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## Silicophytoliths in Holocene peatlands and fossil peat layers from Tierra del Fuego, Argentina, southernmost South America

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### ABSTRACT

Phytolith analyses are practically absent from peatlands, except for studies developed on tropical mires and peat profiles. In Tierra del Fuego, Argentina, peatlands represent the largest surface coverage in the South American continent. Because of their continuous sedimentation pattern, they represent relevant palaeoenvironmental records from which the reconstruction of the latest Pleistocene–Holocene history of this region can be obtained. The aim of the study was to analyze the presence of phytoliths in selected mires and fossil peat layers from Tierra del Fuego, Argentina, and to compare these records with present vegetation. Phytoliths from the most abundant and representative plant species, a minerotrophic mire and an alluvial sequence with fossil peat layers were analyzed and described. Nine of the ten plant families analyzed produced phytoliths. The morphotypes described coincided with previous studies carried on species from other regions. Phytolith assemblages from top soil of both sites mostly coincided with the phytolith assemblages of the plants developed over them, except for tabular and cone sedge phytoliths, which were hardly found in soil samples. A lower silicification level and/or fragmentation processes could account for this absence. Profile analyses showed a low diversity of phytolith morphologies, either due to low plant diversity, a poor phytolith production of the species or to dissolution/fragmentation processes. Besides this low diversity, the phytolith assemblages described reflect the presence of grass communities during the development of these environments, being the Pooideae subfamily the dominant component of these communities. This study is the first to present results of phytolith analyses from cold-temperate, subantarctic peatlands, showing the importance of this proxy as a complement of others, such as pollen or charcoal particles in the palaeoenvironmental interpretation of the region.

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### 1. Introduction

Peatlands are distributed over all continents, covering an area equivalent to around 3% of the Earth surface, representing more than half of all wetlands (Joosten and Clarke, 2002; Pontevedra and Martínez, 2004). Peatlands are ecosystems that, thanks to their capacity of retaining large quantities of water, play relevant roles in hydrological processes (Díaz et al., 2005).

In the island of Tierra del Fuego, peatlands have developed in the central and southern deciduous *Nothofagus* (South American beech) region, representing the largest surface coverage in the South

American continent. They form unique environments due to their geographical location, floristic and hydrological nature and palaeoenvironmental record storage. Because of their continuous sedimentation pattern, they are considered as very good environmental data banks, since uninterrupted palaeoenvironmental records from Late Glacial to present times may be commonly obtained (Rabassa et al., 2006). Moreover, their geomorphologic location and basal peat radiocarbon ages have been used to understand the glaciation–deglaciation processes (Coronato et al., 2006). Many studies have been carried out in these areas and various proxies, such as pollen, spore and charcoal particles, have been thoroughly analyzed in them, allowing the reconstruction of the latest Pleistocene–Holocene history of this region (Heusser, 1989, 1990, 1994, 1998, 2003; Borromei, 1995; Heusser and Rabassa, 1995; Rabassa et al., 2006; Borromei et al., 2007, 2010; Rabassa, 2008). Preliminary

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geochemistry and mineral microparticle content have been reported by Franzen (2006).

Phytoliths are amorphous silica particles that precipitate in and/or between cells of living plant tissues. Once the plant or organ dies, the organic matter decomposes and phytoliths are released directly into the soil. Due to their high taxonomic value and their persistence in soils and sediments, are widely used as indicators of past plant communities, as well as indicators of environmental conditions where these communities developed (Rovner, 1971; Alexandre et al., 1997; Barboni et al., 1999; Hou-Yuan et al., 2006).

With the exception of a few studies carried on tropical mires and peat profiles, phytolith analyses in peatlands are practically absent. Wüst and Bustin (2003) analyzed the presence of biogenic silica content in different tropical mires from West Malaysia, but their study was mainly focused on the biogeochemical cycling of elements, especially Si and Al, under weathering conditions in these environments. Borba-Roschel et al. (2006) analyzed a peat profile of the Uberaba plateau (Minas Gerais-Brazil) focusing their work on the comparison between phytolith assemblages extracted from the peat and the leaves of the main hydromorphic plants. No phytolith studies have been developed until now in temperate-cold subantarctic peatlands, where the processes involved are probably much different from those occurring in tropical environments, especially in relation to phytolith production and preservation. Notwithstanding, in Tierra del Fuego, some phytolith studies have been developed in plant communities from the ecotone (Fernández Pepi et al., 2009, 2010) and in sediments of the archaeological site “Tunel 7”, in the north coast of Beagle Channel (Zurro, 2010).

Due to the great potential that phytoliths have in palaeoenvironmental and palaeobotanical research, especially as a complement to other proxies such as pollen and spores, the aim of the

present paper is to analyze the presence of these biomineralizations in selected mires and fossil peat layers from Tierra del Fuego, Argentina. Also, and with the purpose to compare with the phytolith production of present plants, the most abundant and characteristic plant species in these areas were analyzed. This work represents a first step towards the knowledge of the scientific potential that phytoliths have in these southern Argentina environments as indicators of plant palaeocommunities and palaeoenvironmental conditions.

## 2. Regional setting

The Isla Grande de Tierra del Fuego is located at the southernmost end of South America, between latitude  $53^{\circ}$ – $55^{\circ}$  S and longitude  $66^{\circ}$ – $74^{\circ}$  W (Fig. 1). The Argentine sector occupies the eastern area of the island whereas the rest belongs to Chile. The regional climate of Argentine Tierra del Fuego is cold-temperate-oceanic in the southern part and cold-temperate-subhumid in the northern one, with an overall mean annual temperature of ca.  $5^{\circ}$  C. Moisture is derived primarily from the south and southwest and rainfall shows a strong gradient from the southwest, with 600 mm/y, to the northeast, with less than 300 mm/y (Rabassa et al., 2006). Landscape is almost flat and close to the sea in the northern area, but rugged and mountainous in the southern portion. Most of the island, if not all of it, was glaciated in the Early Pleistocene, and then partially but repeatedly ice covered during the Middle and Late Pleistocene (Rabassa, 2008; Coronato and Rabassa, 2011). During the Last Glacial Maximum, extensive glaciation affected the south-central mountainous region and the Magellan Straits area around 25 cal ka BP. Later, Late Glacial re-advances occurred at around 15–12 cal ka BP, before the final ice-retreat from the lower valleys.

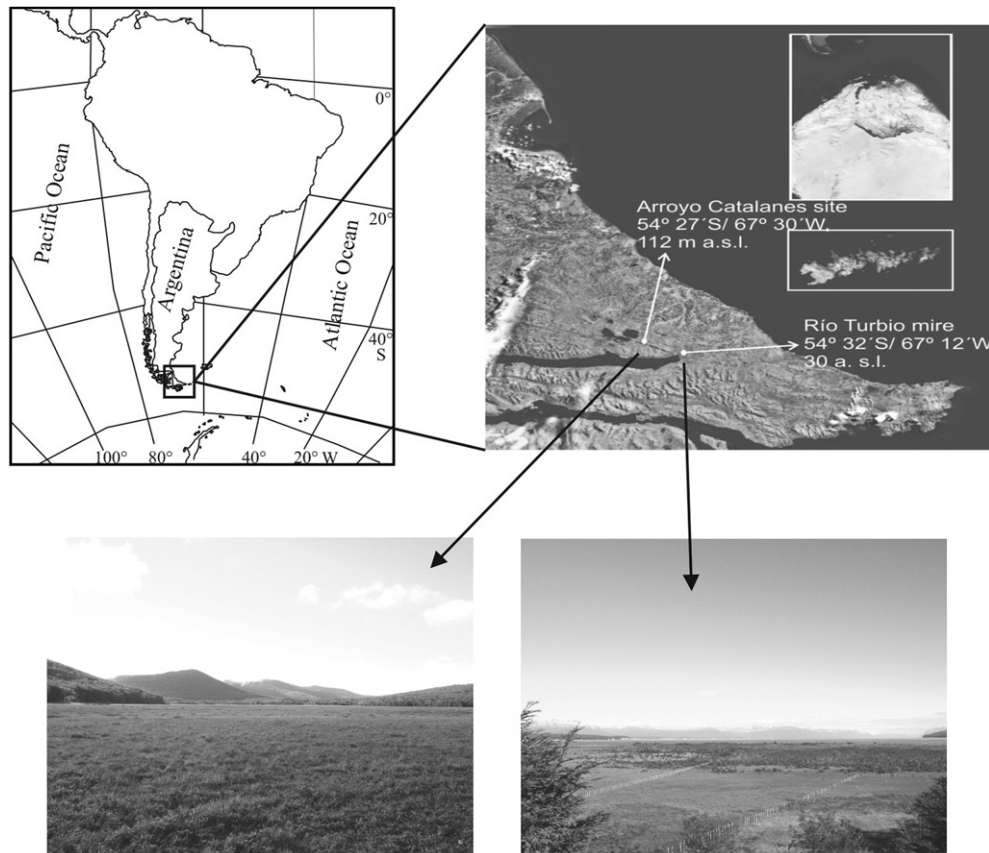


Fig. 1. Location of the two sites studied in Tierra del Fuego, Argentina.

