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New data on *Orthotrichum gigantosporum* Lewinsky (Orthotrichaceae, Bryophyta), a widespread northern Andean-Patagonian endemic moss

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ABSTRACT

The moss family Orthotrichaceae is still poorly known in the southern extreme of South America. This is especially true regarding the morphological variability, geographical distribution, and ecological affinities of the species restricted to the Andean-Patagonian area. These deficiencies are addressed for *Orthotrichum gigantosporum* Lewinsky, one of the least known and most interesting endemics of the area. After examining the rich collections made by our team in southern Chile and Argentina, we have found numerous new localities for the species. *Orthotrichum gigantosporum* has proven to be a widespread moss in the forests and scrublands of the northern sector of the Andean-Patagonian area. In the light of new morphological data, an updated description of the species is presented and the characteristics that allow its differentiation are discussed and illustrated. The ecological data obtained on the populations also help to characterise the distribution of this moss in relation to various environmental factors. An updated list of the accepted species of Orthotrichaceae present in the Andean-Patagonian area is also provided, facilitating an estimate of endemism rates within each genus.

KEY WORDS

Climate,
endemism,
morphology,
vegetation,
Argentina,
Chile.

RÉSUMÉ

Nouvelles données sur Orthotrichum gigantosporum Lewinsky (Orthotrichaceae, Bryophyta), une mousse endémique du nord des Andes de Patagonie largement répandue.

La famille des mousses Orthotrichaceae est encore mal connue dans l'extrême sud de l'Amérique du Sud. Cela est particulièrement vrai en ce qui concerne la variabilité morphologique, la répartition géographique et les affinités écologiques des espèces limitées à la zone andino-patagonienne. Ces aspects ont été abordés pour *Orthotrichum gigantosporum* Lewinsky, l'une des endémies les moins connues et les plus intéressantes de la région. Après avoir examiné les riches collections obtenues par notre équipe du sud du Chili et de l'Argentine, nous avons trouvé de nombreuses nouvelles localités pour l'espèce. *Orthotrichum gigantosporum* s'est avéré être une mousse largement répandue dans les forêts et les formations d'arbustes du secteur nord de la région andino-patagonienne. À la lumière de nouvelles données morphologiques, une description actualisée de l'espèce est présentée et les caractéristiques qui permettent sa différenciation sont discutées et illustrées. Les données écologiques obtenues sur les populations permettent également d'aborder des aspects d'intérêt sur la distribution de cette mousse en relation avec divers facteurs environnementaux. Une liste mise à jour des espèces acceptées d'Orthotrichaceae présentes dans la zone andino-patagonienne est également fournie, ce qui permet d'estimer les taux d'endémicité au sein de chaque genre.

MOTS CLÉS

Climat,
endémicité,
morphologie,
végétation,
Argentine,
Chili.

INTRODUCTION

The territory of the Patagonian Andes is one of the centres of diversity for the Orthotrichaceae, as has already been demonstrated for some of the large genera of the family (Lewinsky 1984, 1987; Garilleti *et al.* 2015). Although southern South America is relatively well known from a bryological point of view (Matteri & Schiavone 2002; Matteri 2003; Larraín 2016), little is known about many of the numerous species of Orthotrichaceae that have been described from this territory. Many have been reported only from the type locality (e.g., Goffinet *et al.* 2007), while others are known only from a few collections and localities (Matteri 2003; Müller 2009). As a consequence, the geographic dispersal and abundance of many Patagonian species is unknown, as well as almost everything about their ecological affinities and possible morphological variability. Against this background, our research team has conducted bryological expeditions in the area to fill these gaps. As a result, numerous new localities have been found for several species and our knowledge on the ecology and morphology of various endemic orthotrichaceous mosses in the Andean Patagonia area has increased considerably (e.g., Muñoz-Puelles *et al.* 2017; Garilleti *et al.* 2020a, b, 2021).

In this paper we focus on *Orthotrichum gigantosporum* Lewinsky, one of the most interesting and least known Andean-Patagonian endemics. This moss, originally named as *O. macrosporum* Lewinsky nom. illeg., was described from a single collection taken from the Argentinian Nahuel Huapi National Park, south of Bariloche (Lewinsky 1984). Since then, it has only been reported once, from the Nahuelbuta National Park in the Araucanía region of Chile (Lewinsky & Deguchi 1989). The most recent reference to the species was only to give it a valid name (Lewinsky 1988). Thus, in more than 35 years since its description, very little new data have been obtained on the distribution, ecological preferences and morphological

variability of this species. However, during our recent surveys we have found numerous populations of this moss in northern Andean Patagonia. Due to its frequent occurrence, it could be considered one of the most representative species of *Orthotrichum* in the area. The scarcity of previous records, despite its widespread distribution, underlines the need to facilitate its recognition. Consequently, it seems pertinent to investigate the morphology of *O. gigantosporum*, as well as its ecological affinities and distribution.

MATERIAL AND METHODS

The Andean-Patagonian area is here considered to comprise the southern section of the Andes Mountains and the surrounding territories at the southern tip of South America south of parallel 37°S, characterized by a temperate or cool-temperate and oceanic climate. In Chile, it includes the regions of Biobío (VIII), Araucanía (IX), Los Ríos (XIV), Los Lagos (X), Aysén (XI), and Magallanes y de la Antártida Chilena (XII). In Argentina, it is limited to a narrow band that reaches the foothills of the mountain range in the provinces of Neuquén, Río Negro, Chubut, and Santa Cruz, as well as most of the province of Tierra del Fuego. In the classification of Luebert & Plischoff (2006), the area considered would be the one coinciding in Chile with the Temperate and Antiboreal macrobioclimates. Although there is no unanimity in establishing the northern limit of the Andean-Patagonian area from a phytogeographical point of view (Moreira-Muñoz 2011), the territory here defined coincides with that understood by Veblen *et al.* (2011), and is basically equivalent to the geographical region of Andean Patagonia as defined by Raffaele *et al.* (2014), except for the Chilean region of Ñuble (XVI). We exclude this region since it has a typically Mediterranean climate that favours the appearance of floristic elements typical of

more northerly sectors of the Andes and that, at the same time, prevents the development of the flora characteristic of Andean Patagonia, which is especially evident in the case of the Orthotrichaceae (Müller 2009).

