



Heloisa Helena Gomes Coe
Margarita Osterrieth
Editors

Synthesis of Some Phytolith Studies in South America (Brazil and Argentina)

Botanical Research and Practices

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BOTANICAL RESEARCH AND PRACTICES

**SYNTHESIS OF SOME PHYTOLITH
STUDIES IN SOUTH AMERICA
(BRAZIL AND ARGENTINA)**

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**HELOISA HELENA GOMES COE
AND
MARGARITA OSTERRIETH
EDITORS**



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Chapter 6

**SILICOPHYTOLITH REFERENCE
COLLECTIONS OF DIFFERENT PLANT
COMMUNITIES FROM ARGENTINA**

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ABSTRACT

The production of silicophytoliths, plant amorphous silica biomineralizations, has a close relation with phylogeny, although environmental and developmental conditions also affect the silicification process. In this sense, different plant communities, depending on their specific composition, will produce different silicophytoliths, both in

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qualitative and quantitative terms. The description of the most abundant and characteristic types of silicophytoliths of a particular plant community is an essential tool for botanical studies and, especially, for the interpretation of the fossil phytolith record, and hence to paleobotanical, archaeological and pedological studies. In the present chapter, the reference collection of the silicophytolith production of species belonging to different plant communities from Argentina, is presented. In particular, the silicophytoliths produced in species developed in natural grasslands (*Paspalum quadrifarium* and “flechillar” communities), grasslands affected by agricultural practices and wetlands from Pampean region, and peatland and grasslands species from Tierra del Fuego are described and compared. The main families represented in these communities are Poaceae, Cyperaceae, Asteraceae and Juncaceae, which greatly differ in their silicophytolith production. Since different subfamilies within Poaceae family characterized the studied grasslands, and silicophytolith production also differs between subfamilies, the grass communities could be differentiated through their phytolith assemblages. In general, silicophytolith production involves the silicification of epidermis, however parenchymatous, sclerenchymatic and xylematic tissues are frequently found silicified.

INTRODUCTION

Numerous studies have related the morphologies of silicophytoliths with plant systematics (Twiss et al., 1969; Brown, 1984; Rapp and Mulholland, 1992; Fernández Honaine et al., 2006). While environmental conditions and plant phenology affect the silicification process, the systematic position of a taxon has more influence on the silicophytolith production of a species (Hodson et al., 2005).

The main silicophytolith producer is Poaceae family, which is also the most studied taxon worldwide (Piperno, 2006). Other monocotyledons such as Cyperaceae and Arecaceae produce abundant silicophytoliths, and their morphologies notably differ from the ones produced by grasses (Tomlinson, 1961; Ollendorf, 1992; Piperno, 2006; Fernández Honaine et al., 2009). Among dicotyledons, many families produce silicophytoliths in diverse proportions and morphologies clearly distinct. The list of families includes species of Asteraceae, Fabaceae, Magnoliaceae, Moraceae, Ulmaceae, Urticaceae, among others (Rapp and Mulholland, 1992; Pearsall, 2000; Wallis,

2003; Piperno, 2006). Gymnosperms also produce silicophytoliths and different morphologies have been described in Araucariaceae, Cupressaceae, Pinaceae, Taxodiaceae and Taxaceae (Carnelli et al., 2004; Piperno, 2006). Finally, silicophytoliths have been observed and described in Pterydophyta (Sundue, 2009) and more recently, in mosses (Benvenuto et al., 2013a).

The first studies that describe these amorphous silica biomineralizations were mainly anatomical works (e.g. Metcalfe, 1960; Ellis, 1979). At present, due to increasing application as indicators of past plant communities, silicophytolith studies in plant species have risen. The description of the most abundant and characteristic morphologies of silicophytoliths of a particular plant community is an essential tool for botanical studies and, especially, for the interpretation of the fossil phytolith record, and hence to paleobotanical, archaeological and pedological studies.

In Argentina, the silicophytolith assemblages of some groups of plant species have been described, principally as belonging to Poaceae family. The studies involve the analysis of silicophytolith production in *Stipa* spp., *Panicum* spp. and *Paspalum* spp. from Entre Ríos province (Zucol 1996, 1998, 2000, 2001), in *Chusquea ramossissima* (Montti et al., 2009), in grassland species from Central Argentina (Gallego and Distel, 2004), in Pampean grasses (Fernández Honaine et al., 2006), in *Celtis tala* (Fernández Honaine et al., 2005), in Cyperaceae and aquatic species (Fernández Honaine et al., 2009, Borrelli et al., 2011), in species of Arecaceae and other monocotyledons related (Patterer, 2013; Benvenuto et al., data not published) and in grasses and peatland species from Tierra del Fuego (Benvenuto et al., 2013 a, b).

In the present chapter, the reference collection of the silicophytolith production of the most representative species belonging to different plant communities from Argentina, is presented and compared. In particular, the silicophytoliths produced in species developed in natural grasslands (*Paspalum quadrifarium* and “flechillar” communities), grasslands affected by agricultural practices and wetlands from Pampean Region, and peatland and grasslands species from Tierra del Fuego are described and compared through multivariate analyses. The reference collection presented in this chapter represents a useful tool for the interpretation of the fossil phytolith record of the region.

METHODOLOGY

1. Study Area and Plant Communities Characterization

The study area involves two phytogeographic regions from Argentina: Pampean Region (*sensu* Cabrera, 1971) or Río de la Plata grasslands (*sensu* Soriano et al., 1992) and the Sub-Antarctic phytogeographic province, Magellanic District (Cabrera, 1971) in the central region of Tierra del Fuego.

In Pampean Region (Southeastern Buenos Aires province), two natural grasslands (*Paspalum quadrifarium* and “flechillar” grasslands) and natural wetlands were analyzed. In Tierra del Fuego, a minerotrophic mire and a grassland associated to peatland were described (Figure 1).