More recently, glaciers advanced several times during the late Holocene until the 19th century in the Andean cirques and hanging valleys, down to the 800 m a.s.l. contour line.

Two sites were specifically selected for this study: the Río Turbio minerotrophic mire and the alluvial sequence with fossil peat layers in the Arroyo Catalanes locality, both located in central Tierra del Fuego, where the forest-steppe transitional environment begins (Fig. 1).

The “Río Turbio” site is a minerotrophic mire formed by Cyperaceae in an environment dominated by *Carex* sp., *Carex gayana*, *Empetrum rubrum*, *Marsippospermum* sp. and *Bolax gumnifera*, among other species. At the surface, few mounds of *Sphagnum magellanicum* in the central areas and *Nothofagus antarctica* specimens in the marginal zone are found (Roig, 2001) (Fig. 1). This mire is developed within a deltaic plain generated by the Río Turbio mouth at the headlands of Lago Fagnano, along which the Magellan-Fagnano transform fault is partially located. The studied sequence presents 2.5 m of peat interbedded with silty-sandy and clayish-silty beds. At the base, at least 0.4 m of blueish lacustrine clays represent the original pond in which the mire was originated. The mineral levels interbedded with peat are interpreted as deposited by the delta stream channels together with ponding due to subsidence by seismo-tectonic activity, as happened during the December 1949 earthquake, of 7.9 magnitude. During this event, the shallow pond that presently floods the southern area of the mire was formed due to the delta dam and the gravel accumulation on the lake shore by seiches. The basal radiocarbon age of this mire yields  $8920 \pm 70$  BP, at 4.57 m depth (Coronato et al., 2006). This mire is located at the foot of an eroded moraine corresponding to the first recessional phase of the paleo Fagnano glacier, immediately after the Last Glacial Maximum (Coronato et al., 2009b).

The Arroyo Catalanes locality is an alluvial sedimentary sequence in a stream bank which drains the northern slope of the Las Pinturas range, north of Lago Fagnano (Fig. 1). This creek is a low discharge stream placed into a vast fluvial valley, later modified by glacial and glaciofluvial processes. It presently corresponds to a wet grassland environment, used for cattle raising (Collado, 2001). The plant cover is composed of *Agrostis* sp., *Carex* sp., *Festuca magellanica*, *Poa* sp., among other species (Lencinas, 2005). This valley does not show clear glacial geomorphological features, although neighbouring valleys were occupied by glaciers flowing north during the Last Glacial Maximum (Coronato et al., 2009a, 2009b) (Fig. 1). This statement gives extremely high interest to the environmental record storage found in this alluvial bank.

The stratigraphic sequences of both localities show tephra deposition as a recurrent process both during Late Glacial and Holocene times. As no active volcanoes are settled in Tierra del Fuego, the provenance of the tephra is related to the volcanic centers located in the Austral Volcanic Zone, Southern Patagonian Andes (Stern, 2008), located northwestwards, between 400 and 1000 km away. At the Arroyo Catalanes site, two different ash layers have been found, whereas only one has been detected so far in the Río Turbio section. Although their geochemistry is still unknown, the stratigraphical position of Arroyo Catalanes tephra layer in between Late Glacial peat could indicate that they belong to the Reclus I eruption, estimated at an average age of  $12,572 \pm 467$  BP, calculated on organic material in soils above and below the ash level in 28 localities of southern Chile (Stern, 2008).

### 3. Material and methods

#### 3.1. Plant selection and phytolith extraction

Ten families and 22 species, corresponding to the main species that characterize the present vegetation of both sites, were selected

(Table 1). The species were sampled at the same places where soil and profile samples were collected: the Río Turbio mire and the Arroyo Catalanes river banks.

Leaves from at least two specimens of each plant species were collected and phytoliths were extracted following a calcination technique (Labouriau, 1983). The samples were first placed in an ultrasound bath for 15–20 min and washed with distilled water to remove mineral contaminants. The material was dried at 56 °C for 24 h, and charred at 200 °C for 2 h. Later, it was boiled in a 5N HCl solution for 10 min, washed with distilled water and filtered with ashless filter paper, until no more chloride ions were detected. Finally, the material was ignited at 760 °C for 3 h. The ashes obtained were mounted with immersion oil and the phytolith morphotypes were observed and described with a Zeiss Axiostar Plus microscope at  $\times 400$  magnification and with a scanning electron microscope (JEOL JSM-6460 LV, Japan) at the Universidad Nacional de Mar del Plata, Argentina. Photographs were taken with a digital camera Cannon Powershot G10. More than 300 phytoliths were counted in each slide and the morphotypes were described according to Twiss (1992), Fredlund and Tieszen (1994), Zucol (1996) and the International Code for Phytolith Nomenclature (Madella et al., 2005).

#### 3.2. Soil and profile sampling and morphological characterization

Eight samples from the first 5 cm of soils at the Río Turbio locality (RT) were collected for phytolith analyses. Due to its heterogeneous micro-relief, samples were taken from mounds (RTM) and hollows (RTH) (Fig. 2A, B). The long pedosedimentary profile was cored using a Russian-type sampler. Eleven samples of 10 cm of sediment, which included a total 2.50 m of depth, were obtained for phytolith extraction (Fig. 2C).

Eight samples from the top soils (first five cm) from the Arroyo Catalanes site were collected (AC 2, 3, 6, 7, 10, 11, 12, 13) (Fig. 3A). Sampling was manually done at a river bank during different field seasons and in different sections, because flooding made some of the sections unreachable. At the beginning of the study (December, 2006), fossil peat layers samples were taken in order to establish

**Table 1**

Plant species examined in this study (listed alphabetically by family). D: dicotyledon. M: monocotyledon. AC: Arroyo Catalanes grassland. RT: Río Turbio mire.

Family	Species	Abbrev.	Collection site
Asteraceae (D)	<i>Senecio magellanicus</i> Hook. & Arn.	SM	RT
Berberidaceae (D)	<i>Berberis buxifolia</i> Lam.	BB	AC
Caryophyllaceae (D)	<i>Cerastium arvense</i> L.	CA	RT
	<i>Colobanthus quitensis</i> (Kunth) Bartl.	CQ	RT
Cyperaceae (M)	<i>Carex magellanica</i> Lam.	CM	RT
	<i>Carex</i> sp.	Csp	RT
Gunneraceae (D)	<i>Gunnera magellanica</i> Lam.	GM	RT
Juncaceae (M)	<i>Luzula alopecurus</i> Desv.	LA	AC
Nothofagaceae (D)	<i>Nothofagus pumilio</i> (Poepp. & Endl.) Krasser	NP	AC
Poaceae (M)	<i>Alopecurus magellanicus</i> Lam.	AM	AC
	<i>Deschampsia antarctica</i> E. Desv.	DA	RT
	<i>Deschampsia flexuosa</i> (L.) Trin.	DF	AC
	<i>Deyeuxia poaeoides</i> (Steud.) Rúgolo	DP	RT
	<i>Elymus agropyroides</i> J. Presl.	EA	AC
	<i>Festuca arundinacea</i> Schreber	FA	AC
	<i>Festuca magellanica</i> Lam.	FM	AC
	<i>Phleum alpinum</i> L.	PA	AC
	<i>Puccinellia magellanica</i> (Hooker f.) Parodi	PM	AC/RT
	<i>Trisetum spicatum</i> (L.) K. Richt.	TS	AC/RT
Ranunculaceae (D)	<i>Ranunculus</i> sp.	Rsp	AC
Rosaceae (D)	<i>Acaena magellanica</i> (Lam.) Vahl	Am	AC
	<i>Rubus geoides</i> Sm.	RG	AC