The geographical limits of the Andean-Patagonian area are relevant in delimiting the list of Orthotrichaceae present there (Table 2), which is based on the reviews of Lewinsky (1984, 1987) and Calabrese (2006), the compilations of Matteri (2003) and Müller (2009), as well as the most recent bryological contributions related to the study area. The taxonomic framework and nomenclature have been updated according to Draper *et al.* (2021).

The results of the present study are based on collections from 152 localities between latitudes 39°08'S and 55°43'S. Thus, the area sampled comprises a large part of the Andean-Patagonian area of Chile and Argentina, as defined above. Selected localities were sampled during three bryological expeditions, especially concentrated in the northern and southern sectors of the area (Fig. 1). A first reconnaissance was carried out in the austral summer of 2005-2006, visiting representative points throughout the territory. A second visit took place in January 2012, focusing on the Cape Horn archipelagos of the Magallanes Region. The third, was conducted in the austral summer of 2016-2017 and focused on the survey of the Chilean regions of Los Lagos and Aysén, as well as the Argentinean provinces of Neuquén, Río Negro and Chubut. Additional samples collected by W. Buck, J. Shevock and J. Larraín at Cape Horn area, and by J. Larraín in the Capitán Prat Province (Aysén) were also examined.

To understand the climatic affinity of *Orthotrichum gigantosporum* through the distribution of its known populations, a cartographic study was performed using climatic data. Figure 1 was created with the open-source software QGIS 3.10.14 (available at www.qgis.org site) and using the Köppen-Geiger climate classification world map developed by Beck *et al.* (2018). This world map (downloaded from www.gloh2o.org/koppen in GeoTIFF format) has a resolution of 0.0083°, nearly 1 km at the equator, which ensures a highly detailed and accurate cartography, particularly in regions with sharp spatial or elevational gradients, as is the case in the western façade of the Andean Cordillera.

RESULTS

Orthotrichum gigantosporum was found in a total of 24 new localities, six from Argentina and 18 from Chile (Appendix 1). These must be added to the two previously known localities (Lewinsky 1984; Lewinsky & Deguchi 1989) (Fig. 1). It has always been found as an epiphyte, growing on the trunks, branches and twigs of a wide variety of trees and shrubs (Table 1).

The abundance of samples obtained across such a wide geographic area has made it possible to provide a complete morphological circumscription of this moss. The variability of its characters and some new observations are synthesized in the following updated description.

TABLE 1. — Trees and shrubs, arranged by families, found colonized by *Orthotrichum gigantosporum* Lewinsky. The most frequent phorophytes are marked in **bold**. Allochthonous trees and shrubs are identified by an asterisk (*).

Families	Phorophytes
Araliaceae	<i>Raukua laetevirens</i> (Gay) Frodin
Berberidaceae	<i>Berberis ilicifolia</i> L. f. <i>Berberis microphylla</i> G. Forst.
Cunoniaceae	<i>Eucryphia cordifolia</i> Cav.
Elaeocarpaceae	<i>Aristotelia chilensis</i> (Molina) Stuntz
Ericaceae	* <i>Rhododendron</i> sp.
Escalloniaceae	<i>Escallonia</i> sp.
Myrtaceae	<i>Amomyrtus luma</i> (Molina) D. Legrand & Kausel <i>Luma apiculata</i> (DC.) Burret
Nothofagaceae	<i>Nothofagus betuloides</i> (Mirb.) Oerst. <i>Nothofagus dombeyi</i> (Mirb.) Oerst.
Onagraceae	<i>Fuchsia magellanica</i> Lam.
Rosaceae	* <i>Rosa</i> sp. * <i>Malus domestica</i> (Suckow) Borkh.
Salicaceae	<i>Azara lanceolata</i> Hook. f. * <i>Salix</i> sp.

Family ORTHOTRICHACEAE Arn.

Genus *Orthotrichum* Hedw.

Orthotrichum gigantosporum Lewinsky

(Figs 2; 3)

Lindbergia 14: 183 [1988(1989)].

Orthotrichum macrosporum Lewinsky hom. illeg. *Lindbergia* 10: 91. figs 150-161. (Lewinsky 1984[1985]). — non *O. macrosporum* Müll. Hal., *Nuovo Giornale Botanico Italiano*, n. s. 5: 185 (Müller 1898).

TYPE. — **Argentina**. Rio Negro: Bariloche, Pampa del Toro, road to Lago Steffen; 41°31'S, 71°28'W; Rahn 4593 p.; 27.II.1979. holo- C.

DESCRIPTION

Plants

Up to 0.8(-1.7) cm tall, in lax or rarely compact irregular tufts or patches, up to 2 cm in diameter, frequently mixed with other species, olive green to brownish below.

Stems

Rounded-pentagonal in section, with all cells thick walled, orange to deep red, the 1(-2) external rows smaller with narrow lumina; axillary hairs scarce, of 1 short slightly coloured basal cell and 1-2 elongated hyaline distal cells.

Rhizoids

Mostly in basal parts of stems, scattered in median and upper branches, reddish, smooth.

Leaves

Erect to erect-appressed when dry, scarcely sinuose but frequently loosely and irregularly oriented, when moist patent to spreading, ovate-lanceolate to lanceolate with oval base, more or less concave, lamina narrowly triangular, slightly carinate, (0.8-)1.0-1.5 × 0.2-0.3 mm; leaf apex acute to acuminate, frequently ending in a row of up to 7 cells; costa single, ending well below apex to subpercurrent, 25-50 µm wide at base and