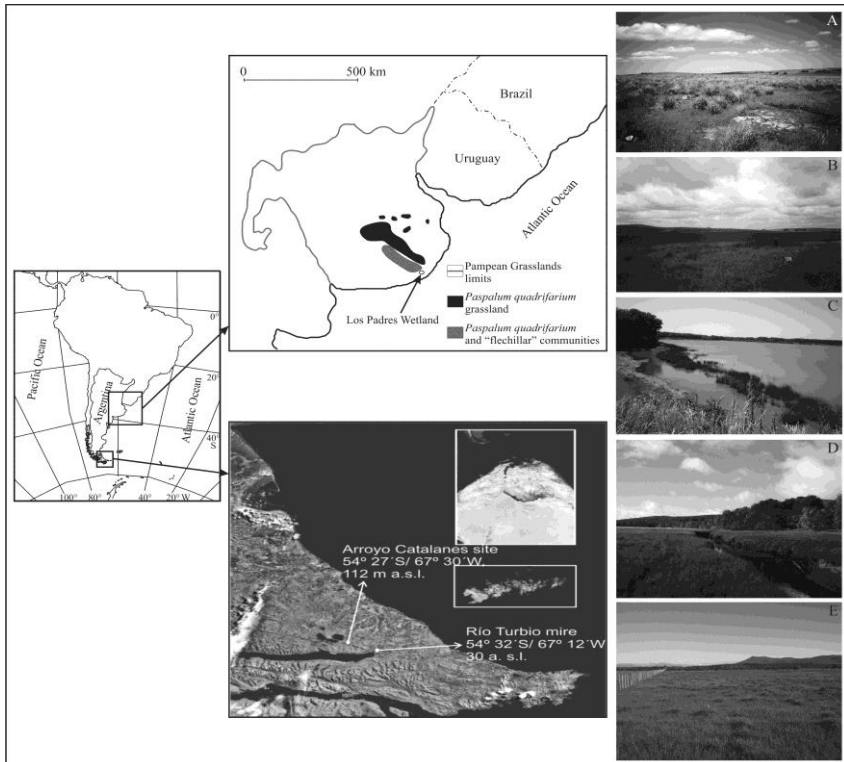


Figure 1. Location of the plant communities studied and photographs of the environment: A – B. *Paspalum quadrifarium* grassland mixed with “flechillar” community. C. Los Padres Wetland. D. Grassland associated to peatland, Arroyo Catalanes Site. E. Minerotrophic mire, Río Turbio Mire.

Pampean Region - Río De La Plata Grassland

This region can be considered as a vast and continuous plain with rocky outcrops hills with a maximum elevation of 500 m.a.s.l. in the south-central area of the region (Ventania and Tandilia systems) (Soriano et al., 1992).

In particular, the plant communities studied in this chapter correspond to the southern Pampa, which includes Tandilia system as well as their pediments and coastal plains (Soriano et al., 1992). It is a mesothermic subhumid–humid area with null or little water deficiency and an annual rainfall of about 800 mm/y (Burgos and Vidal, 1951).

The mean monthly temperatures for the warmest and coldest month are 23 and 13 °C, respectively (Soriano et al., 1992).

Three geological units are differentiated: crystalline basement (metamorphic and pegmatitic rocks of pre-Cambrian age), a sedimentary layer of quartzites from Paleozoic age and a Quaternary loess layer. In this area three geomorphological units are developed: Ranges, Perirange eolian hills and fluvioeolian plain (Martinez, 2001). The Ranges unit consists of a group of table-like hills of flat summit. The Perirange eolian fringe comprises a relief of morphologically complex hills, with relative heights of up to 30 m and concave–convex profiles with intermediate straight patches and slopes between 6% and 8% (Osterrieth et al., 1998). It originated from processes of primary eolian accumulation, modified later by superficial wash (Osterrieth and Martínez, 1993). Soils have developed from the Quaternary loess that covers the Paleozoic quartzites and the most dominant are Typical Hapludolls and Argiudolls (Osterrieth and Cionchi, 1985; INTA, 1989; 1991a).

In this unit, some permanent waterbodies are also developed. The Pampean lagoons are very shallow plain lakes, without thermal stratification and highly fluctuating in salinity and water renewal time. They are eutrophic and undergo environmental stress due to the nutrient loading from agriculture activities and urbanization (Cionchi et al., 1982). The soils developed on flood plains are poorly drained and are directly affected by seasonal variations in water level of wetland (Soil Survey Staff, 1999).

The *Paspalum quadrifarium* grassland is a native monospecific community that is mixed with the “flechillar”, another typical and native Pampean grassland. The most common “flechillar” species are *Bothriochloa laguroides*, *Briza* spp., *Bromus* spp., *Stipa* spp., *Piptochaetium* spp., *Bromus* spp., among others. The distribution of both grasslands in the southern Pampas is largely restricted to the foothills of the Tandilia System, where the poorly developed soil has prevented its replacement by crops (Frangi, 1975; Herrera

and Laterra, 2011). However, some areas of the region are grazed, or subject to winter burnings to increase forage quality (Laterra et al., 1998).

As a consequence, the floristic characteristics have been modified, with a noticeable increase in the number of Asteraceae species at the expense of native Poaceae species.

At burned sites, there is a predominance of *Achillea* sp., whereas at grazed sites the main species found are *Carduus acanthoides*, *Cirsium vulgare* and *Taraxacum officinale*, accompanied by grasses such as *Dactylis glomerata* (Herrera, 2007; Herrera and Laterra, 2011).

Species from the typical Pampean wetlands include Cyperaceae species such as *Schoenoplectus californicus*, *Cyperus* spp., *Eleocharis* spp. and *Carex* spp. Other common hydrophytes found in these communities are *Typha latifolia*, *Typha dominguensis*, *Juncus* spp. and *Solanum glaucophyllum* (Cabrera, 1976; Soriano et al., 1992).

Central Region of Tierra Del Fuego

The Isla Grande de Tierra del Fuego is located at the southernmost end of South America, between latitude 53°-55° S and longitude 66°-74° W. 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).

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°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).

The Fuegian landscape presents two large topography areas: Cordilleran or Andean area and extra Andean or with plains and terraces. According to this classification, the study area is located in Cordilleran or Andean area. It is characterized by a cordilleran basement composed of metamorphic rocks which was covered by different sequences of volcanic and sedimentary rocks and several marine sedimentations.

During the Quaternary, erosive processes shaped the landscape highlighting in particular the relief created by the glaciers (Bondel, 1988; Martinez and Coronato, 2008). The soils are highly complex due to the variability of landforms, parental materials and vegetation, hence Mollisols,

Entisols, Inceptisols, Aridisols, Espodosols and Histosols can be identified in this region (Soil Survey Staff, 1999).

The minerotrophic 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 typical vegetation developed in this site is characterized by Cyperaceae in an environment dominated by *Carex* spp., *Carex magellanica*, *Trisetum* sp., *Agrostis inconspicua*, *Deschampsia kingii*, *Deyeuxia poaeoides*, *Marsippospermum grandiflorum*, *Juncus* sp., *Gunnera magellanica* and *Acaena magellanica*, among other species (Roig et al., 2001).

