Journal of Paleolimnology (2005) 34: 433–444
DOI 10.1007/s10933-005-5804-8

The fossil record of freshwater micro-algae *Pediastrum* Meyen (Chlorophyceae) in southern South America

María del C. Zamaloa* and Guillermo Tell
*Departamento de Ecología, Genética y Evolución, Universidad de Buenos Aires, Intendente Güiraldes 2620, C1428EHA Buenos Aires, Argentina; *Author for correspondence (e-mail: mzamaloa@bg.fcen.uba.ar)*

Received 21 October 2004; accepted in revised form 2 April 2005

Key words: Chlorococcales, Cretaceous, Fossil, Micro-algae, Miocene, Paleogene, Paleolimnology, *Pediastrum*, South America

Abstract

The fossil record of *Pediastrum* Meyen (Chlorophyceae) in southern South America is revised and 10 species/varieties are recognised within the genus. Previously published material is identified and new data are included. The oldest and most widespread variety for the region is *P. boryanum* var. *boryanum*, which appears in the Late Cretaceous age. *P. tetras* is recorded in the Early Eocene in Patagonia. *P. boryanum* var. *brevicorne*, *P. boryanum* var. *longicorne*, *P. duplex*, *P. integrum*, *P. kawraiskyi*, *P. leonensis*, *P. mustersii* and *P. simplex* are present in numerous Miocene assemblages. Assemblages of different species and mass production episodes are also detected in the fossil record. New examples of the value of *Pediastrum* species as paleoenvironmental markers are presented.

Introduction

Coenobial green algae belonging to the genus *Pediastrum* Meyen are recorded from all over the world in a great number of papers dealing with freshwater phytoplankton communities. Some species are endemic, and others are cosmopolitan or restricted to cold, temperate or warm regions. The species geographical distribution is mainly determined by two factors: global distribution responds to temperature, whereas regional distributions are more closely explained by water quality (Tell 2004).

The main diagnostic features of the genus are inner and marginal cell morphology and the presence/absence of clatrations or perforations in the coenobium. Fossil and subfossil coenobia are frequently found in palynological assemblages owing to the resistance of cell walls to diagenetic processes. According to Batten (1996) species of *Pediastrum* are known to have existed since the Early Cretaceous and at this time only compact coenobia were present. During the Cenozoic, the genus became a common component of many planktonic paleocommunities and the oldest perforated species appeared in the Eocene. Hence the genus has been largely used as a biological indicator of freshwater paleoenvironments and temperate (or warm) climate. Some authors have referred fossil forms to extant taxa (e.g., Evitt 1963; Starck and Anzótegui 2001), while others preferred to erect new taxa for fossil forms (Wilson and Hoffmeister 1953; Singh and Khanna 1978).

Pediastrum is frequently found in Cenozoic southern South America (sSA) deposits, however most of the records lack descriptions and illustrations and only mention *Pediastrum* spp. in taxonomic lists. In some cases, there is an indication of the probable species affiliation. Accurate identifications, adequately illustrated, have been

attempted in comparatively few papers. Nevertheless, fossil species differentiation and their comparison with extant taxa are not difficult when the specimens are moderately well preserved. This approach, based in the assumption that the past ecological requirements of the species/varieties were similar to those of the living representatives, greatly improves the paleoenvironmental interpretations derived of the presence of the genus. The paleoecolgical value, not only of *Pediastrum* species but also of some other algal families such as Zygnemataceae, Oedogoniaceae and Cyanophyceae, has been demonstrated in previous palynological studies mainly of northern hemisphere Quaternary deposits (see Komárek and Jankovská 2001 and references therein).

The aim of this contribution is to review the fossil record of *Pediastrum* in sSA (latitudes higher than 24° S approximately) with emphasis in pre-Quaternary deposits on the basis of available literature and some unpublished data from the authors. Identification of the illustrated specimens and their relationship with extant taxa are also attempted in order to contribute to a better understanding of the biogeographical history of the genus in southern latitudes. Finally, some interpretations about the depositional conditions of the sedimentary basins containing *Pediastrum* are discussed.