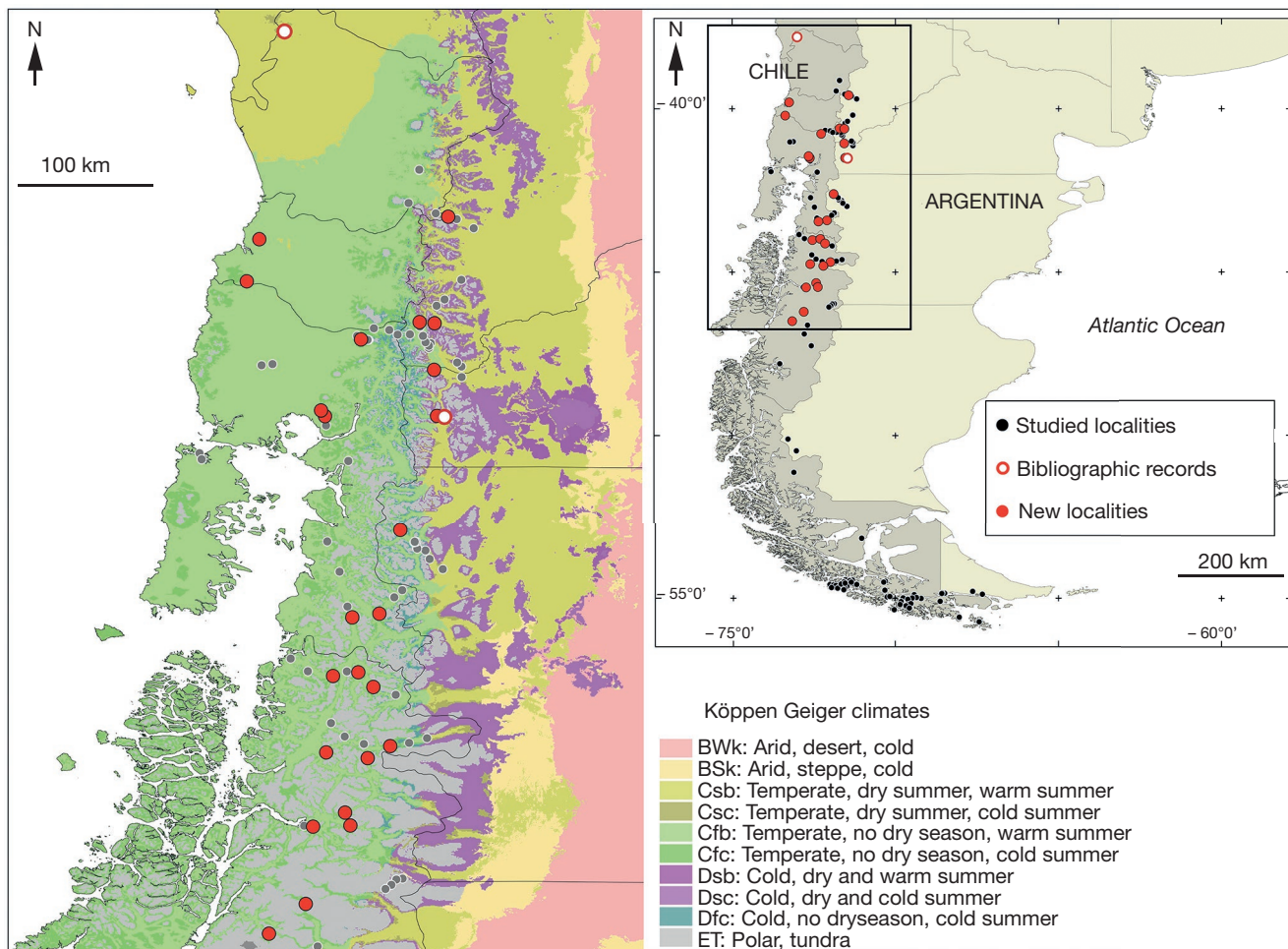


FIG. 1. — *Orthotrichum gigantosporum* Lewinsky: known distribution superimposed on a Köppen-Geiger climate map. Previous bibliographic records and other studied localities are indicated.

at mid-leaf; leaf margins entire to papillose-crenulate, usually completely plane, sometimes finely and irregularly recurved in part of their length; lamina unistratose throughout; upper and median leaf cells (6-)10-15(-16) × (6-)10-15(-20) μm, isodiametric or somewhat elongate or oblate, with moderately thickened walls, with (1-)2(-3) simple papillae on both surfaces; basal cells (10-)15-40(-50) × 5-10 μm, mostly rectangular, sometimes fusiform, with thin to moderately thickened smooth or somewhat nodulose walls, towards margins usually shorter, short rectangular to quadrate. Brood bodies not seen.

Cladautoicous.

Perigonia

Bud-shaped, terminal on branches and main axes; perigonal leaves (0.2-)0.3-0.7(-1.2) mm long.

Perichaetial leaves

Similar to vegetative leaves, somewhat larger, (0.9-)1.1-1.9(-2.1) × 0.2-0.4(-0.5), with a longer ovate base that reaches 2/5 to 1/2 leaf.

Vaginula

Cylindric to oblong, 0.4-0.6 mm long, strongly hairy, with hairs up to more than 1 mm long, 1(-2)-seriate, barely papillose.

Calyptra

Mitrate, conic-oblong, 1.3-1.5 mm long, yellowish to orange with a dark orange beak, naked, plicate, almost smooth to papillose at plicae.

Seta

(1.1-)1.5-2.7 mm long.

Capsule

Exserted, ovoid when moist, urceolate to pyriform and constricted below mouth when dry, unribbed except near mouth or very faintly in the upper half, (1.1-)1.2-1.5(-1.8) mm long, including a 0.3-0.5 mm long neck, gradually narrowing to seta; exothelial cells rectangular, yellowish, arranged in vertical sinuous lines with external walls thickened; exothelial bands differentiated in the distal part of urn, orange tinted, of (2-)3(-4) rows of enlarged cells with extra-thickened



FIG. 2. — *Orthotrichum gigantosporum* Lewinsky: **A**, habit; **B**, mature capsules with exostome teeth both in pairs and divided, compare with the peristome in **E**; **C**, calyptra; **D**, mature operculated capsule; **E**, mature capsule with exostome teeth completely divided in 16; **F**, vegetative leaf; **G**, setae of two capsules showing the vaginula hairs protruding from the perichaetial leaves; **H**, operculum beginning its dehiscence from the capsule; **I**, vegetative leaf base; **J**, apicule of a single row of cells in a vegetative leaf. A-C, E, H, from Garilleti 2016-199a; D, G, I, from Garilleti 2016-198a; F, J, from Garilleti 2016-177. Scales bars: A, 1 mm; B-E, G, 0.5 mm; F, 0.2 mm; H, 0.25 mm; I, 100 μ m; J, 50 μ m.

walls, extending 130–200 µm from mouth, 2 rows weakly differentiated beyond, sometimes up to the middle of the capsule; stomata immersed, almost to completely covered by well differentiated exothecial cells, located in the upper half of capsule, not reaching urn base nor mouth vicinity.