The grassland associated to peatland is developed on an alluvial sedimentary sequence next to a stream bank which drains the northern slope of the Las Pinturas range, north of Lago Fagnano in the marginal Cordillera of the Cordilleran or Andean area.

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., *Acaena magellanica*, among other species (Lencinas, 2005).

2. Silicophytolith Description of Plant Communities

The most representative species from each plant community were selected for the analysis (Table 1). Leaves and/or culms from at least two specimens of each species were collected, and silicophytoliths 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 were mounted with immersion oil and the silicophytolith morphologies were observed and described with Leitz WetzlarD 35780 and Zeiss Axiostar plus microscopes at x400 magnification and a scanning electron microscope (JEOL JSM-6460 LV, Japan) at Universidad Nacional from Mar del Plata, Argentina. Photographs were taken with a digital camera Canon Powershot G10. More than 200 silicophytoliths were counted in each slide and the morphologies

were described according to ICPN descriptors (Madella et al., 2005). For each morphology the relative frequency was calculated.

The silicophytolith assemblages of each species are described in detail in the different studies previously mentioned (Fernández Honaine et al., 2006, 2009; Borrelli et al., 2011; Benvenuto et al., 2013 a, b).

3. DATA ANALYSIS

Silicophytolith assemblages of each plant community was built according to the silicophytolith assemblage of the species that dominate or differentiate the community (see Table 1).

Table 1. Species selected for the study

Region	Plant community	Family	Subfamily	Species
Pampean	F	Poaceae	Arundinoideae	<i>Danthonia montevidensis</i>
	F	Poaceae	Panicoideae	<i>Sorghastrum pellitum</i>
	F	Poaceae	Pooideae	<i>Briza subaristata</i>
	F	Poaceae	Pooideae	<i>Bromus auleticus</i>
	F	Poaceae	Pooideae	<i>Bromus catharticus</i>
	F	Poaceae	Pooideae	<i>Festuca arundinacea</i>
	F	Poaceae	Pooideae	<i>Melica brasiliana</i>
	F	Poaceae	Stipoideae	<i>Piptochaetium bicolor</i>
	F	Poaceae	Stipoideae	<i>Piptochaetium hackelii</i>
	F	Poaceae	Stipoideae	<i>Piptochaetium lasianthum</i>
	F	Poaceae	Stipoideae	<i>Piptochaetium medium</i>
	F	Poaceae	Stipoideae	<i>Nasella neesiana</i>
	F	Poaceae	Stipoideae	<i>Achnatherum papposum</i>
	F	Poaceae	Stipoideae	<i>Nasella trichotoma</i>
	F	Poaceae	Pooideae	<i>Hordeum pusillum</i>
	F/ FG	Poaceae	Panicoideae	<i>Bothriochloa laguroides</i>
	F/ FG	Poaceae	Pooideae	<i>Vulpia dertonensis</i>
	F/ FG	Poaceae	Pooideae	<i>Dactylis glomerata</i>
	FG/ FB	Asteraceae		<i>Carduus acanthoides</i>
	FG/ FB	Asteraceae		<i>Cirsium vulgare</i>
	FB	Asteraceae		<i>Achillea millefolium</i>
	W	Asteraceae		<i>Bidens laevis</i>
W	Asteraceae		<i>Mikania parodii</i>	
W	Cyperaceae		<i>Schoenoplectus californicus</i>	

Region	Plant community	Family	Subfamily	Species
	W	Cyperaceae		<i>Carex chilensis</i> Brongn
	W	Cyperaceae		<i>Carex phalaroides</i> Kunth
	W	Cyperaceae		<i>Carex tweediana</i> Nees
	W	Cyperaceae		<i>Cyperus digitatus</i> Roxburgh
	W	Cyperaceae		<i>Cyperus eragrostis</i> Lam.
	W	Cyperaceae		<i>Cyperus reflexus</i> Vahl s.s.
Pampean	W	Cyperaceae		<i>Eleocharis bonariensis</i>
	W	Cyperaceae		<i>Eleocharis macrostachya</i>
	W	Cyperaceae		<i>Rhynchospora corymbosa</i> var. <i>bonariensis</i>
	W	Juncaceae		<i>Juncus imbricatus</i>
	W	Juncaceae		<i>Juncus microcephalus</i>
	W	Ranunculaceae		<i>Ranunculus apiifolius</i>
	W	Solanaceae		<i>Solanum glaucophyllum</i>
PQ	Poaceae		<i>Paspalum quadrifarium</i>	
Tierra del Fuego	RT	Asteraceae		<i>Senecio magellanicus</i>
	RT	Cyperaceae		<i>Carex magellanica</i>
	RT	Cyperaceae		<i>Carex</i> sp
	RT	Gunneraceae		<i>Gunnera magellanica</i>
	RT	Poaceae	Pooideae	<i>Deyeuxia poaeoides</i>
	GP	Berberidaceae		<i>Berberis buxifolia</i>
	GP	Juncaceae		<i>Luzula alopecurus</i>
	GP	Nothofagaceae		<i>Nothofagus pumilio</i>
	GP	Poaceae	Pooideae	<i>Alopecurus magellanicus</i>
	GP	Poaceae	Pooideae	<i>Deschampsia antarctica</i>
	GP	Poaceae	Pooideae	<i>Deschampsia flexuosa</i>
	GP	Poaceae	Pooideae	<i>Elymus agropyroides</i>
	GP	Poaceae	Pooideae	<i>Festuca magellanica</i>
	GP	Poaceae	Pooideae	<i>Festuca arundinacea</i>
	GP	Poaceae	Pooideae	<i>Phleum alpinum</i>
	GP	Ranunculaceae		<i>Ranunculus</i> sp
	GP	Rosaceae		<i>Acaena magellanica</i>
	GP	Rosaceae		<i>Rubus geoides</i>
	GP/RT	Poaceae	Pooideae	<i>Puccinellia magellanica</i>
	GP/RT	Poaceae	Pooideae	<i>Trisetum spicatum</i>
GP/RT	Polytrichaceae		<i>Polytrichum strictum</i>	

F: flechillar, FB: flechillar at burned sites, FG: flechillar at grazed sites; GP: grassland associated to peatlands; PQ: *Paspalum quadrifarium* grassland; RT: Río Turbio mire; W: wetlands.