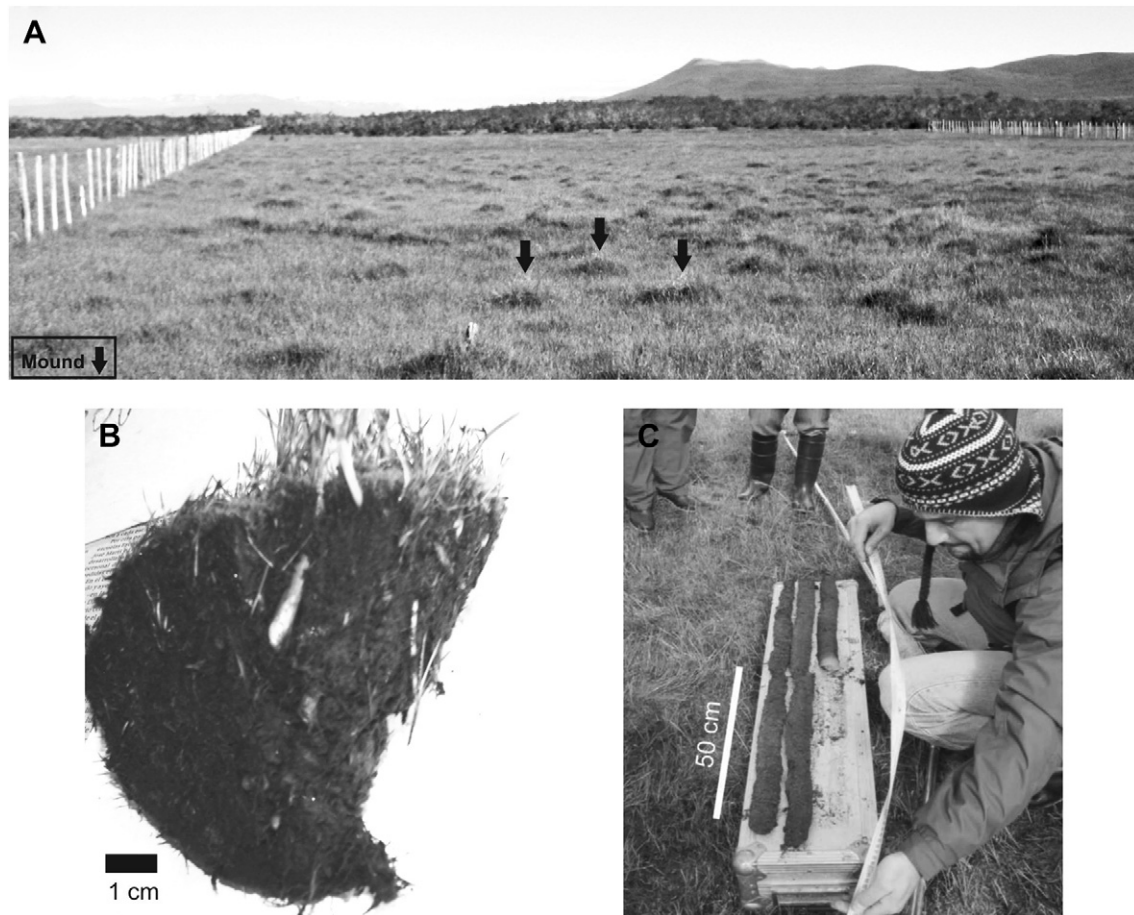


Fig. 2. Río Turbio samples. (A) Panoramic view of mounds and hollows. (B) Top soils collected. (C) Río Turbio profile.

the radiocarbon age of the alluvial sequence and tephra layers. During the next field season (2007), the site was partially flooded by a beaver (*Castor canadensis*; introduced in the island in 1946) dam and sampling could be done only from the first layers, composed by alluvial sediments and fossil peat. The last sampling, completed in 2010, was done 400 m downstream from the original column due continued flooding. Seventeen samples, each of 5 cm in thickness, were collected for phytolith analyses from different strata. Ten continuous samples which included a total depth of 60 cm were collected from the present soil and alluvial silty-clay deposit (ACS2 1–10). Four samples were taken from fossil peat layers: UP2 in the 2007 section and UP 1, MP and LP in the 2010 section. Three samples from alluvial deposits were obtained in 2007 (AL 1–3). Stratigraphy and sample position details are shown in Fig. 3.

Morphological descriptions were made from all collected samples, according to the Soil Survey Staff (1996) standards. Color was determined according to the Munsell Soil Color Chart (1973). Radiocarbon dates were performed on samples of the fossil peat layers at the NSF Facility Lab (University of Arizona, USA). They were later calibrated with Quickcal2007 ver.1.5., CalPal2007 HULU curve, from the Cal Pal Online Radiocarbon Calibration website.

### 3.3. Phytolith extraction from soil and sediments

Due to the differences observed in the material of the samples from both profiles, different methodologies were applied for phytolith extraction. Because the Río Turbio profile is a minerotrophic

mire but the main material component is organic, a calcination technique was herein applied. Between 1 and 2 g from each sample were subject to the same calcination methodology used for plant phytolith extraction (Labouriau, 1983).

Phytoliths from soil samples and the Arroyo Catalanes pedoseimentary column samples were extracted following the technique described by Alvarez et al. (2008) and between 4 and 6 g of each sample were analyzed. Carbonates (with HCl 10%), organic matter (with heat and H<sub>2</sub>O<sub>2</sub> 30%) and clays (with Calgon 0.5% and centrifugation at 1000 rpm for 3 min) were eliminated (Alvarez et al., 2008). The material obtained was mounted on immersion oil and Canada balsam and was then observed with a Zeiss Axiostar Plus microscope and with a scanning electron microscope (JEOL JSM-6460 LV, Japan) at the Universidad Nacional de Mar del Plata, Argentina.

In all cases, a minimum of 400 particles were counted. The relative frequencies of diatoms, Crysophyceae stomatocysts, sponge spicules, phytoliths and other mineral particles were calculated. Phytolith morphologies were classified as it was described in Section 3.1.

## 4. Results

### 4.1. Descriptions of leaf phytolith assemblages

Phytoliths were observed in all but one (Caryophyllaceae) of the 10 plant families studied. The morphotypes appeared in articulated and isolated forms in all species analysed (Fig. 4).

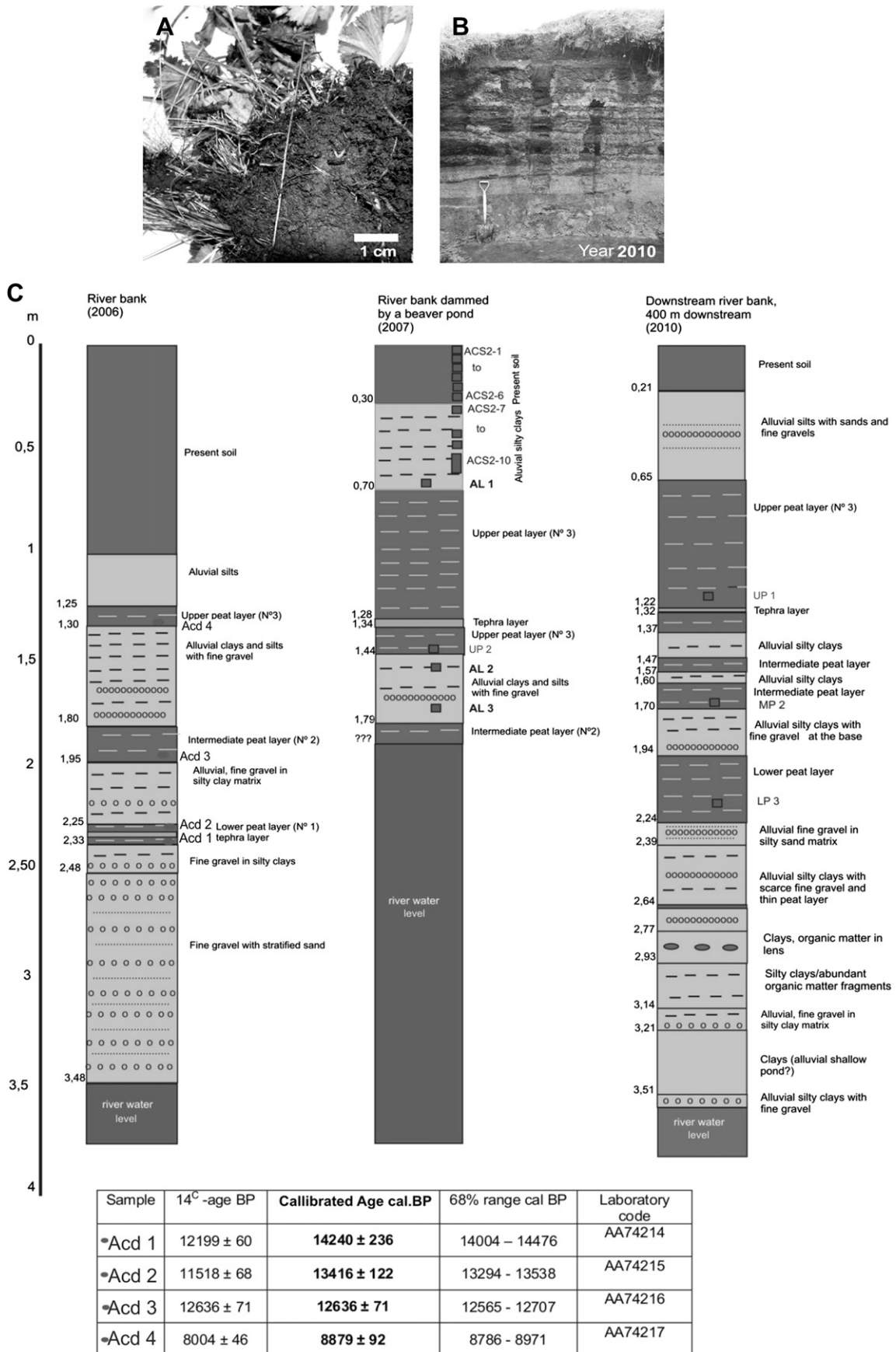
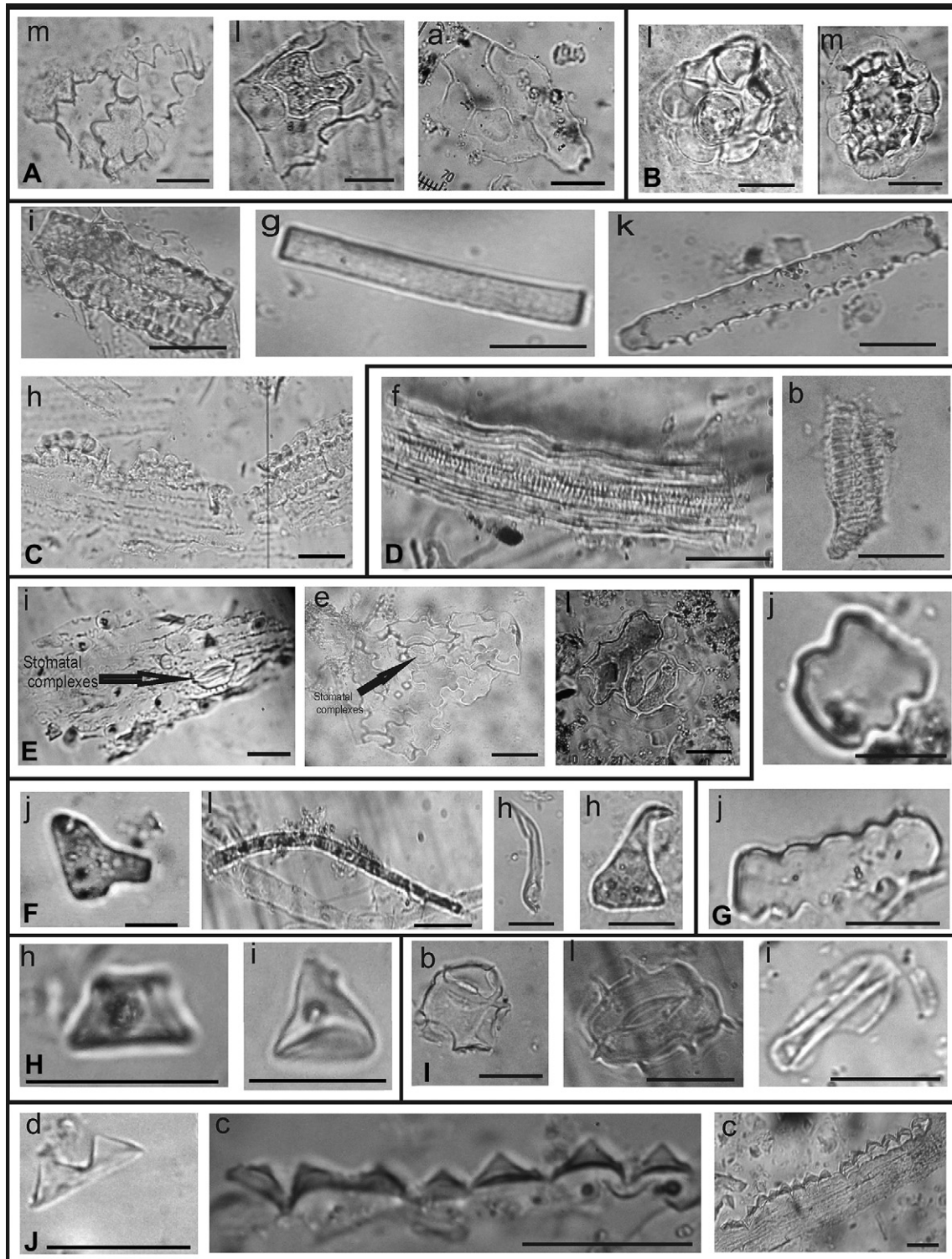