Operculum

350–550 µm in diameter, shortly rostrate, convex, with a broad reddish basal rim.

Peristome

Double; small basal remnants of prostome sometimes present; exostome of 8 pairs of teeth, completely splitting into 16 or some pairs remaining after hygrometric movements, reflexed to revolute when dry, yellowish to light orange, (190–)220–330 µm long; outer peristomial layer (OPL) densely papillose throughout; exostomial primary peristomial layer (PPL) finely ornamented, with vertical lines and some intercalated papillae in basal part, papillose at apex; endostome of 16 segments, lanceolate, relatively broad, with margins frequently irregular, the intermediate ones more slender, paler and somewhat shorter than teeth, united by a thin connecting membrane of 2–3 cell rows tall, the upper cell row papillose like the segments; endostomial PPL faintly carinate, finely ornamented with vertical or oblique lines, usually papillose, centred on the cell surface; inner peristomial layer (IPL) biseriate in main segments, uniseriate to partially biseriate in intermediate segments, densely covered with tall papillae, becoming low in distal part.

Spores

Unicellular, (27–)30–50(–55) µm, yellowish brown, spherical to ellipsoidal, verrucose, the largest spores sparsely ornamented after the verrucae are partially detached.

DISCUSSION

The Orthotrichaceae are known to be diversified in the temperate and humid zone of the southern tip of South America, but the extent to which this family is important in the flora of Andean Patagonia is an aspect that has not been previously appreciated.

The list compiled in Table 2 brings the total number of species and subspecific taxa present in this area to 66. These are distributed in 12 genera, which in order of richness are: *Ulota* (18), *Lewinskya* (11), *Orthotrichum* (10), *Macromitrium* (9), *Zygodon* (8), *Australoria* (2), *Macrocoma* (2), *Matteria* (2), *Codonoblepharon* (1), *Leratia* (1), *Pentastichella* (1), and *Plenogemma* (1).

The overall degree of endemism for this area in the family is very high (67%), reaching extraordinary proportions in several large genera: *Ulota* (94%), *Macromitrium* (89%), and *Lewinskya* (73%). Moreover, the bispecific genera *Australoria* and *Matteria* are endemic to the area. Within this framework, *Orthotrichum* (40%) has an endemism rate below average, as only four of the ten recognized species are considered endemic

to the Andean–Patagonian area. Additionally, *O. tristriatum* could be considered a quasi-endemic since it has only been reported elsewhere from the Metropolitan District of Chile. Significantly, all of these endemic or near-endemic species, except *O. inclinatum*, are very poorly recorded (Müller 2009). However, the apparent rarity of these mosses may reflect a lack of bryological knowledge of the area rather than an intrinsic characteristic of the taxa. The discovery of a high number of new localities for *O. gigantosporum* (Fig. 1), some of whose populations are extensive, seems to confirm this hypothesis. As noted in the introduction, the same situation has been demonstrated for several endemics in *Ulota*: *U. pygmaeothecia* (Muñoz-Puelles et al. 2017), *U. glabella* (Garilleti et al. 2020a), *U. maltana* (Garilleti et al. 2020b), and *U. macrodontia* (Garilleti et al. 2021).

DISTRIBUTION AND ECOLOGY

We now know that *Orthotrichum gigantosporum* extends over most of the northern sector of the Andean–Patagonian area (Fig. 1). The identified localities lie between latitude coordinates 37°46'S (approximately, cf. Lewinsky & Deguchi 1989) and 46°29'S; the outer longitude coordinates are 71°25'W and 73°15'W. The extensive sampling carried out could justify discounting the presence of the species in the Chilean region of Magallanes and in the Argentine provinces of Santa Cruz and Tierra del Fuego. In Argentina, it has not been found in the provinces of Río Negro and Chubut either, but its presence in the border zones of these provinces cannot be ruled out. In the Chilean region of Araucanía, with very few points sampled, only the locality reported by Lewinsky & Deguchi (1989) is known; the Biobío region has not been studied by our team, and it is possible that the distribution of *O. gigantosporum* extends northwards through the Andean areas into that region. The altitudinal range of the distribution of the species is quite wide, as in Chile the localities are located between 10 and 800 m, while in Argentina they are located between 525 and 1060 m.

From a climatic point of view, most of the confirmed localities for *O. gigantosporum* are located in areas under the influence of the Oceanic climate (Cfb) in the Köppen–Geiger classification system (Fig. 1). Only a few populations seem to thrive under other types of Patagonian climate: Subpolar oceanic (Cfc) and Mediterranean with warm/cool summer (Csb). These localities under an atypical climate are probably situated in transitional areas where the climatic conditions might be attenuated.

Orthotrichum gigantosporum has been found in several vegetation types corresponding to the North Patagonian and Valdivian rainforests (Luebert & Plischoff 2006; Moreira-Muñoz 2011). It is most frequently found associated with evergreen *Nothofagus* forests, both those dominated by *N. dombeyi*, sometimes with *Fitzroya cupressoides* (Molina) I.M. Johnst. or *Araucaria araucana* (Molina) K. Koch, and those dominated by *N. betuloides*. More rarely it is associated with deciduous forests and thickets dominated by *N. antarctica* (G. Forst.) Oerst. This moss grows in forests, often in the more open ones, but especially on the bushes associated with them. In fact, all the most frequently