The final assemblage was the result of the sum of the silicophytoliths morphologies of each species. Principal component analysis was performed in order to establish the relative importance of silicophytoliths morphologies in the differentiation of plant communities.

Data were standardized with arcsine square root transformation and a variance-covariance matrix was used (McCune and Mefford, 1999).

RESULTS

Paspalum quadrifarium Grassland

Since it is a monospecific community, silicophytolith description corresponds to a unique species. *Paspalum quadrifarium* is characterized by bilobates, crosses and elongate silicophytoliths, which derive from the silicification of short (bilobates and crosses) and long (elongate) epidermal cells (Figure 2 A-C, E). Bulliform silicophytoliths are also commonly produced (Figure 2D).

“Flechillar” Grassland

The silicophytoliths that characterized “flechillar” community are derived from short epidermal cells such as bilobates (*Stipa*-type, Panicoid-type and simple lobates) (Figure 3), trapeziform crenates and rondels (Figure 4). Elongate silicophytoliths derived from long epidermal cells and hooks and prickles were also described (Figure 5).

The phytolith assemblage of this community at grazed sites is characterized by the presence of Asteraceae silicophytoliths such as tabular polygonals, derived from epidermal cells (Figure 6 C-F) and Pooideae silicophytoliths, such as trapeziform crenates (Figure 4).

Flechillar community at burned sites differed by the presence of Asteraceae silicophytoliths: tabular lobate and tabular polygonal, both derived from epidermal cells (Figure 6).

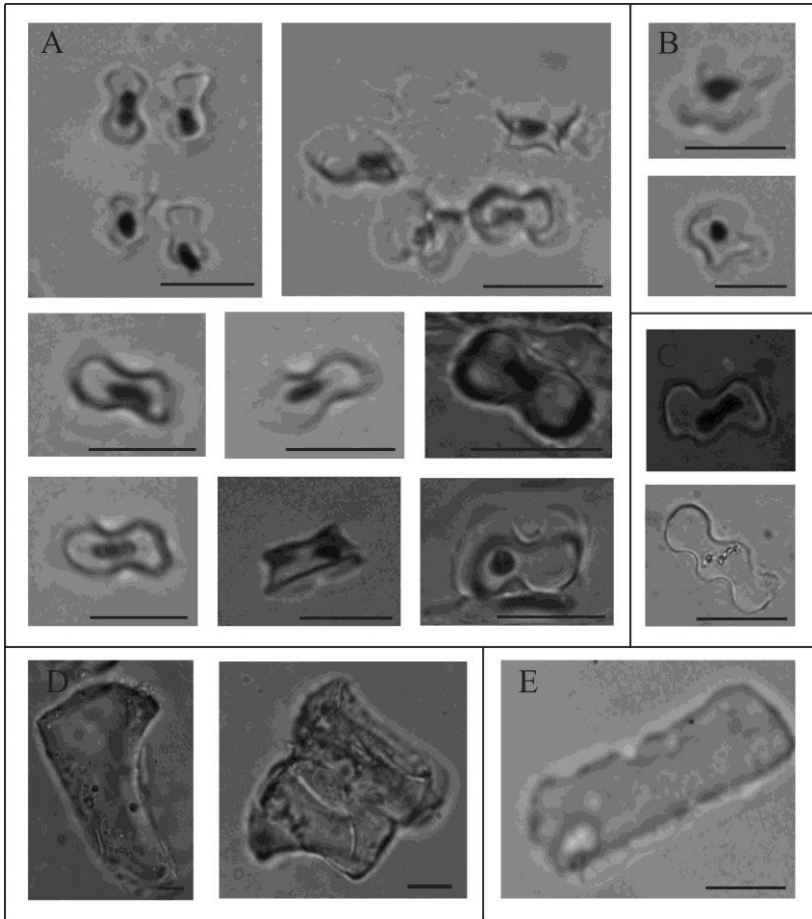


Figure 2. *Paspalum quadrifarium* leaf silicophytoliths. A. Panicoid and simple bilobates. B. Crosses. C. Polylobates. D. Silicified bulliform cells. E. Elongates. Bar 10 μm .

Pampean Wetlands

Cone silicophytoliths produced in epidermal cells of sedges, elongate silicophytoliths derived from fibers, and tabular lobate and tabular polygonal silicophytoliths derived from epidermal cells of dicotyledons, are the main morphologies produced by wetland communities (Figure 7).

Also, pointed shape silicophytoliths derived from trichomes (Figure 7 O-Q) and tracheid cells derived from xylem tissue are described (Figure 7 K, L).

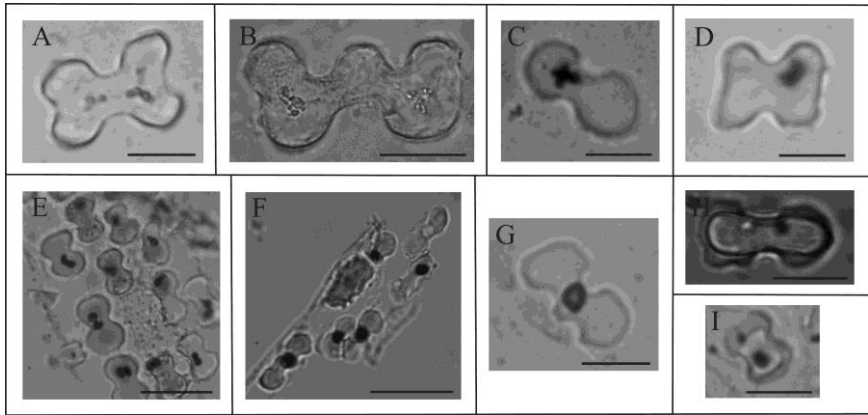


Figure 3. Bilobate and polilobate silicophytoliths from “flechillar” communities. A. Panicoid bilobate in *Bothriochloa laguroides*. B. Polylobate in *Bothriochloa laguroides*. C, E. Simple lobate in *Danthonia montevidensis*. D. Panicoid bilobate in *Danthonia montevidensis*. F-G Polilobates and bilobates in *Melica brasiliiana*. H-I *Stipa*-type bilobates in *Piptochaetium bicolor* and *Piptochaetium hackelii*, respectively. Bar 10 μm , except in E and F (25 μm).