Fig. 3. Arroyo Catalanes samples (rectangular marks). (A) Top soil samples. (B) General view of the 2010 section. (C) pedosedimentary scheme of the sampled columns.

#### 4.1.1. Asteraceae (*Senecio magellanicus*)

Tabular polygonal and tabular lobate phytoliths were the most frequent morphologies in this species, with percentages of 53.8 and 10.4, respectively (Fig. 4A). Both morphologies are derived from

epidermal tissues. Elongate psilate (18.7%) and elongate crenate (1.2%) phytoliths and stomatal complexes (1%) were also observed. The rest of the morphologies (elongate fusiform phytoliths and cylindrical sulcate tracheids, among others) were present with a less than 1% frequency.



**Fig. 4.** Silicophytoliths in selected species. (A) Articulated tabular lobate phytoliths. (B) Silica skeletons composed by orbicular cell arranged in radiated form. (C) Elongate phytoliths. (D) Cylindrical sulcate tracheids. (E) Silica skeletons composed by tabular polygonal and stomatal complexes. (F) Apex of sharp-pointed shapes (hairs, prickles or hooks). (G) Trapeziforms phytoliths. (H) Rondels. (I) Stomatal complexes. (J) Cones. a, *Senecio magellanicus*; b, *Berberis buxifolia*; c, *Carex magellanica*; d, *Carex* sp.; e, *Gunnera magellanica*; f, *Luzula alopecurus*; g, *Deschampsia flexuosa*; h, *Festuca arundinacea*; i, *Festuca magellanica*; j, *Phleum alpinum*; k, *Puccinellia magellanica*; l, *Ranunculus* sp.; m, *Acaena magellanica*. Scale bar = 25  $\mu$ m.



#### 4.1.2. Berberidaceae (*Berberis buxifolia*)

Only three morphotypes of phytoliths were found in the species analyzed: cylindrical sulcate tracheids (63.3%) (Fig. 4D), silica skeletons composed by tabular polygonal epidermal cell and stomatal complexes (23.3%) (Fig. 4I), and tabular polygonal phytoliths (10%).

#### 4.1.3. Cyperaceae (*Carex magellanica* and *Carex* sp.)

Both species produced similar phytolith morphologies and they were observed in articulated as well as in isolated forms. The most abundant phytolith morphology were silica skeletons composed by cones and elongate psilate phytoliths (19.5% in *C. magellanica* and 6.4% in *Carex* sp.) and isolated cones (20% in *C. magellanica* and 47.3% in *Carex* sp.) (Fig. 4C, D), followed by elongate psilate (32% in *C. magellanica*, and 16% in *Carex* sp.), elongate crenate (10.4%) and elongate echinate (6%) phytoliths, these latter found only in *Carex* sp. Other morphologies, such as stomatal complexes, cylindrical sulcate tracheid and elongate fusiform phytoliths, were found in low frequency (less than 5%).

#### 4.1.4. Gunneraceae (*Gunnera magellanica*)

This species was characterized by tabular polygonal epidermal cell phytoliths (55.5%), tabular lobate phytoliths (40.7%) and silica skeletons composed by tabular polygonal and stomatal complexes (1.8%) (Fig. 4E).

#### 4.1.5. Juncaceae (*Luzula alopecurus*)

Phytolith assemblages were mainly represented by silicification of vascular tissue. Particularly, cylindrical sulcate tracheids (57%) (Fig. 4D), elongate psilate phytoliths (16%), elongate fusiform phytoliths, derived from silicification of fibers (12.9%) and silica skeletons composed by elongate fusiform phytoliths and cylindrical sulcate tracheids (12.9%) were observed.

#### 4.1.6. Nothofagaceae (*Nothofagus pumilio*)

Phytolith assemblages were mainly represented by silicification of vascular tissue and stomatal complexes. Silica skeletons composed by cylindrical sulcate tracheids and mesophyll tissue (39.3%), elongate psilate phytoliths (9%), and stomatal complexes (1.3%) were described.

#### 4.1.7. Poaceae

As it was expected, the ten grasses analyzed produced similar phytolith morphologies, since all of them belong to the same Pooideae subfamily. In all species, elongate psilate phytoliths were the most abundant morphology with percentages higher than 25% (Fig. 4C). Elongate sinuate phytolith presented percentages lower than 15% and elongate echinate phytoliths were scarce (less than 3%). Short cells silicifications were observed in all species: rondels were more abundant in *Festuca arundinacea* (27%) and *F. magellanica* (25.8%) (Fig. 4H), whereas trapeziform short cells were more abundant in *F. magellanica* (24.7%). Trapeziform phytoliths (psilate and/or sinuate) were found in all species. Trapeziform sinuate phytoliths were more abundant in four species: *Phleum alpinum* (28.2%) (Fig. 4G), *Deyeuxia poaeoides* (27.3%), *Elymus agropyroides* (26.5%) and *Trisetum spicatum* (23.8%), while trapeziform psilate were common in *E. agropyroides* (11.7%) and *Deschampsia flexuosa* (5.5%). Apex of sharp-pointed shapes (hairs or hooks) and silica skeletons composed of elongate fusiform phytoliths were observed with percentages lower than 15% in most of the species except in *Alopecurus magellanicus* and *Puccinellia magellanica* (values between 15% and 2%), *Deschampsia flexuosa*, *Deschampsia antarctica* and *T. spicatum* (with hairs with percentages higher than 20%) and *Festuca arundinacea* (with hooks with percentages of 15.8) (Fig. 4F). Cylindrical sulcate tracheids and stomatal complexes were observed in scarce percentages in all species.

