. Lobe laminal cells with thick walls, 10.5 × 7.5 µm; Gemmae elliptical, without acute projections .... *Cephaloziella hampeana* (Nees) Schiffn.

***Cephaloziella hampeana* (Nees) Schiffn. *ex* Loeske,** Loeske, *Moosfl. d. Harzes* 92. 1903 **Figs 1-4**

Jungermannia hampeana Nees, *Naturgesch. Eur. Leberm.* 3: 560. 1838

Plants small, whitish to brownish, occasionally purplish. Stems decumbent, delicate, scarcely branched, less than 1 cm long; cortical cells elliptical to rectangular, 12-15 µm long, 9-6 µm wide. Rhizoids scarce on the ventral side of the stem, mainly whitish. Leaves ovate, apex bifid, 0.10-0.12 mm long; lobes triangular, ending in an acute whitish two-celled apex; laminal cells elliptical to quadrate towards the margins, with homogeneously thickened walls, 9-12 µm long, 6-9 µm wide. Underleaves absent. Perigonia terminal on branches; bract margins serrulate. Female gametangia terminal on branches, bract and bracteole margins toothed (the latter conspicuously toothed). Perianth cylindrical, hyaline throughout, margins denticulate.



Figs 1-4. *Cephaloziella hampeana* (Nees) Schiffn. *ex* Loeske **1.** Fertile branch showing bracts and gemmae. **2.** Non-gemmiparous leaves with an acute tip. **3.** Leaves lobes without the acute tip (*Suárez 615d*). **4.** Capsule and hyaline perianth.

Capsule rounded, reddish to purple, valves 0.50-0.52 µm long; wall cells with nodular thickenings. Spores brown, alete (monolete?), coarsely verrucose, 6-9 µm diameter. Elaters purplish, with two helical bands, attached to the valve inner surface. Gemmae elliptical, brownish to reddish, two-celled, 15-18 µm long; each cell with homogeneously thickened walls, and papillae-like projections at the tips, 3-6 µm long.

Specimens examined: ***Cephaloziella hampeana*** (Nees) Schiffn. *ex* Loeske – **NORTH AMERICA. Canada.** Ontario. Open sand in gravel pit. Norway Lake, *Cain 4281* (F). **USA.** New York. In small patches on rather dry soil, *Schuster 24250* (F). Tennessee. Abrams Falls Trails, moist soil, *A. J. Sharp s/n* (F). Minnesota. Grand Marais, over moist sandy soil, *Schuster 13795* (F). over peaty log, *Schuster & Winne* (F). Winston-Salem, on sandy soil, *A. W. Evans 2157* (F). **SOUTH AMERICA. Argentina.** Tucumán, Tafí del Valle, “La Cienaga”, cañada frente al rio, más sombreado, 2600 m, 12/09/2009, *G. Suárez 651d* (LIL). ***Cephaloziella granatensis*** (J.B. Jack) Fulford – **SOUTH AMERICA. Colombia**. Dept. Cundinamarca, Chipaqué, along the road to Bogotá just W of the village, 3100 m, *E. Linares & S. R. Gradstein 1467* (F). **Bolivia**. Santa Cruz, forming greenish to blackish mats, *S. R. Gradstein et al. H34* (F).

As exemplified by Gradstein & Costa (2003), species of *Cephaloziella* are easily confused. Among these, *C. hampeana* and *C. granatensis* share several characters and are potentially confusing species. These species have entire leaf margins (excepting gemmiparous leaves), broad lobes ending in a two celled tip, and gemmae formed by two cells. Although the colour of the mature plants has been widely used to distinguish these species (Fulford, 1976), this character was highly variable among the observed specimens of *C. granatensis*. Table 1 lists several useful morphological characters differentiating between the two species, including the distinctive morphology of the gemmae. *Cephaloziella fragillima*, a species present in Bolivia, is recognized by the three-keeled perianth with crenulate margins. Additionally, the margins of the male bracts and the dimensions of the lobe cells were valuable characters to distinguish *C. fragillima* from *C. hampeana* and *C. granatensis*.