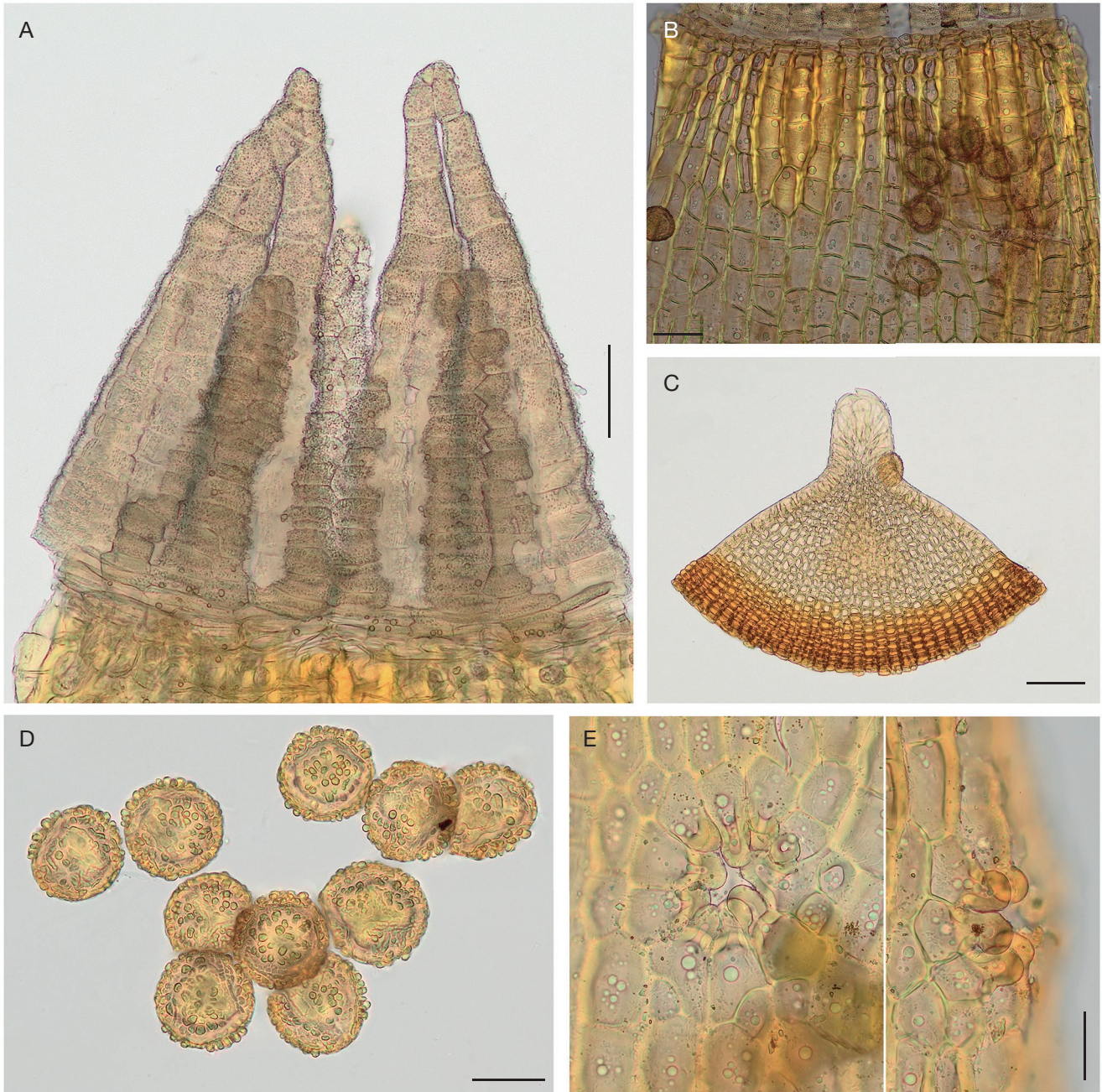


FIG. 3. — *Orthotrichum gigantosporum* Lewinsky: **A**, peristome showing the endostome in first plane, note the teeth pair on left joined by the tip; **B**, detail of the exothecium with the short exothecial bands shining in polarized light; **C**, operculum; **D**, spores; **E**, upper and lateral view of stomata. A, B, E, from Garilleti 2016-198a; C, from Lara s.n. 30-12-2005; D, from Garilleti 2016-236g. Scale bars: A-C, 50 μ m; D, E, 30 μ m.

colonized phorophytes are heliophilous shrubs (Table 1). *Orthotrichum gigantosporum* also occurs on trees, native or introduced, in open spaces (riparian forests, roadsides, fruit trees in crops), which is a characteristic behaviour of the species of the genus, in accordance with its photophilous character and high tolerance to desiccation. Nevertheless, this moss seems to inhabit only areas with high levels of precipitation. This is evidenced by the composition of the epiphytic communities in which *O. gigantosporum* occurs, which are completely dominated by highly hygrophilous species of the genus *Ulota*; these communities may contain several species of *Lewinskya*

but lack other *Orthotrichum* species. Very few other species of the genus *Orthotrichum* have adapted to such ecological conditions, which are very humid and at the same time very exposed to plant desiccation. Interestingly, the New Zealand endemic *O. calvum* Hook.f. & Wilson, a moss growing in very similar environments and epiphytic communities, has also been morphologically compared with *O. gigantosporum* (Lewinsky 1984).

MORPHOLOGY

Due to its exerted capsules, narrow leaves and small size, wet specimens of *Orthotrichum gigantosporum* look quite like the

TABLE 2. — Species and subspecific taxa recognized for the Andean Patagonia. Endemics for the area are marked with *. The numbers accompanying each genus indicate: total amount of taxa/number of endemics – percentage of endemism.