#### 4.1.8. Ranunculaceae (*Ranunculus* sp.)

Phytolith assemblages were mainly represented by elongate psilate phytoliths (33.5%), tabular lobate phytoliths (20.7%) (Fig. 4A), tabular polygonal (19.6%) and elongate fusiform phytoliths (15.4%). Silica skeletons composed by orbicular cell arranged in radiated form (5.1%) (Fig. 4B), in some cases with a silicified hair in the middle, were also common. Stomatal complexes, hairs and cylindrical sulcate tracheids were scarce (less than 3%).

#### 4.1.9. Rosaceae (*Acaena magellanica* and *Rubus geoides*)

This family was characterized by tabular polygonal (51.7% in *A. magellanica* and 12.6% in *R. geoides*), silica skeletons composed by orbicular cell arranged in radiated form (25.4% in *A. magellanica* and 12.2% in *R. geoides*) (Fig. 4B), tabular lobate phytoliths (11.2% in *A. magellanica* and 2.4% in *R. geoides*) (Fig. 4A), elongate psilate phytoliths (4% in *A. magellanica* and 47% in *R. geoides*), stomatal complexes (0.27% in *A. magellanica* and 6.5% in *R. geoides*) and elongate sinuate phytoliths (5.3% in *A. magellanica* and 0.54% in *R. geoides*). Hairs and cylindrical sulcate tracheids were scarce in both species.

### 4.2. Río Turbio mire

#### 4.2.1. Soil and sediment descriptions

Río Turbio mire soil is composed by organic and saturated horizons, characterized by a dark reddish brown color (5YR 3/3, 2/2) in mound sectors (RTM samples) and very dark grey (5YR 3/1), dark grey (5YR 4/1) and dark brown (7.5YR 3/2) colors in hollows (RTH samples). Roots were very abundant (Fig. 2A, B).

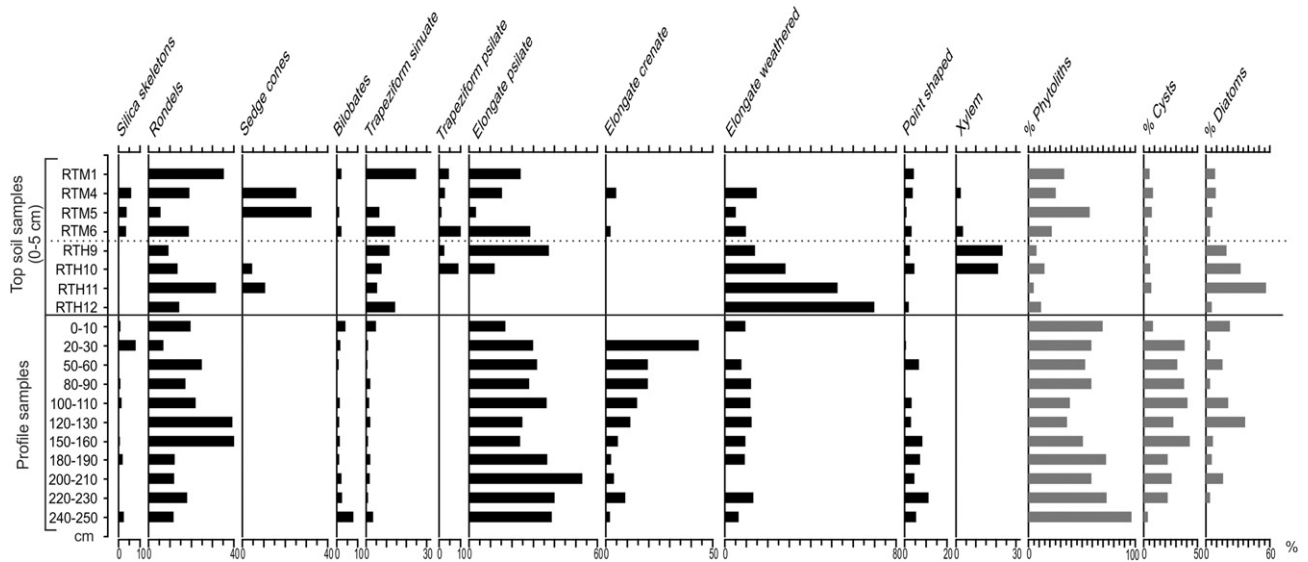
The studied sequence presents 2.5 m of peat interbedded with silty-sandy and clayish-silty beds. All samples had a high percentage of macroscopic rests, a massive structure and colors that vary between dark reddish brown (5YR 3/3, 2/2) to dark (5YR 2/1, 10YR 2/1) (Fig. 2C).

#### 4.2.2. Phytolith description

4.2.2.1. *Phytolith assemblages of modern soil.* The 0–5 cm of analyzed top soil showed some differences between mounds and hollows on the relative frequencies of phytoliths in relation to other particles, diatoms and Crysophyceae stomatocysts. Phytoliths were scarcer in hollows (4–11%) than in mounds (21–57%), while diatoms and rests of diatoms were more abundant in hollows (5.5–56.3%) than in mounds (3.8–9.2%) (Fig. 5).

The analyses of the phytolith assemblages showed that rondels, which are assigned to pooid grasses, and elongate phytoliths, which are derived from grasses and many dicots, were the main morphologies found both in hollows (53–84%) and mounds (13–61%) (Fig. 6A). However, some differences can be found between them. Mounds had a greater diversity of elongates (psilate, crenate and echinate), whereas hollows had a higher percentage of weathered elongates. Bilobates and silica skeletons composed by cones sedges, cylindrical sulcate tracheids or elongate psilate phytoliths were only observed in mounds. Grass phytoliths are also represented in all samples by trapeziform crenate phytoliths, which are mainly produced by pooid species of the area such as *D. poaeoides* and *Trisetum spicatum*. In four samples sedge cones were observed in rather high frequency; these morphologies are produced by Cyperaceae, such as *C. magellanica* and *Carex* sp. Lastly, trapeziform phytoliths, derived from grasses, pointed shaped (which included hooks, prickles and hairs, mostly produced by grasses) and xylem tissues were observed in many samples of both sectors.

4.2.2.2. *Phytolith assemblages of the profile.* In the profile samples the relative frequencies of phytoliths in relation to diatoms, Crysophyceae stomatocysts and sponge spicules were higher than



**Fig. 5.** Percentage of the most abundant phytolith morphologies and total biogenic silica (phytoliths, diatoms and cysts) in present soils (RTM: mound sectors; RTH: hollow sectors) and profile samples from the Río Turbio mire. (Percentage of phytoliths, diatoms and cysts in top soil samples are relative to total particles).

50%, except for samples of the levels 1–1.1 m and 1.2–1.3 m, where diatoms and Crysophyceae stomatocysts were dominant (Figs. 5 and 6B).

As observed in top soil samples, rondels and elongates were the main morphologies observed along the profile. However, two groups of samples can be differentiated: levels 0–10 cm, 180–190 cm, 200–210 cm, 240–250 cm, where rondels and elongates summed between 46 and 68% of total morphologies; and levels between 20–30 and 150–160 cm, and 220–230 cm, where these morphologies represented between 78 and 88% of total phytoliths. Also, in this last group, a higher diversity of elongates (psilate, crenate and echinate) was observed. It is interesting the presence of silica skeletons composed by elongate phytoliths in many samples. Other morphologies produced by grasses, besides rondels, were observed along the profile. Trapeziform phytoliths and bilobates, which frequencies were generally lower than the first one, were described in almost all samples. The frequencies of the grass phytoliths were rather low along the entire profile, in the 240–250 cm level a higher percentage was detected, probably indicating some change in surrounding vegetation with an enrichment of grass species. Finally, the presence of prickles and weathered prickles increased with depth. As grasses are the main producer of these morphologies, this pattern could be indicating a higher abundance of Poaceae in the area.

### 4.3. Arroyo Catalanes site

#### 4.3.1. Soils and sediment descriptions

Soils from Arroyo Catalanes were characterized by organic and saturated horizons, variability in color properties, and presence of roots (Table 2). The sequence analyzed included the present soil, alluvial deposits and fossil peat layers (Fig. 3B, C). The morphological and color properties of each sample are described in Table 2.

The alluvial sequence allows inferring that lateral fluvial dynamics occurred during the Early Holocene, between 14.2–8.0 <sup>14</sup>C ka BP, generating secondary or abandoned, low depth stream beds, ponding shallow waters which were colonized by peat-producer vegetation. Biogenic accumulation would have been interrupted several times both due to the deposition of volcanic ash and due to the formation of pond environments fed by surficial runoff discharge.

#### 4.3.2. Phytolith description

**4.3.2.1. Phytolith assemblages of present soil.** The analyzed top soil (0–5 cm) showed higher relative frequencies of phytoliths (49–71%) in relation to other particles (22–44%), diatoms (1–5%) and Crysophyceae stomatocysts (0.5–15%) in all samples but one (AC3 sample). In this case the percentages were 32.82 (phytoliths), 51.19 (other particles), 3.06 (diatoms) and 12.93 (Crysophyceae stomatocysts) (Fig. 7).