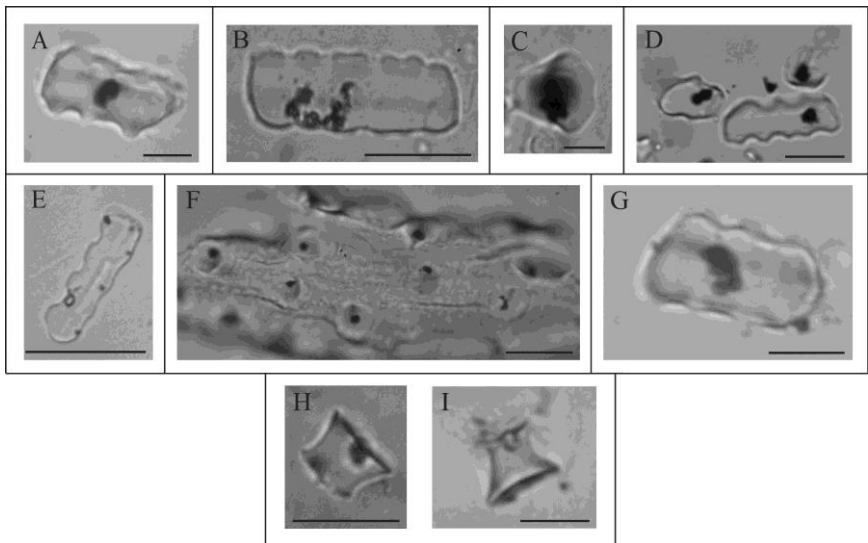


Figure 4. Rondels (C, F, H, I) and trapeziform crenate (A, B, D, G) silicophytoliths from “flechillar” communities. A. *Bromus auleticus*. B. *Bromus catharticus*. C-D. *Briza subaristata*. E. *Dactylis glomerata*. F. *Festuca arundinacea*. G. *Hordeum pusillum*. H. *Piptochaetium bicolor*. I. *Piptochaetium hackelii*. Bar 10 μm except in B, E and F (25 μm).

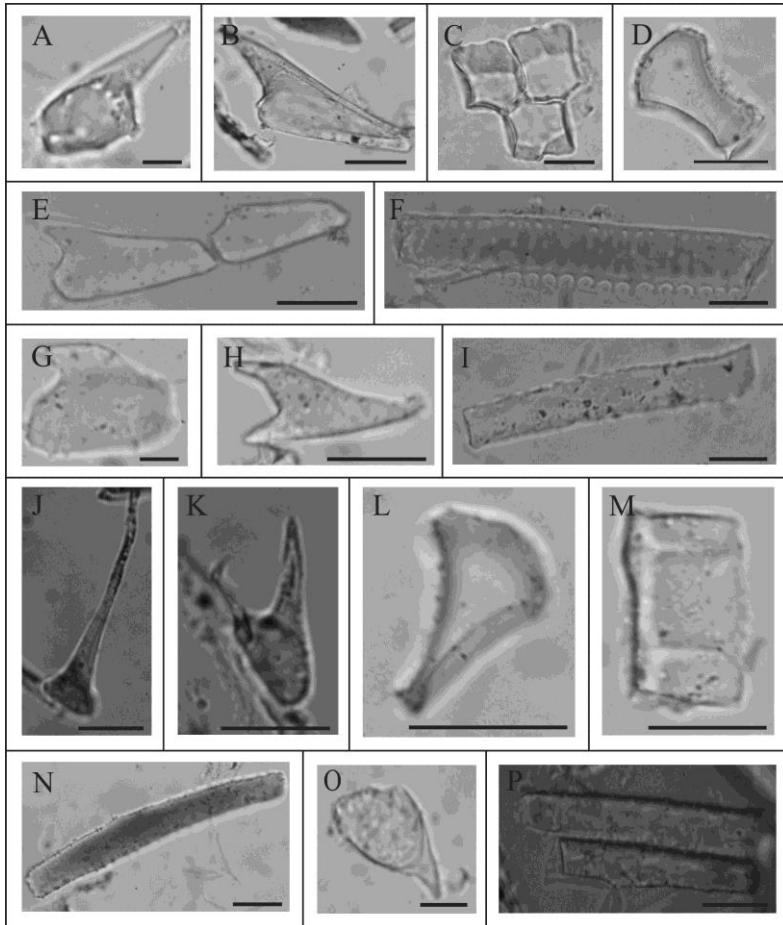


Figure 5. Other silicophytolith morphologies from “flechillar” communities. C-D, L-M. Silicified bulliform cells. F, I, N, P. Elongates. A-B, E, G-H, J-K, O. Trichomes. A. *Bromus auleticus*. B. *Bromus catharticus*. C-D. *Bothriochloa laguroides*. E-G. *Briza subaristata*. H. *Dactylis glomerata*. I. *Festuca arundinaceae*. J-K. *Melica brasiliana*. L-M. *Piptochaetium bicolor*. N-O *Piptochaetium hackelii*. P. *Piptochaetium lasianthum*. Bar 25 μm except in A, D, G, N and O (10 μm).

Minerotrophic Mire Vegetation

The silicophytoliths that characterized this community are derived from epidermal cells of monocotyledons such as elongates (psilates, sinuates and echinates), trapeziforms (psilates and sinuates), rondels and sedge cones.

Also, dicotyledon silicophytoliths such as tabular polygonal and tabular lobate are common. Other morphologies described in a minor proportion but in all the species are cylindrical sulcate tracheids (derived from silicification of vascular tissue), stomatal complexes and apex of sharp-pointed shapes (hairs or hooks) (Figure 8 A-P).