Methods and materials

All the literature dealing with *Pediastrum* found in sedimentary basins of Chile, Argentina and Paraguay was considered for this review. Table 1 includes all well documented and illustrated records of the genus in sSA. The contributions that contain lists of taxa without illustrations were not included. Whenever poor quality photographs or poorly preserved material did not allow for definite identifications of the taxonomic affiliation to *Pediastrum*, it is indicated as 'aff.' The iconography of all published taxa of *Pediastrum* is reproduced in Plate 1; only one photograph is reproduced from papers containing more than one picture of the same taxon.

Additionally, several samples belonging to other Patagonian sites with algal remains (Zamaloa 1993, 1996, 2000, 2004) were incorporated in this study. Material from the Miocene Cullen and Pinturas Formations was examined for this purpose. The samples were processed following standard palynological techniques consisting of acid treatment (HF and HCl), dilute HCl washing, fine and coarse sieving, heavy liquid separation and acetolysis, and mounted in glycerin jelly.

Palynological samples derived from the Cullen Formation that crops out in the North-East of Tierra del Fuego Island (ca. 52° S lat.) yielded scarce *Pediastrum* specimens. Contrarily, some levels of the Pinturas Formation exposed in North-West Santa Cruz Province (ca. 46° S lat.) are completely dominated by *Pediastrum*. This new material is described below and is illustrated in Plate 2.

Results

The southern South American fossil record

Some comments followed by a brief description of the identified species and varieties, as well as their ecology, recent distribution and known fossil record in sSA, are summarised forthwith in the text and in Table 1. Figure 1 illustrates the known fossil and recent records in sSA.

Pediastrum boryanum (Turp.) Menegh. (Plate 1, figures 1–13)

This is the most widely distributed and variable species. Many recent infraspecific taxa have been described all over the world based on coenobia and cell morphology, and ultrastructural patterns. The absence of holes in the coenobia and the external cells with two horns in the same plane clearly distinguish the species. The species is a common component of the phytoplankton of eutrophic to mesotrophic lakes, found mostly in temperate regions, frequently associated with other species of 'small' Chlorococcales.

The type species and two fossil varieties have been recorded in sSA. Those fossil specimens identified as *Pediastrum* spp. and *P.* sp. aff. *boryanum* by different authors (Quattrocchio and Volkheimer 1988, 1990; Guerstein 1990; Papú and Sepúlveda 1997) are here allocated in *P.* sp. aff. *boryanum* (Plate 1, figures 9–12). Other specimens figured by Papú (1990) and Barreda et al. (2003) are confirmed as *P. boryanum* (Plate 1, figures 1–2).

Table 1. Southern South American illustrated records of *Pediastrum* (ordered by geological ages).