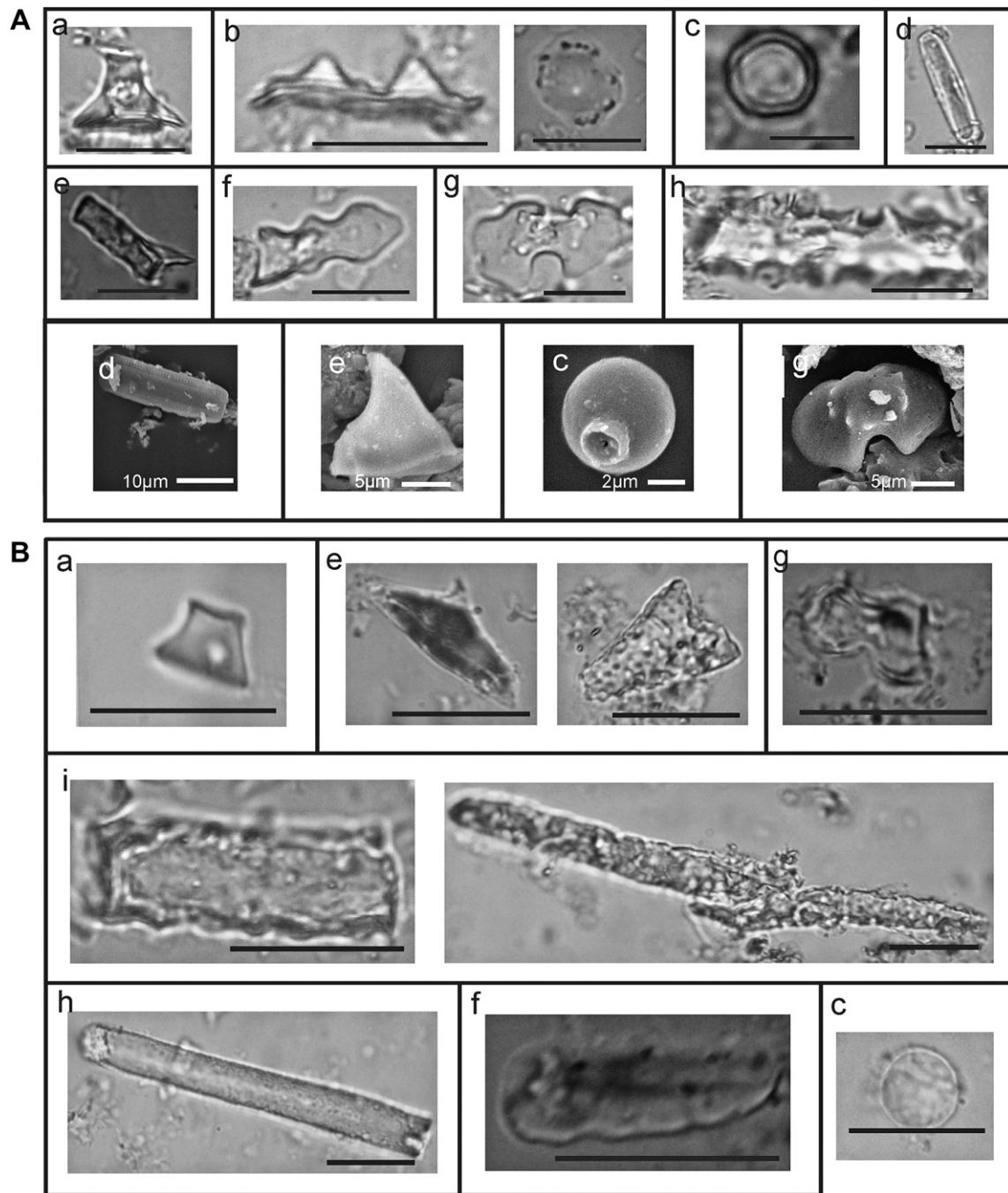
The dominant phytolith morphotypes were isolated phytoliths such as rondels (31–70%), elongate phytoliths (17–28%), trapeziform psilate (11–23%) and trapeziform sinuate/polylobate phytoliths (8–28%). Other phytoliths produced by grasses were also observed, such as bilobates and point shaped. In some samples the presence of sedges were evidenced by a high percentage of cones (samples AC3 and AC11) (Figs. 7 and 8A).

**4.3.2.2. Phytolith assemblages of profile samples.** Phytolith percentages of the first 60 cm of the profile analyzed decreased from top (35.3%) to bottom (4.6%), with intermediate samples with lower values (1.5 and 1.3%, at depths 40–45 cm and 45–50 cm, respectively). Samples from alluvial deposits (AL 1–3) showed low values of phytolith content (between 4.9 and 5.2%), whereas samples from peat levels (UP, MP, LP) had a higher content (between 23.8 and 72.6%), except for inferior peat level, where no phytoliths were observed. The presence of diatoms and Crysophyceae stomatocysts were very low along the profile (<4%) (Figs. 7 and 8B).

The main morphologies observed along the first 60 cm of the profile, which included the present soil and alluvial deposits, were elongates (psilate and crenate) (18.5–71.4%), rondels (9.3–38.3%) and trapeziform crenate phytoliths (20–44%) (Fig. 8B). It is interesting the inverse relationship in the percentages of rondels and elongate psilate phytoliths that was observed along the profile. In samples where rondels increased, elongate phytoliths decreased, and vice-versa. The percentages of trapeziform sinuate phytoliths ranged between 20 and 28% along all the samples, except for the sample from 30 to 35 cm, where the value reached 44%. It is also interesting the presence of pointed shaped phytoliths (which includes hooks, prickles and hairs, mostly derived from grasses) along the profile.

The Upper peat level (UP1) showed that elongate psilate phytoliths (38%), rondels (33%) and trapeziform crenate phytoliths





**Fig. 6.** Silicophytoliths in Rio Turbio mire. (A) Phytoliths from modern soil. (B) Phytoliths from profile. (a) Rondels. (b) Cones. (c) Cryosphyceae stomatocysts. (d) Diatom. (e) Point-shaped. (f) Trapeziform phytoliths. (g) Bilobate. (h) Elongate phytoliths. (i) Weathered elongate phytoliths. Scale bar = 25 μm (except for MEB photographs).

(19%) were the most abundant morphologies. Elongate crenate, elongate weathered and pointed shaped phytoliths were found with values lower than 5%. Instead, the other sample corresponding to the same peat level (UP2) was characterized by elongates (67%), derived from grasses and/or dicots, and pointed shaped phytoliths (prickles, hooks and hairs; 15%), mostly derived from grasses. In the intermediate peat level (MP) the most abundant phytolith were elongate psilate (77%); the rest of the morphologies (rondels, trapeziform crenate phytoliths, elongate weathered and pointed shaped) were found with values lower than 10%.

Other grass morphologies, such as trapeziform (25.5% in AL1, 7.54% in AL2 and 4.31% in AL3) and rondels (14% in AL1 and AL2, and

4.31% in AL3) were observed in samples from alluvial deposits, where total percentage of phytoliths was very low (between 4.9 and 5.2%).

## 5. Discussion

### 5.1. Phytoliths in plants

All except one of the ten families analyzed produce silicophytoliths, indicating an important input of phytoliths from local and present vegetation into present soils.

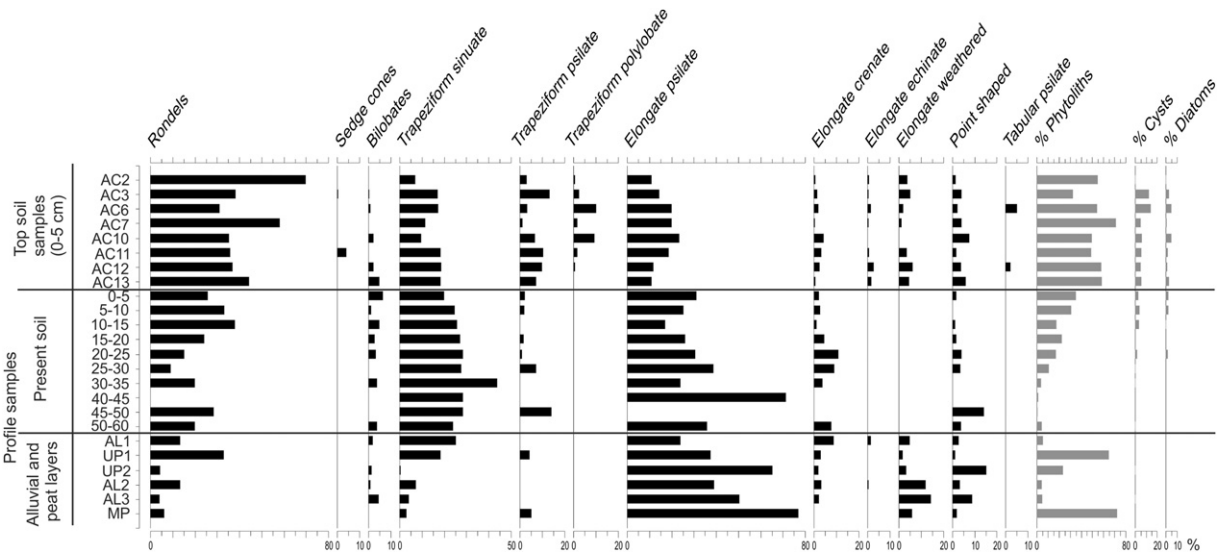
**Table 2**

Morphological description of samples from the Arroyo Catalanes profile. NP: no plastic; NA: no adhesive; SP: slightly plastic; SA: slightly adhesive. The number of X indicates the relative abundance of roots.