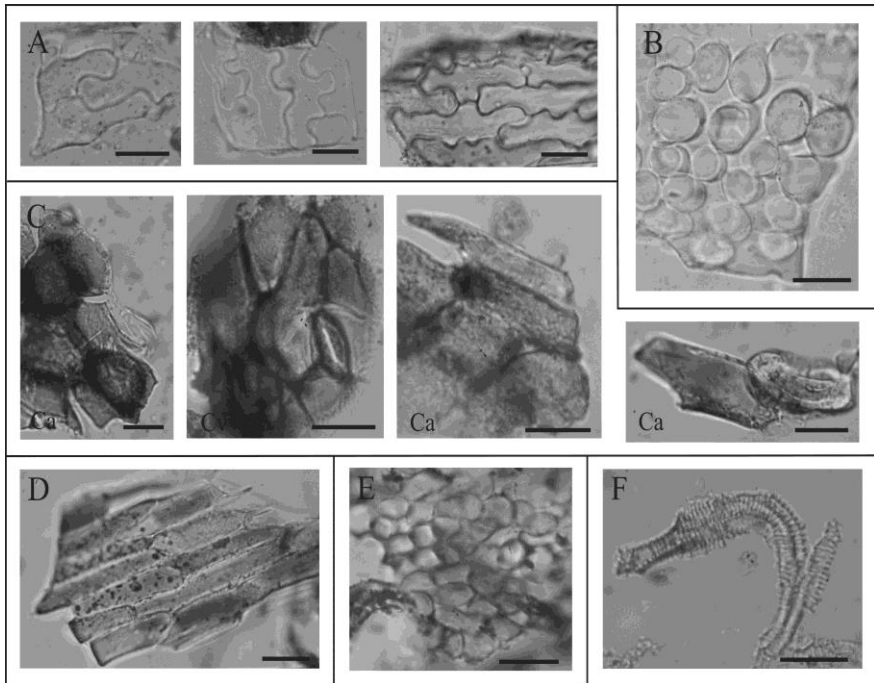


Figure 6. Leaf silicophytoliths from Asteraceae species common in grazed and burned grasslands. A. Tabular lobate in *Achillea millefolium*. B. Papillae-like silicifications in *Achillea millefolium*. C. Tabular polygonals and elongates in *Carduus acanthoides* (Ca) and *Cirsium vulgare* (Cv). D. Elongate in *Carduus acanthoides*. E. Subepidermic silicified elements in *Cirsium vulgare*. F. Silicified xylem in *Carduus acanthoides*. Bar 25 μ m.

Silica skeletons composed by thin elongated silicophytoliths with blunt, round, or acute ends were only observed in the gametophyte from *Polytrichum strictum* (Figure 8 Q-R).

Grassland Associated to Peatland

The silicophytoliths mainly represented in this community are derived from epidermal cells of monocotyledons and dicotyledons such as elongates (psilates, sinuates and echinates), trapeziforms (psilates and sinuates), rondels, tabular polygonal and tabular lobate (Figure 9 A-M).

Other morphologies such as cylindrical sulcate tracheids and elongate fusiform silicophytoliths, derived from silicification of vascular tissue and fibers, are described in this community. Stomatal complexes and apex of sharp-pointed shapes (hairs or hooks) are less common (Figure 9 N-X).

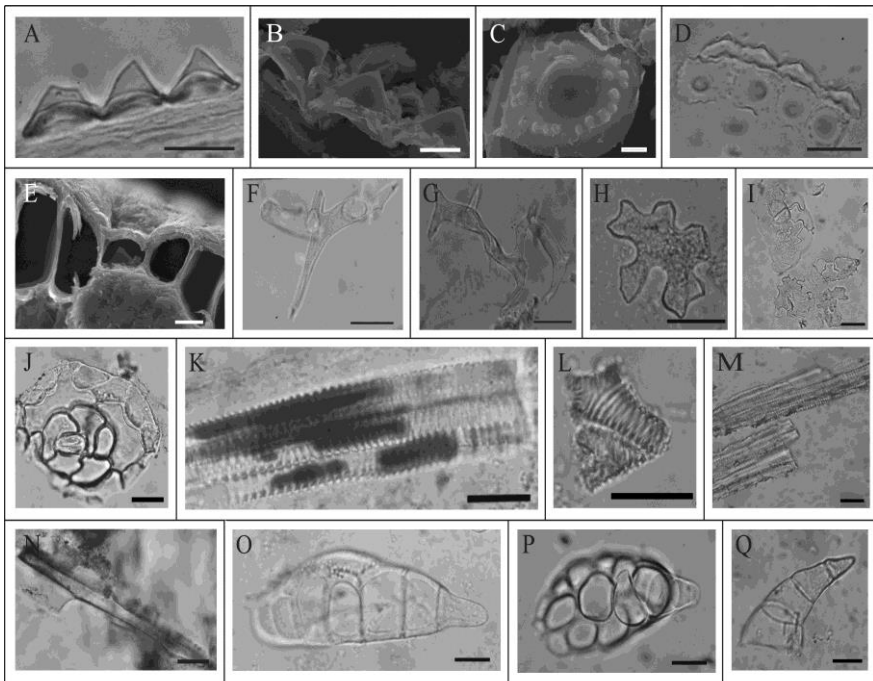


Figure 7. Leaf silicophytoliths from wetland species. A-E. Cones. A. *Carex phalaroides*. B-C. *Cyperus odoratus*. D. *Cyperus reflexus*. E. Transverse sections showing cone location (arrows) in *Schoenoplectus californicus*. F-G. Stellate in *Rynchospora corymbosa*. H-I. Tabular lobates in *Bidens laevis*. J. Articulated tabular polygons in *Solanum glaucophyllum*. K-L. Silicified xylem in *Bidens laevis* (K) and *Solanum glaucophyllum* (L). M-N. Silicified xylem and elongates in articulated form in *Juncus* spp. O-P. Multicellular silicified hairs from *Bidens laevis*. Q. Multicellular silicified hairs from *Mikania parodii*. Bar 25 μm , except in B, C and E (5 μm).