Species and subspecific	Total amount of taxa/ number of endemics – percentage of endemism
<i>Australoria</i> F.Lara, Garilleti & Draper	2/2 – 100%
* <i>A. bartramioides</i> (Dusén ex Malta) F.Lara, Garilleti & Draper (synonym of <i>Zygodon bartramioides</i> Malta)	
* <i>A. chilensis</i> (Calabrese & F.Lara) F.Lara, Garilleti & Draper (synonym of <i>Z. chilensis</i> Calabrese & F.Lara)	
<i>Codonoblepharon</i> Schwägr.	1/0 – 0%
<i>C. menziesii</i> Schwägr. [synonym of <i>Zygodon menziesii</i> (Schwägr.) Arn.]	
<i>Leratia</i> Broth. & Paris	1/0 – 0%
<i>L. obtusifolia</i> (Hook.) Goffinet (synonym of <i>Zygodon obtusifolius</i> Hook.)	
<i>Lewinskya</i> F.Lara, Garilleti & Goffinet	11/8 – 73%
* <i>L. anaglyptodon</i> (Cardot & Broth.) F.Lara, Garilleti & Goffinet (synonym of <i>Orthotrichum anaglyptodon</i> Cardot & Broth.)	
* <i>L. anaglyptodon</i> var. <i>ochyrarum</i> Plášek	
* <i>L. brotheri</i> (Dusén ex Lewinsky) F.Lara, Garilleti & Goffinet (synonym of <i>O. brotheri</i> Dusén ex Lewinsky)	
* <i>L. densa</i> (Lewinsky) F.Lara, Garilleti & Goffinet (synonym of <i>O. densum</i> Lewinsky)	
* <i>L. elegantula</i> (Schimp. ex Mitt.) F.Lara, Garilleti & Goffinet (synonym of <i>O. elegantulum</i> Schimp. ex Mitt.)	
<i>L. hortensis</i> (Bosw.) F.Lara, Garilleti & Goffinet (synonym of <i>O. hortense</i> Bosw.)	
* <i>L. incana</i> (Müll.Hal.) F.Lara, Garilleti & Goffinet (synonym of <i>O. incanum</i> Müll.Hal.)	
* <i>L. ludificans</i> (Lewinsky) F.Lara, Garilleti & Goffinet (synonym of <i>O. ludificans</i> Lewinsky)	
<i>L. rupestris</i> (Schleich. ex Schwägr.) F.Lara, Garilleti & Goffinet (synonym of <i>O. rupestre</i> Schleich. ex Schwägr.)	
<i>L. rupestris</i> var. <i>papillosa</i> (Lewinsky) F.Lara, Garilleti & Goffinet (synonym of <i>O. rupestre</i> var. <i>papillosum</i> Lewinsky)	
* <i>L. truncata</i> (Lewinsky & Deguchi) F.Lara, Garilleti & Goffinet (synonym of <i>O. truncatum</i> Lewinsky & Deguchi)	
<i>Macrocoma</i> (Hornsch. ex Müll.Hal.) Grout	2/0 – 0%
<i>M. brasiliensis</i> (Mitt.) Vitt	
<i>M. tenuis</i> subsp. <i>sullivantii</i> (Müll.Hal.) Vitt [synonym of <i>M. sullivantii</i> (Müll.Hal.) Grout]	
<i>Macromitrium</i> Brid.	9/8 – 89%
* <i>M. bifasciculare</i> Müll.Hal. ex Dusén	
* <i>M. campoanum</i> Thér.	
* <i>M. crassiusculum</i> Lorentz	
* <i>M. krausei</i> Lorentz	
<i>M. longirostre</i> (Hook.) Schwägr.	
* <i>M. microcarpum</i> Müll.Hal.	
* <i>M. pertriste</i> Müll.Hal.	
* <i>M. saddleanum</i> Besch. ex Müll.Hal.	
* <i>M. tenax</i> Müll.Hal.	
<i>Matteria</i> Goffinet	2/2 – 100%
* <i>M. gracillima</i> (Besch.) Goffinet	
* <i>M. papillosula</i> (Thér.) Goffinet	
<i>Orthotrichum</i> Hedw.	10/4 – 40%
<i>O. anomalum</i> Hedw.	
<i>O. assimile</i> Müll.Hal.	
<i>O. crassifolium</i> Hook.f. & Wilson	
<i>O. cupulatum</i> var. <i>austroamericanum</i> Lewinsky	
<i>O. diaphanum</i> var. <i>podocarpj</i> (Müll.Hal.) Lewinsky	
* <i>O. freyanum</i> Goffinet, W.R.Buck & M.A.Wall	
* <i>O. gigantosporum</i> Lewinsky	
* <i>O. inclinatum</i> Müll.Hal.	
* <i>O. perexiguum</i> Dusén ex Lewinsky	
<i>O. tristriatum</i> Lewinsky	
<i>Pentastichella</i> Müll.Hal.	1/0 – 0%
<i>P. pentasticha</i> (Mont.) Müll.Hal. ex Thér. [synonym of <i>Zygodon pentastichus</i> (Mont.) Müll.Hal.]	
<i>Plenogemma</i> Plášek, Sawicki & Ochyra	1/0 – 0%
<i>Plenogemma phyllantha</i> (Brid.) Sawicki, Plášek & Ochyra (synonym of <i>Ulota phyllantha</i> Brid.)	
<i>Ulota</i> D.Mohr	18/17 – 94%
* <i>U. billbuckii</i> Garilleti, Mazimpaka & F.Lara	
* <i>U. carinata</i> Mitt.	
* <i>U. fuegiana</i> Mitt.	
* <i>U. fuegiana</i> subsp. <i>darwinii</i> (Mitt.) Malta	
<i>U. germana</i> (Mont.) Mitt.	
* <i>U. glabella</i> Mitt.	
* <i>U. larrainii</i> Garilleti, Mazimpaka & F.Lara	
* <i>U. lativentrosa</i> Müll.Hal. ex Malta	
* <i>U. luteola</i> (Hook.f. & Wilson) Wijk & Margad.	
* <i>U. macrocalycina</i> Mitt.	
* <i>U. macrodontia</i> Dusén ex Malta	
* <i>U. magellanica</i> (Mont.) A.Jaeger	

TABLE 2. — Continuation.

Species and subspecific	Total amount of taxa/ number of endemics – percentage of endemism
* <i>U. maltana</i> Garilleti & F.Lara	
* <i>U. pusilla</i> Malta	
* <i>U. pycnophylla</i> Dusén ex Malta	
* <i>U. pygmaeothecia</i> (Müll.Hal.) Kindb.	
* <i>U. streptodon</i> Garilleti, Mazimpaka & F.Lara	
* <i>U. ventricosa</i> (Müll.Hal.) Malta	
<i>Zygodon</i> Hook. & Taylor	8/3 – 37%
<i>Z. hookeri</i> Hampe var. <i>hookeri</i>	
<i>Z. hookeri</i> var. <i>leptobolax</i> (Müll.Hal.) Calabrese	
<i>Z. intermedius</i> Bruch & Schimp.	
* <i>Z. jaffuelii</i> Thér.	
* <i>Z. magellanicus</i> Dusén ex Malta	
* <i>Z. papillatus</i> Mont.	
<i>Z. pichinchensis</i> (Taylor) Mitt.	
<i>Z. reinwardtii</i> (Horns.) A.Braun	

Ulotia species with which it is usually intermixed, so it easily goes unnoticed in the field. Its naked calyptrae, in contrast what happens with the New Zealand *O. calvum* (Sainsbury 1955), are not sufficient to rule out the genus *Ulotia*, since in the Andean-Patagonian area there are two species of this group with hairless calyptrae (Garilleti *et al.* 2020a).