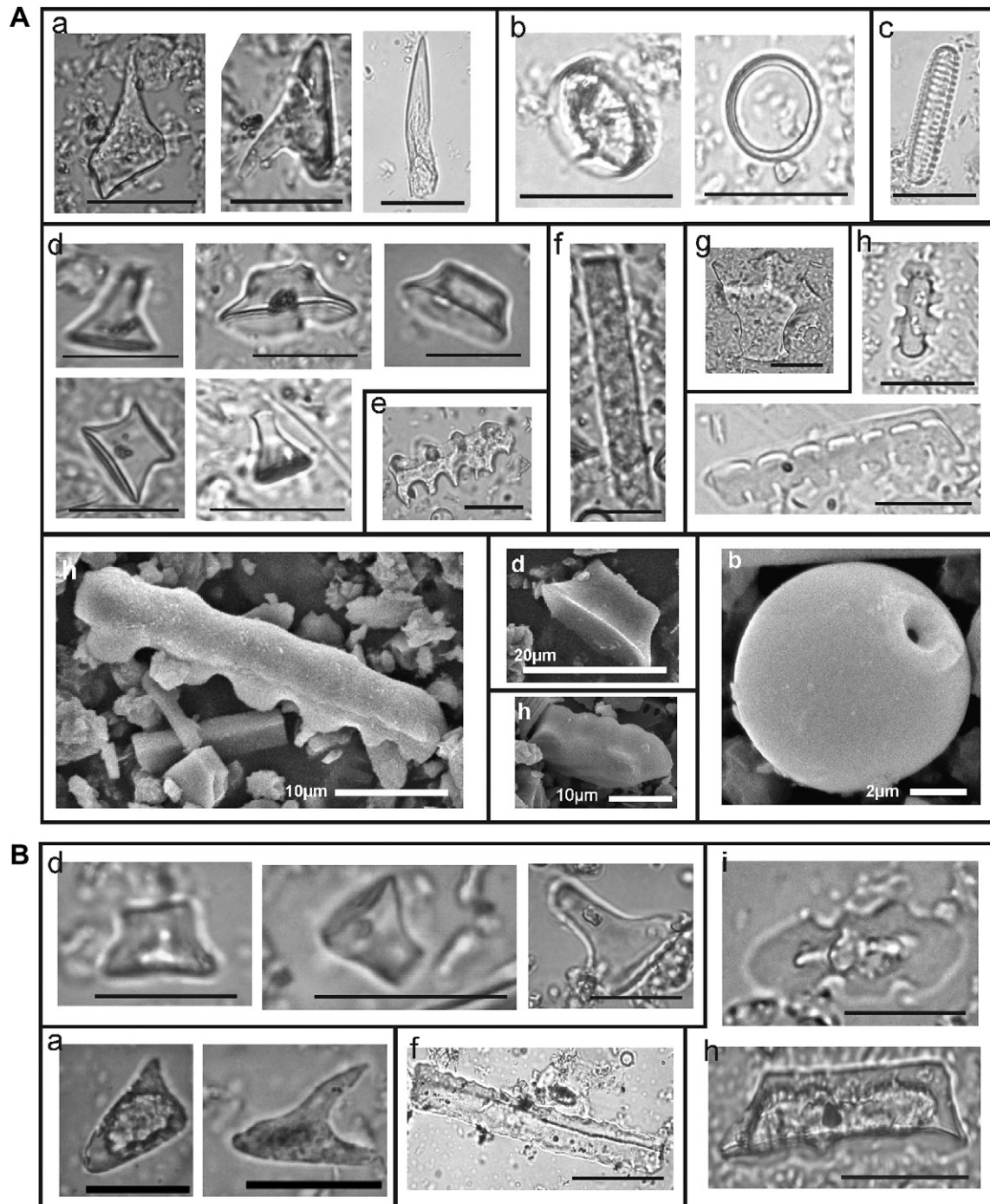
Sample depth (cm) or code	Color		Texture	Structure	Consistency	Roots
	Dry	Wet				
0–5	7.5YR 5/2	7.5YR 3/2	Siltyclay	Granular Fine Weak	NP-NA	XXXXX
5–10	10YR 5/3	10YR 3/2	Siltyclay	Granular Fine Weak	NP-NA	XXXXX
10–15	10YR 5/3	10YR 3/3	Siltyclay	Granular Fine Weak	SP-SA	XXXXX
15–20	10YR 6/4	10YR 4/4	Siltyclay	Granular Fine/Blocky Subangular Fine Moderate	SP-SA	XXX
20–25	10YR 5/4	10YR 4/4	Siltyclay	Blocky Thick Strong	SP-SA	X
25–30	10YR 5/3	10YR 3/3	Siltyclay	Blocky Thick Strong	SP-SA	–
30–35	10YR 5/2	10YR 4/2	Siltyclay	Blocky Thick Moderate	SP-SA	–
40–45	10YR 6/4	10YR 4/3	Siltyclay	Blocky Thick Moderate	SP-SA	–
45–50	10YR 5/4	10YR 3/3	Siltyclay	Massive	–	–
50–60	10YR 5/2	10YR 4/1	Siltyclay	Massive	–	–
AL1	2.5Y 6/2	5Y 5/2	Siltyclay	Massive	–	–
UP1	5YR 2/1	5YR 2/2	Siltyclay	Massive	–	–
UP2	7.5YR 3/2	10YR 2/2	Siltyclay	Massive	–	–
AL2	2.5Y 7/0	5Y 3/2	Siltyclay	Massive	–	–
AL3	5Y 7/1	5Y 3/2	Siltyclay	Massive	–	–
MP	10YR 2/1	5YR 2/1	Siltyclay	Massive	–	–
LP	5YR 3/2	5YR 2/1	Siltyclay	Massive	–	–

The descriptions of silicophytoliths in the studied taxa coincide with previous work in species of the same families from other regions, especially in Asteraceae, Cyperaceae, Juncaceae, Poaceae, Ranunculaceae and Rosaceae. In Asteraceae, silicification is variable and it has been thoroughly studied (Piperno, 1988; Pearsall, 2000; Wallis, 2003; Thorn, 2004; Fernández Honaine et al., 2006; Morris et al., 2009; Borrelli et al., 2011). In most of these studies, the authors found morphologies derived from epidermal tissues such as tabular polygonal and tabular lobate phytoliths which are consistent with the phytolith assemblages described for *Senecio magellanicus* in this work. Borrelli et al. (2011) also found abundant phytoliths derived from epidermal cells (such as tabular lobate and polygonal phytoliths) in *Ranunculus* sp. (Ranunculaceae); however, they did

not describe the silica skeletons composed by orbicular cell arranged in radiated form observed in the Ranunculaceae species during the present study. In the Rosaceae family, Thorn (2004) reported silicified hairs bases, subsidiary epidermal cell and solid hairs in *Acaena minor* var. *antarctica* and in *Acaena anserinifolia*, which are consistent with the silica skeletons composed by orbicular cell arranged in radiated form found in *Ranunculus* sp. and *A. magellanica* and *R. geoides* too. The results about silicophytolith production in Poaceae family are similar to those observed by other authors in the Pooide subfamily (Brown, 1984; Mulholland, 1989; Twiss, 1992; Fernández Honaine et al., 2006). The dominant morphotypes found in the species of this study were rondels, elongate psilate and elongate sinuate phytoliths, all characteristic of the Pooideae subfamily.



**Fig. 7.** Percentage of the most abundant phytolith morphologies and total biogenic silica (phytoliths, diatoms and cysts) in present soils and profile samples from the Arroyo Catalanes site.



**Fig. 8.** Silicophytoliths in Arroyo Catalanes site. (A) Phytoliths from modern soils. (B) Phytoliths from profile. (a) Apex of sharp-pointed shapes (hairs, prickles or hooks). (b) Cryosphyceae stomatocysts (c) Diatoms. (d) Rondels. (e) Elongate echinate phytoliths. (f) Elongate psilate and crenate phytoliths. (g) Tabular polygonal. (h). Trapeziforms phytoliths. (i) Polylobate. Scale bar = 25 μm (except for MEB photographs).