Age	Formation	Approximate latitude	Author	Plate/Figure (as originally published)	Published as:	Identified in this paper as:
Late Cretaceous	Malargüe	35°29′ S	Papú 1990	Pl. III, fig. 6–7	*Pediastrum* sp.	*P. boryanum*
Maastrichtian	C. Río Guaco	30° S	Limarino et al. 2000	Fig. 7, 13–14	*Pediastrum* sp. aff. *P. boryanum*	*P. boryanum* var. *boryanum*
Maastrichtian	Loncoche	36° S	Papú 2002	Fig. 5E	*Pediastrum* sp.	*P. boryanum* var.*boryanum*
Paleocene	Tunal	25° S	Quattrocchio and Volkheimer 1988	Pl. B, fig. 26, 30	*Pediastrum* sp.	*P.* sp. aff. *boryanum*
Paleocene	Tunal	25° S	Quattrocchio and Volkheimer 1990	Fig. 6, 18	*Pediastrum* sp.	*P.* sp. aff. *boryanum*
Late Paleocene or Early Eocene?	Río Chico	45° S	Papu and Sepúlveda 1997	Pl. I, fig. 4	*P.* aff. *P. boryanum*	*P.* sp. aff. *boryanum*
Early Eocene	Huitrera	41° S	Melendi et al. 2003	Fig. 8, 6	*Pediastrum* cf. *tetras*	*P. tetras*
Late Eocene to Miocene?	Pachaco	32° S	Prámpano et al. 1996	Pl. III, 6	*P.* sp. aff. *P. duplex*	*P. duplex* var. *duplex*
Miocene	Chinches	32° S	Ottone et al. 1998	Pl. 3, fig. 11–12	*Pediastrum* sp.	*P. boryanum* var. *boryanum*
Early Miocene	Monte León	50° S	Barreda and Palamrczuk 2000	Fig. 5, A–B	*Pediastrum* spp.	*P. kawraiskyi*
Early Miocene	Monte León	50° S	Barreda and Palamrczuk 2000	Fig. 5, D	*Pediastrum* sp.	*P. leonensis*
Early Miocene	Monte León	50° S	Barreda and Palamrczuk 2000	Fig. 5, C, E, F	*Pediastrum* spp.	*P. mustersii*
Early Miocene	Monte León	50° S	Tell 2004	Pl. I, Figs a–b	*P. kawraiskyi*	*P. kawraiskyi*
Early Miocene	Monte León	50° S	Tell 2004	Pl. I, Fig. f	*Pediastrum* sp.	*P. leonensis*
Early Miocene	Monte León	50° S	Tell 2004	Pl. I, Figs. c–e	*P. mustersii*	*P. mustersii*
Early Miocene	Monte León	50° S	Tell and Zamaloa 2004	Fig. 4(a)	*P. kawraiskyi*	*P. kawraiskyi*
Early Miocene	Monte León	50° S	Tell and Zamaloa 2004	Fig. 3(a)–(f)	*P. leonensis*	*P. leonensis*
Early Miocene	Monte León	50° S	Tell and Zamaloa 2004	Fig. 4(b)	*P. mustersii*	*P. mustersii*
Early Miocene (Barreda and Bellosi 2003)	Chenque	45°30′ S	Barreda 1997	Pl. I, fig. 10	*Pediastrum* sp.	*P. mustersii*
Late Early-Miocene (Fleagle et al. 1995)	Pinturas	46° S	This paper	Pl. 2, fig. 1–2		*P. duplex* var. *duplex*
Late Early-Miocene (Fleagle et al. 1995)	Pinturas	46° S	This paper	Pl. 2, fig. 3		*P. boryanum* var. *brevicorne*
Early or Middle Miocene	Cerro Morado	29°33′ S	Barreda et al. 2003	Fig. 4, L-N	*Pediastrum* sp.	*P. boryanum*
Early or Middle Miocene (Zamaloa 2004)	Cullen	52° S	This paper	Pl. 2, fig. 4–5		*P. boryanum* var. *brevicorne*
Early or Middle Miocene (Zamaloa 2004)	Cullen	52° S	This paper	Pl. 2, fig. 6 –7		*P. integrum* var. *integrum*
Middle to Late Miocene	Barranca Final	38°30′ S	Guerstein 1990	Pl. VI, fig. 14	*Pediastrum* sp.	*P.* sp. aff. *boryanum*
Middle to Late Miocene	Barranca Final	41° S	Guler et al. 2002	Fig. 4, K	*Pediastrum* sp.	*P. boryanum* var. *boryanum*
Middle to Late Miocene	Barranca Final	41° S	Guler et al. 2002	Fig. 4, L	*Pediastrum* sp.	*P. mustersii*
Late Miocene	Palo Pintado	26° S	Starck and Anzótegui 2001	Fig. 6, 1–2	*P. simplex*	*P. simplex*
Late Miocene	Palo Pintado	26° S	Starck and Anzótegui 2001	Fig. 6, 3	*P. boryanum*	*P. boryanum* var. *longicorne*
Holocene	Not indicated	35°37′ S	Fernández 1993	Pl. 3, fig. 1–2	*P. boryanum*	*P. boryanum* var. *boryanum*
Holocene (This paper)	Not indicated	39° S	Tell 2004	Pl. III, fig. a–b	*P. boryanum* var.*boryanum*	*P. boryanum* var. *boryanum*
Holocene (This paper)	Not indicated	39° S	Tell 2004	Pl. III, fig. c–d	*P. mustersii*	*P. mustersii*