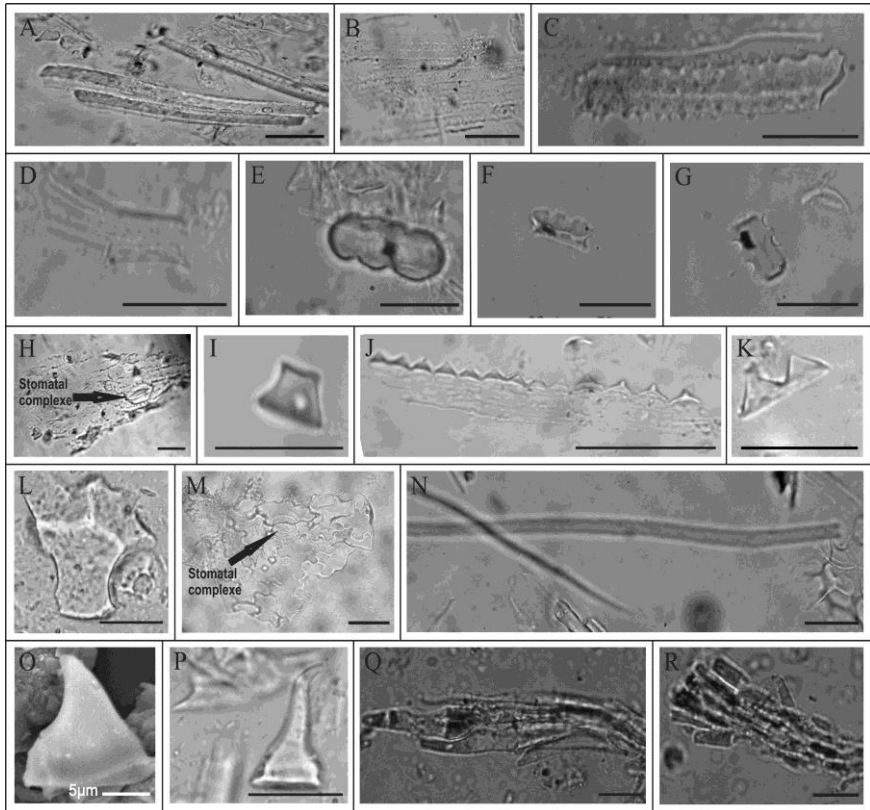


Figure 8. Leaf silicophytoliths from minerotrophic mire species. A. Elongate psilate in *Deyeuxia poaeoides*. B-C. Elongate sinuate (B) and Elongate echinate (C) in *Carex* sp. D. Trapeziform psilate in *Puccinellia magellanica*. E-G. Trapeziform crenate in *Deyeuxia poaeoides*. H. Silicification of epidermal cells and stomatal complexes (arrows) in *Puccinellia magellanica*. I. Rondel in *Trisetum spicatum*. J-K. Conical silicophytoliths in articulated form in *Carex magellanica* (J) and *Carex* sp.(K). L. Silica skeletons composed by tabular lobate and stomatal complexes (arrows) in *Gunnera magellanica*. M. Tabular polygonal in *Senecio magellanicus*. N. Elongate fusiform silicophytoliths derived from silicification of fibers in *Puccinellia magellanica*. O-P. Pointed shaped silicophytoliths derived from trichomes in *Puccinellia magellanica* (O) and *Trisetum spicatum* (P). Q-R. Silicophytolith morphology observed in the gametophyte from *Polytrichum strictum*: silica skeletons composed by thin elongated silicophytoliths with blunt, round, or acute ends. Bar 25µm.

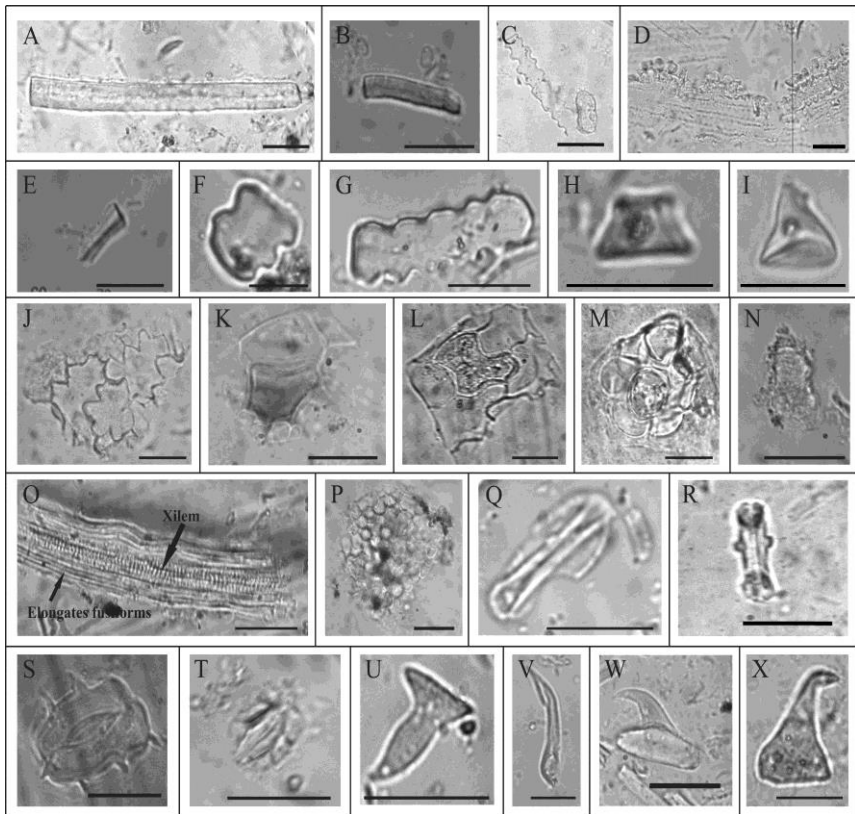


Figure 9. Leaf silicophytoliths from grassland species associated to peatland. A-B. Elongate psilate in *Deschampsia flexuosa*. C. Elongate sinuate in *Elymus agropyroides*. D. Articulated elongate echinate silicophytoliths in *Festuca arundinacea*. E. Trapeziform psilate in *Puccinellia magellanica*. F-G. Trapeziform crenate in *Phleum alpinum*. H-I. Rondel in *Festuca arundinacea* (H) and *Festuca magellanica* (I). J-K. Articulated tabular polygonal silicophytoliths in *Acaena magellanica* (J) and *Nothofagus pumilio* (K). L. Articulated tabular lobate silicophytoliths in *Ranunculus* sp. M. Silica skeletons composed by orbicular cell arranged in radiated form in *Ranunculus* sp. N. Cylindrical sulcate tracheids in *Berberis buxifolia*. O. Silica skeletons composed by cylindrical sulcate tracheids and elongate fusiform silicophytoliths in *Luzula alopecurus*. P. Silica skeletons composed by silicified cells from mesophyll tissue in *Nothofagus pumilio*. Q-T. Stomatal complexes. Q. *Festuca magellanica*. R. *Alopecurus magellanicus*. S. *Ranunculus* sp. T. *Berberis buxifolia*. U-X. Pointed shaped silicophytoliths derived from trichomes. U. *Deschampsia flexuosa*. V. *Festuca arundinacea*. W. *Deschampsia antartica*. X. *Festuca arundinacea*. Bar 25 μ m.