Phytolith assemblages in Cyperaceae were characterized by the typical 'cones', morphologies that have been largely described for this family by other authors (Metcalf, 1971; Ollendorf, 1992; Kealhofer and Piperno, 1998; Wallis, 2003; Fernández Honain et al., 2009b). Although previous studies in Juncaceae concluded that the species analyzed were non-producers (Pearsall, 2000; Wallis, 2003; Morris et al., 2009), in this study the phytolith assemblage of *L. alopecurus* was mainly represented by silicifications of vascular tissue. These results, however, coincide with the findings made by Borrelli et al. (2011) in *Juncus* sp. collected in the Pampean

region of Argentina. Likewise, Hart (2007) reported the presence of Caryophyllaceae type phytoliths in vascular tissue in the leaf of *Silene inflata* in England, whereas in the current study no phytoliths were observed in those specimens examined (*Cerastium arvense* and *Colobanthus quitensis*) from the Río Turbio mire. Differences between studies could be the consequence of differences in maturity stage of individuals or differences in the environmental conditions of sites where specimens were collected (Jones and Handreck, 1967; Motomura et al., 2004), factors that might be affecting the abundance and production of phytoliths.



The results obtained for Berberidaceae and Nothofagaceae can be considered the first descriptions of phytoliths for these families, as no previous investigations are available. Tabular polygonal and tabular lobate phytoliths, both derived from epidermal tissue, and stomatal complexes were the main morphologies found in these three families. However, due to the multiplicity and redundancy of these phytolith morphologies (they can be found in many others dicotyledons), they do not have a high taxonomic relevance. The only taxonomic usefulness could be the identification of a dicotyledon species.

### 5.2. Río Turbio mire analyses

The phytolith assemblages of top soils described for mounds and hollows mostly coincide with the phytoliths produced by local vegetation, which was mainly represented by grasses and sedges. The exception was the phytoliths produced by the Asteraceae or Gunneraceae families, represented by tabular lobate and tabular psilate phytoliths. These morphologies, due to their low silicification degree, could be probably more susceptible to degradation and prevent their presence in soils, as it was mentioned by other authors (Thorn, 2004; Fernández Honaine et al., 2009a).

Some quantitative and qualitative differences in phytolith content between mounds and hollows were observed, probably due to the micro-topographic characteristic of both sectors, which in turn determine the taphonomic processes. For instance, the presence of silica skeletons in mounds can be associated with a higher stability of these sectors, since these morphologies are quickly fragmented once they are deposited (Osterrieth et al., 2002; Osterrieth and Fernández Honaine, 2007). Instead, the low percentage of phytoliths, the absence of silica skeletons and the high percentage of weathered elongate phytoliths observed in hollows, could be indicating a higher rate of degradation and/or dissolution of phytoliths, probably due to the water movement of this sector.

As observed in present soil phytolith assemblages, rondels and elongates were the dominant morphotypes found along the profile. Elongate phytoliths are derived both from dicotyledons and monocotyledons, while rondels are produced by Poaceae, mainly Pooideae and Stipoideae subfamilies. These results may indicate the presence of Poaceae along the development of this mire, in particular, species belonging to Pooideae and Stipoideae subfamilies, the same taxa represented actually in the area (Twiss, 1992; Fredlund and Tieszen, 1994; Fernández Honaine et al., 2006). Other grass phytoliths, such as bilobates and trapeziform, support this conclusion. Even though rondels are dominant along the samples, the last 70 cm (180–250 cm) of depth showed some change in their percentages, in relation with the other grass phytoliths, such as bilobates. This slightly difference may indicate some change of grass subfamilies from Pooideae (0–180 cm) to Panicoideae (180–250), since bilobates are mainly produced by this last taxa. Finally, although Cyperaceae species are an important component of this mire, and typical “cones” were observed in modern soils, no sedge phytoliths were described along the profile. As in the case of Asteraceae phytoliths, fragmentation processes could be acting on these morphologies, preventing their preservation along the column. Borba-Roschel et al. (2006) found similar results in tropical mires in Brazil.

### 5.3. Arroyo Catalanes site analysis

The percentages of phytoliths reached 50% in all top soil samples, except for sample AC3. This result could be related to the plant species that are developed on this soil sample, since in this sector only *Polytrichum juniperinum* (Bryophyte) was present, a species whose phytolith production is scarce (Benvenuto et al.,

2009). The phytolith assemblages of the samples of top soils of the Arroyo Catalanes site mostly coincide with the phytolith assemblages of the main plant species of the area. In particular, rondels and trapeziform phytoliths, the most abundant morphotypes found in soil samples, are derived from silicifications of short cells of epidermis of Pooid grasses (Metcalf, 1960; Twiss, 1992), the grass subfamily which is dominant in local vegetation. Elongates and point shaped are derived both from grasses and dicots families, and they are present in almost all the species analyzed in this study.

In general, the phytolith morphotypes found along the profile, including alluvial deposits and peat layers coincided with the phytolith morphotypes found at local vegetation and at top soils samples. Exceptions are the cones phytoliths, produced by sedges, and tabular phytoliths, produced by Asteraceae and other dicots. As at the Río Turbio site, several fragmentation processes could be acting preferentially on these morphotypes, which could be considered as more fragile than grass phytoliths (Thorn, 2004; Osterrieth et al., 2009; Fernández Honaine et al., 2009a).

The decrease of the relative frequencies of total phytoliths with depth, in the first 60 cm analyzed, is a common result found in soil profiles from other regions, such as the Pampean (Osterrieth, 2000, 2006; Borrelli et al., 2008). Phytolith content in alluvial deposits (AL1 to 3) is low, compared with peat layers, where phytolith content reached 70%. These results are in close relationship with phytolith input of the plant species developed in peatlands. The only exception was the lower peat (LP) where no phytoliths were found. The absence of phytoliths in this last sample could be associated to the plant that originated the peat level. For example, if this sector was derived from a *Sphagnum* peat, a species that almost does not produce any phytoliths (Benvenuto et al., 2009), it is expected that no phytoliths would be found. Also, probably some environmental conditions, such as higher degradation processes, could be the cause of the absence of these biomineralizations.

Phytolith assemblages described in upper peat levels (UP1 and UP2) differed not only in phytolith content but also in the relative frequencies of several morphologies. This could indicate differences in the development of the peat, either the plant species and/or the micro-relief of the sector analyzed, which could be affecting the preservation of some morphotypes. As UP2 is at the base of the upper peat level and very close to the limit with the alluvial level, it can be considered as a sector of initial stage of the peat development, where the input of phytoliths could be consider recently and therefore, low. Instead, UP1 represents a sector where the development of the peat is higher, and also the phytolith input. Finally, UP1 is dominated by Pooid phytoliths (rondels and trapeziforms), whereas in UP2 elongate phytoliths (derived from dicotyledons as well as grasses) dominated the assemblage. This result could account for a difference in species peat component between upper peat sectors (Pooid grasses in UP1 and dycotyledons/monocotyledons in UP2). Intermediate peat (MP) phytolith assemblage resemble more to UP2 assemblage, with higher percentages in elongate phytoliths, indicating a similar plant composition, but probably a higher abundance of plants (since the percentage of total phytoliths reached 72%).

Besides the quantitative differences in total phytolith content detailed above and some differences in the percentages of specific morphotypes, the phytoliths found in all samples (rondels and trapeziforms) support the presence of grasses during the development of these environments, especially Pooid grasses (Twiss, 1992).

## 6. Conclusions

This paper is one of the first contributions to (1) the comprehension of the phytolith production, deposition and incorporation processes in modern soils/peats from cold-temperate, subantarctic

peatlands, (2) the understanding of the development of the plant paleocommunities of Tierra del Fuego, Argentina, and (3) the interpretation of fossil phytolith records in this region.

Nine from ten families analyzed produced phytoliths, indicating an important input of phytoliths from local and present vegetation into present soils. Phytolith assemblages were first described for Berberidaceae and Nothofagaceae, and some species of Asteraceae, Cyperaceae, Juncaceae, Poaceae, Ranunculaceae and Rosaceae.

Phytolith assemblages of top soil analyzed at both sites (the Río Turbio mire and the Arroyo Catalanes site) coincide with the phytoliths produced by local vegetation, except for the tabular lobate and tabular psilate morphologies produced by Asteraceae, Gunneraceae, Berberidaceae, Ranunculaceae and Rosaceae, which were hardly found in soil samples. These results can be explained through qualitative or quantitative differences in silicification process in plant species, or dissolution or physical fragmentation of phytoliths once they are deposited on soils. The high percentage of grass phytoliths in almost all samples, including those where grasses were not the dominant species, could be indicating an overrepresentation of this family. These results can be explained due to a greater production and higher resistance to degradation of grass phytoliths.

Although there was a low diversity of phytolith morphologies along the two profiles analyzed, either due to a poor phytolith production of the species or to a dissolution/fragmentation processes, phytolith assemblages showed that grass communities were present along the development of these environments. Within Poaceae phytoliths the morphologies produced by Pooideae subfamily were the dominant component of the assemblages, reflecting the abundance of this plant group over other grass taxa.

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