In the northwest of Argentina, *C. hampeana* was found at 2600 m in “La Cienaga” (Tafí del Valle). This seasonal area is dominated by cloudy grasslands and wetlands. As with others species in the Neotropics, *C. hampeana* was found on soil, associated with wetlands. Species such as *C. divaricata*, *C. granatensis* and *C. fragillima* are not only found in open areas (mostly in Páramo region) but also in montane forest. This variety of inhabited environments may explain some of the observed morphological differences (e.g. cell wall thickening; Table 1).

Table 1. Morphological differences among the species of *Cephaloziella* registered for the southern limit of the Neotropics (*C. stellulifera* not considered)

	Lobe cell dimensions & cell wall thickness	*Gemmae length*	*Male bract margins*	*Colour*
C. hampeana	10.5 × 7.5 µm (thick walled)	15-18 µm (not clustered)	Serrulate	Whitish to brownish
C. granatensis	13.5 × 9 µm (thin walled)	(6-)9 µm (not clustered)	Sometimes with a single tooth	Variable (whitish to purple)
C. fragillima	10 × 8 µm (thin walled)	Not seen	Sometimes with a single tooth	Whitish
C. divaricata	12.5 × 12.5 µm (thick walled)	Not measured (clustered)	Serrate	Dark purple

In terms of biogeography, *Cephaloziella hampeana* is widely distributed along the Holarctic region (Northern Hemisphere of Old and New World) and has a quite disjunct distribution involving the northern and southern limits of the Neotropics (Mexico-Guatemala and subtropical Argentina, respectively; Fig. 5). A similar pattern, within the New World, has been found for both liverworts and hornworts (Gradstein *et al.*, 2001; Hässel de Menéndez & Rubies, 2009; Flores & Suárez, 2015). Hässel de Menéndez & Rubies (2009) enumerated several examples of disjunct distribution. Such disjunction between North and South America comprises species of a broad taxonomic range (e.g. *Lejeunea* aff. *dimorphophylla* R. M. Schust., *Riccia austini* Steph. and *Anthoceros lamellatus* Steph.; Hässel de Menéndez & Rubies, 2009).

Unsurprisingly, species of both liverworts and mosses restricted to grasslands are found along high mountains within the Neotropics (Bischler-Causse *et al.*, 2005; Vanderpoorten & Goffinet, 2009; Suárez *et al.*, 2010; Flores & Suárez, 2015). Because of the presence of *Cephaloziella* in boreal and Antarctic areas, it is easy to consider this genus as a bipolar intermediate taxon (Bednarek-Ochyra *et al.*, 2000; Ochyra *et al.*, 2008). The nearly disjunct distribution between poles is commonly explained by the "American pathway" (Ochyra *et al.*, 2008). This is, the displacement between polar regions might have occurred along the high mountains within the tropics. Records within the South American tropics, including this new record of *Cephaloziella hampeana*, reinforce such a hypothesis. However, significant gaps remain with our knowledge of South American bryoflora (Matteri, 2000). This raises the question on the role of mountainous systems play in dispersing species throughout tropical South America. Many of the currently recognised disjunct distributions could actually be instances of continuous distributions along the high-mountain grasslands. The Andean uplift has been regarded as a crucial geological

Fig. 5. Distribution of *Cephaloziella hampeana* in America. Previously known distribution in the Americas (grey dots) and current record from Argentina (black pentagon).

event that allowed the movement of temperate biota towards the tropics (Segovia & Armesto, 2015) and speciation as well (Gregory-Wodzicki, 2000). Several authors found molecular evidence of long-dispersion involving different continents (Shaw *et al.*, 2003; Hartmann *et al.*, 2006; Feldberg *et al.*, 2007; also see review and cites within Heinrichs *et al.*, 2009) and cryptic speciation in bryophytes (McDaniel & Shaw, 2003). Whether the high mountains environments represent a biological corridor which facilitate dispersion shall be clarified by conducting an exhaustive samples inside the region.

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