The differentiation of *O. gigantosporum* offers no difficulties in the laboratory. It is a very characteristic species, unmistakable by the following set of characters: 1) small plants, not appearing crisped when dry (Fig. 2A); 2) narrow leaves with plane or scarcely recurved margins and oval bases (Fig. 2F, I); 3) leaf apex frequently ending in a long uniseriate row of cells (Fig. 2F, J); 4) naked calyptrae (Fig. 2C); 5) vaginula with many long hairs (Fig. 2G); 6) capsules visibly exerted, urceolate to pyriform when dry, with very short ribs extending just below the mouth (Figs 2A, B, D, E, H; 3B); 7) stomata at mid capsule, widely covered by the exothecial cells (Fig. 3E); 8) operculum shortly rostrate with a broad reddish basal rim (Figs 2D, H; 3C); 9) exostome of eight pairs of teeth easily splitting into 16 (Figs 2B, E; 3A); 10) endostome of 16 broad, papillose segments (Figs 2B; 3A); and 11) spores unicellular but very large, verrucose (Fig. 3D).

Because several of these features are unique within *Orthotrichum* (Lara *et al.* 2016), no other Patagonian or Australasian species can be confused with *O. gigantosporum*. In fact, Lewinsky (1984) suggested the possibility that *O. gigantosporum* could be placed in its own subgenus, due to its unparalleled stout papillose endostome and the very large spores that give the moss its name. Indeed, these are two extraordinary features, although as far as the peristome is concerned we now know of one other species with the same peristomial arrangement: *O. spiculatum* F.Lara, Garilleti & Mazimpaka. This xerophytic moss from central Argentina also has 16 stout endostomial segments although it can be easily differentiated by its acuminate-dentate leaves and almost immersed capsules, among other characteristics (Lara *et al.* 2007).

As for the spores, there are other species of *Orthotrichum* in which they become very large, but in such cases multicol-

ular spores are involved. In these species sporeling development takes place inside the spore cell wall that stretches without breaking, and it occurs during the maturation of the capsule, before the separation of the operculum. However, the spore size of *O. gigantosporum* is exceptional in the genus because these are unicellular spores. In this case, there is no endosporic germination, but it is evident that in a proportion of the spores the cell expands abnormally before release. As can be easily observed in every capsule of *O. gigantosporum*, the walls of the larger spores, those close to 50 µm in diameter, have expanded as is evident from the distancing of the verrucae ornamenting the surface and the detachment of many of them. The detachment of a proportion of the perine structures of the spore surface as the spore wall stretches has been observed in multicellular spores of *Ulotia* (Caparrós *et al.* 2011; Garilleti *et al.* 2012, 2015), but as far as we know it has not been previously described for the genus *Orthotrichum*.

The morphological re-examination of *O. gigantosporum* based on a large number of specimens has shown that the original description (Lewinsky 1984) contained some shortcomings or inaccuracies. The most important of these undoubtedly concerns the peristomial structure, which, when used in the available identification key (Lewinsky 1984), can lead to confusion. In this key the peristome of *O. gigantosporum* is described as: “exo- and endostome with 16 teeth each, equally tall and well developed”. However, the exostome of *O. gigantosporum* does not consist of 16 independent teeth, but of eight pairs that usually split easily, although irregularly. Therefore, capsules can be found showing three apparently different peristome arrangements: 1) all pairs of teeth intact or almost intact; 2) some pairs split and others intact; and finally, 3) all pairs split or with the exostomial teeth paired only at their bases. Only in the latter case can 16 independent teeth be observed. The degree of scission of the teeth pairs is usually related to the age of the capsules, so that in recently deoperculate capsules many of the teeth remain paired, while in those that have already released their spores the teeth are

detached in most cases. Occasionally, however, old capsules are found with exostomial teeth that remain paired.

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APPENDIX

APPENDIX 1. — New localities (selected specimens for each locality are indicated).

MATERIAL. — **Argentina**, Neuquén, Departamento Huiliches: Parque Nacional Lanín, Lago Tromen, $39^{\circ}34'15''\text{S}$, $71^{\circ}25'07''\text{W}$, 1060 m, 21.XII.2005, *F. Lara* s/n & *E. San Miguel* (MAUAM 4687); Departamento Los Lagos: Parque Nacional Nahuel Huapi, río Ruca Malén en la desembocadura en el Lago Correntoso, $40^{\circ}36'12''\text{S}$, $071^{\circ}42'21''\text{W}$, alt. 800 m, 10.I.2017., *R. Garilleti 2017-066* & *F. Lara* (Herb. Garilleti); Parque Nacional Nahuel Huapi, ruta prov. 65 al Lago Traful, 1.2 km al W de Puerto Arrayanes, $40^{\circ}36'52''\text{S}$, $71^{\circ}33'41''\text{W}$, alt. 820 m, 10.I.2017, *F. Lara 1701/82* & *R. Garilleti* (MAUAM). — Río Negro, Departamento Bariloche: Parque Nacional Nahuel Huapi, Lago Nahuel Huapi, Circuito Chico al S de Villa Tacul, entre la ruta prov. 77 y la Bahía de Los Troncos, $41^{\circ}03'48''\text{S}$, $71^{\circ}33'57''\text{W}$, alt. 780 m, 9.I.2017, *R. Garilleti 2017-058a* & *F. Lara* (Herb. Garilleti); Parque Nacional Nahuel Huapi, Lago Steffen, Camping agreste Bahía Steffen y márgenes del río Giacovo, $41^{\circ}30'24''\text{S}$, $71^{\circ}32'16''\text{W}$, alt. 540 m, 8.I.2017, *R. Garilleti 2017-050a* & *F. Lara* (Herb. Garilleti). — Chubut, Departamento Futaleufú: Parque Nacional Los Alerces, Lago Menéndez, Alerzal Milenario, pasarela bordeando el Río Cisne desde Puerto Sagrario al Lago Cisne, $42^{\circ}36'37''\text{S}$, $71^{\circ}53'27''\text{W}$, alt. 525 m, 7.I.2017, *R. Garilleti 2017-042a* & *F. Lara* (Herb. Garilleti).