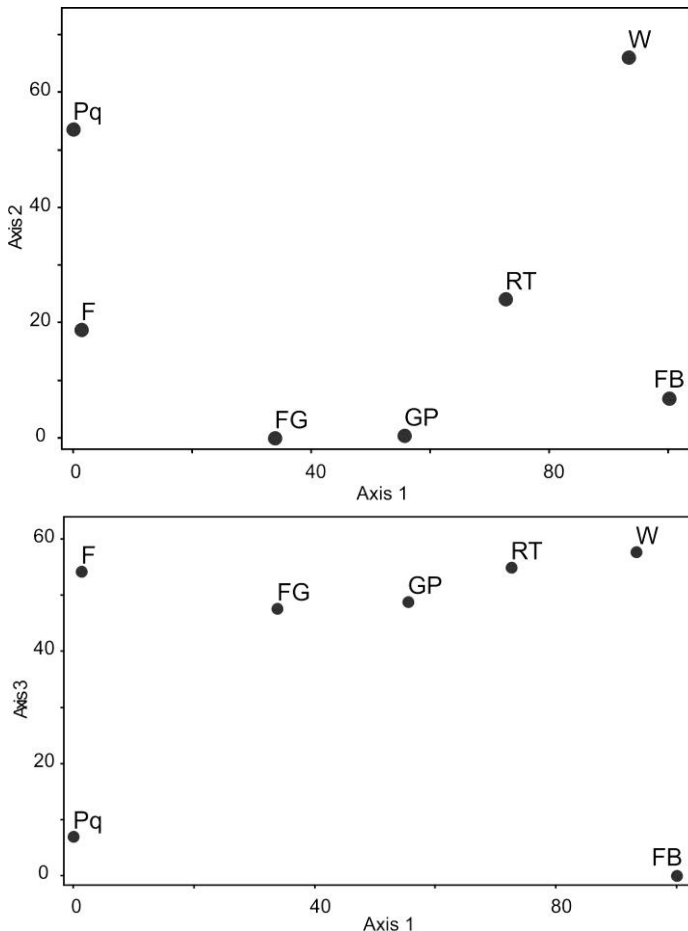
Multivariate Analysis

Principal component analysis was carried on with the purpose of analyze the relevance of silicophytolith assemblages on plant community differentiation. The first three axes of the PCA amount to 92% of the total variance (54% for axis 1, 21% for axis 2, 17% for axis 3). Tabular lobate and tabular polygonal silicophytoliths, sedge cones and short cell silicophytoliths contribute to axis 1, which allows the separation between Pampean grasslands (left side) from wetlands and grasslands affected by agricultural activities (burned flechillar, FIB) (right side) (Figure 10). The communities from Tierra del Fuego are placed between the above-described communities, since they are characterized by tabular lobate and also short cells silicophytoliths. Cyperaceae cones mainly contribute to axis 2, and separate wetland community from the rest. The main morphotypes that contribute to axis 3 are simple lobates, trapeziforms, tabular lobates, tabular polygonals and point shaped silicophytoliths. This axis allows the separation between the different types of grasslands analyzed, especially *Paspalum quadrifarium* community from the rest.

Pampean grasslands (*P. quadrifarium* and “flechillar” communities) are mainly characterized by bilobates (simple lobates, Panicoid-type bilobates and *Stipa*-type bilobates) and crosses, while Tierra del Fuego grasslands are characterized by poid silicophytoliths, such as trapeziforms and rondels, and elongate silicophytoliths.

CONCLUSION

Silicophytolith description of local and regional plant communities constitutes a fundamental tool for the adequate interpretation of fossil phytolith record in soils and sediments. In the present chapter, the production of silicophytoliths of species from two phytogeographic, climatic and environmentally different regions of Argentina was described and compared. Pampean grasslands are characterized by Poaceae species mainly belonging to Panicoideae, Pooideae and Stipoideae subfamilies; while Pampean wetlands are dominated by Cyperaceae and Asteraceae species. Communities from Tierra del Fuego are dominated by Poaceae species (Pooideae subfamily) and, in a lesser degree, by Cyperaceae and Asteraceae species, among others.



F: “flechillar”; FG: “flechillar” at grazed sites; FB: “flechillar” at burned sites; GP: Grassland associated to peatland; Pq: *Paspalum quadrifarum* grassland; RT: minerotrophic mire from Tierra del Fuego; W: Pampean wetland.

Figure 10. PCA of plant communities based on their silicophytolith assemblages. Axes 1 vs. 2 and axes 1 vs. 3 are shown.

All the families and subfamilies studied produce silicophytoliths in different amounts, and these morphological and quantitative differences allowed the separation between communities.

The results of the multivariate analysis reaffirm the usefulness of silicophytolith assemblages in the differentiation of plant communities (e.g. Ollendorf et al., 1988; Krishnan et al., 2000; Blinnikov, 2005).

The silicophytolith production of Pampean grasslands (*Paspalum quadrifarium* and “flechillar”) includes the silicification of the typical short cells that characterized each subfamily of Poaceae, allowing the differentiation between these grasslands. *Paspalum quadrifarium* produces panicoid silicophytoliths (crosses and bilobates), while “flechillar” species production includes poid and stipoid silicophytoliths (rondels and trapeziforms, and *Stipa*-type bilobates, respectively). At the same time, the silicophytolith production in grasslands associated to peatlands is differentiated from the Pampean grasslands by the dominance of poid silicophytoliths (rondels and trapeziforms) and the absence of bilobates. Finally, the presence of phytoliths produced by dicotyledons, such as tabular lobates and tabular polygonals, differentiates Tierra del Fuego grasslands from Pampean ones.

Wetland communities are mainly characterized by silicophytoliths produced by Cyperaceae and Asteraceae species, which greatly differ from the morphologies produced by Poaceae species. Cone silicophytoliths, produced by sedges, and tabular polygonal and tabular lobate silicophytoliths, produced by dicotyledons, are the main elements in the silicophytolith assemblages of wetland communities. In all the families studied, the production of silicophytoliths mainly involved the silicification of epidermis. Typical short cells from grasses (bilobates, rondels, trapeziforms), long cells (elongate silicophytoliths), bulliform and epidermal cells from dicotyledons (tabular lobate, tabular polygonal silicophytoliths) and trichomes (hooks, prickles, multicellular hair silicophytoliths) are the most abundant types of cells that are silicified. Xylem, parenchyma and sclerenchyma (elongate silicophytoliths) are sometimes silicified.

The results shown in this chapter will contribute to the understanding on silicophytolith production of the different plant communities of Argentina, its relation with systematics and represent an important tool for the interpretation of regional fossil phytolith record.

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