Chile, IX Región de Los Ríos, Prov. de Valdivia: Comuna de Valdivia, Jardín Botánico de Valdivia, $39^{\circ}48'20''\text{S}$, $73^{\circ}15'08''\text{W}$, 10 m, 26.XII.2005, *F. Lara* s/n & *E. San Miguel* (MAUAM 3584); Prov. del Ranco: Comuna de La Unión, ruta T-80 en la confluencia con la ruta T-850, $40^{\circ}12'40''\text{S}$, $073^{\circ}22'23''\text{W}$, alt. 705 m, 15.I.2017, *R. Garilleti 2017-108f* & *F. Lara* (Herb. Garilleti). — X Región de Los Lagos, Prov. de Osorno: Comuna de Puyehue, Parque Nacional Puyehue, ruta U-485 por encima de las Termas Aguas Calientes, Lago Toro, $40^{\circ}46'13''\text{S}$, $72^{\circ}16'16''\text{W}$, alt. 720 m, 14.I.2017, *F. Lara 1712/108* & *R. Garilleti* (MAUAM); Prov. de Llanquihue: Comuna de Puerto Montt, Parque Nacional Alerce Andino, sector Sargazo, sendero entre el puesto de guardaparques y la laguna Sargazo, $41^{\circ}30'34''\text{S}$, $072^{\circ}37'06''\text{W}$, alt. 340-430 m, 22.XII.2016, *R. Garilleti 2016-177* & *F. Lara* (Herb. Garilleti); Comuna de Puerto Montt, proximidades del P.N. Alerce Andino, sector Correntoso, ruta V-657 cerca de la confluencia con la V65, $41^{\circ}27'13''\text{S}$, $72^{\circ}39'25''\text{W}$, alt. 147 m, 22.XII.2016, *F. Lara 1612/18* & *R. Garilleti* (MAUAM); Prov. de Palena: Comuna de Palena, ruta 231 junto al río Futaleufú, al norte del hotel Raudal, $43^{\circ}25'05''\text{S}$, $72^{\circ}05'35''\text{W}$, alt. 65 m, 25.XII.2016, *F. Lara 1612/38 - 41* & *R. Garilleti* (MAUAM); Ibidem, *R. Garilleti 2016-198a*, *199a* & *F. Lara* (Herb. Garilleti); Comuna de Chaitén, Parque Nacional Corcovado, río Frío, ruta Austral (7) c. 5 km al sur de Villa Santa Lucía, $43^{\circ}27'12''\text{S}$, $72^{\circ}21'17''\text{W}$, alt. 220 m, 26.XII.2016, *F. Lara 1612/50 - 51* & *R. Garilleti* (MAUAM); Ibidem, *R. Garilleti 2016-208b* & *F. Lara* (Herb. Garilleti). — XI Región Aysén del General Carlos Ibáñez del Campo, Prov. de Aysén: Comuna de Cisnes, Ruta X-12, a 15 km al W de La Junta, $44^{\circ}01'06''\text{S}$, $072^{\circ}32'25''\text{W}$, alt. 45 m, 27.XII.2016, *R. Garilleti 2016-2016pp* & *F. Lara* (Herb. Garilleti); Comuna de Cisnes, Ruta X-13, a 10 km al E de La Junta, $43^{\circ}58'57''\text{S}$, $072^{\circ}17'48''\text{W}$, alt. 95 m, 27.XII.2016, *R. Garilleti 2016-219pp* & *F. Lara* (Herb. Garilleti); Comuna de Cisnes, Ruta X-13, a 37 km al E de La Junta, $44^{\circ}07'27''\text{S}$, $072^{\circ}09'05''\text{W}$, alt. 220 m, 27.XII.2016, *R. Garilleti 2016-220a* & *F. Lara* (Herb. Garilleti); Comuna de Cisnes, Puerto Cisnes, ruta X-25 a 8 km al E del pueblo, $44^{\circ}45'15''\text{S}$, $072^{\circ}36'23''\text{W}$, alt. 20 m, 29.XII.2016, *R. Garilleti 2016-236g* & *F. Lara* (Herb. Garilleti); Comuna de Aysén, Río Mañihuales, 6 km al E de Las Turbinas por la ruta X-50, $45^{\circ}20'01''\text{S}$, $72^{\circ}25'28''\text{W}$, alt. 40 m, 30.XII.2016, *F. Lara 1612/91* & *R. Garilleti* (MAUAM); Comuna de Aysén, Lago Riesco, El Salto, $45^{\circ}28'09''\text{S}$, $72^{\circ}43'59''\text{W}$, alt. 20 m, 30.XII.2016, *F. Lara 1612/92 - 94* & *R. Garilleti* (MAUAM); Comuna de Aysén, Río Simson, Reserva Nacional Río Simson, c. cascada La Virgen, a 31 km al E de Puerto Aysén por la ruta 240, $45^{\circ}27'30''\text{S}$, $72^{\circ}22'23''\text{W}$, alt. 70 m, 30.XII.2016, *F. Lara 1612/96* & *R. Garilleti* (MAUAM); Prov. de Coyhaique: Comuna de Lago Verde, Valle del río Cisnes, Choyquemoro, Ruta X-25, 22 km al E del cruce con la ruta 7 en Villa Amengual, $44^{\circ}41'36''\text{S}$, $071^{\circ}59'18''\text{W}$, alt. 440 m, 29.XII.2016, *R. Garilleti 2016-241a* & *F. Lara* (Herb. Garilleti); Comuna de Lago Verde, Laguna de Las Torres, Reserva Nacional Lago Las Torres, Ruta Austral (7), 8 km al S de Villa Amengual, $44^{\circ}48'33''\text{S}$, $72^{\circ}12'22''\text{W}$, alt. 290 m, 30.XII.2016, *F. Lara 1612/87* & *R. Garilleti* (MAUAM); Prov. de General Carrera: Comuna de Río Ibáñez, Ruta Austral (7), 2.9 km al S de Puente Las Ovejas, c. valle del río Murta, $46^{\circ}12'48''\text{S}$, $72^{\circ}48'13''\text{W}$, alt. 325 m, 31.XII.2016, *F. Lara 1612/115*, *117* & *R. Garilleti* (MAUAM); Comuna de Chile Chico, Parque Nacional Laguna de San Rafael, sector Exploradores, Mirador Glaciar Exploradores, $46^{\circ}29'57''\text{S}$, $73^{\circ}09'31''\text{W}$, alt. 200 m, 1.I.2017, *F. Lara 1701/009* & *R. Garilleti* (MAUAM).