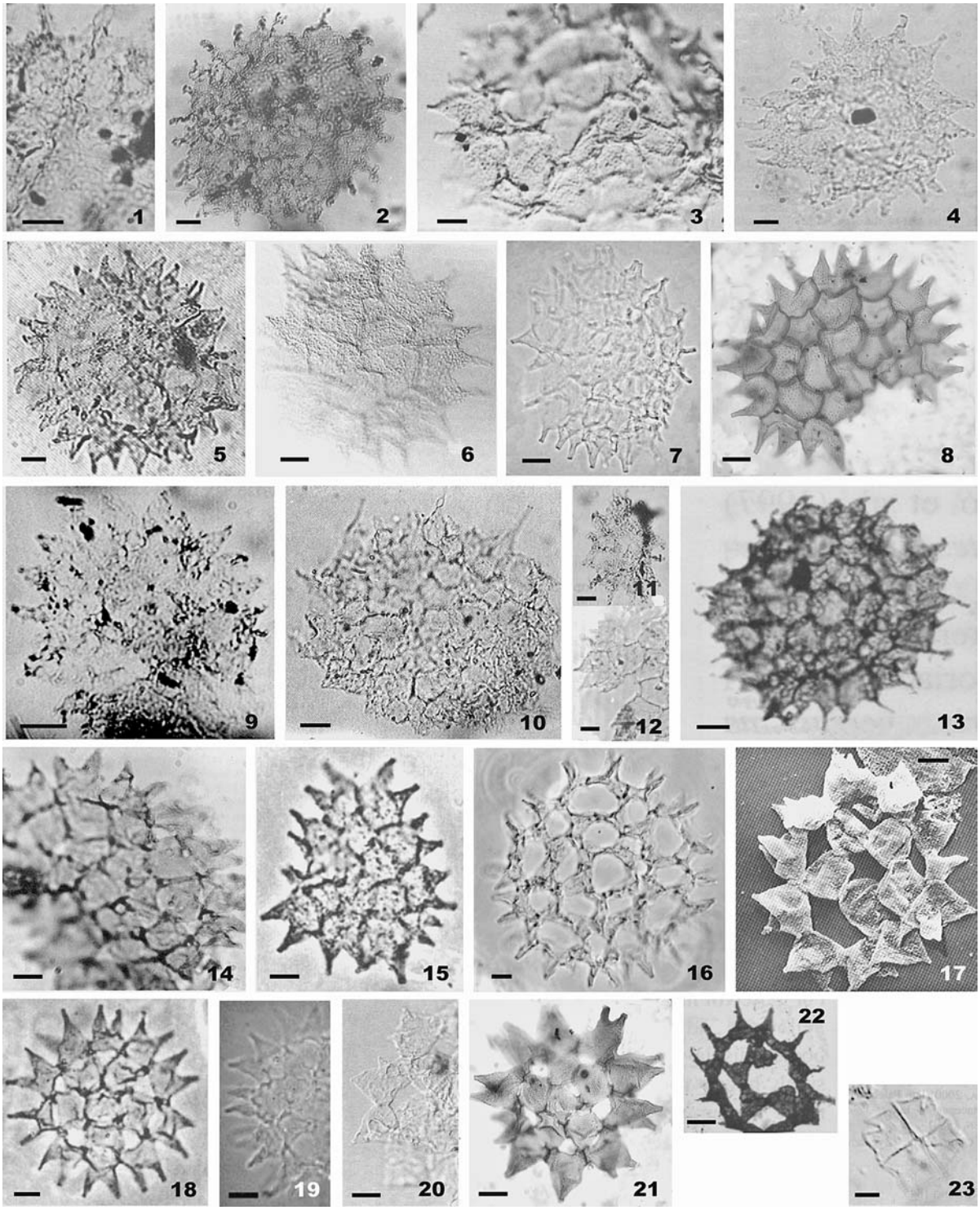
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23

Plate 1. 1, *Pediastrum boryanum* (from Papú 1990); 2, *P. boryanum* (from Barreda et al. 2003); 3, *P. boryanum* var. *boryanum* (from Fernández 1993); 4, *P. boryanum* var. *boryanum* (from Ottone et al. 1998); 5, *P. boryanum* var. *boryanum* (from Limarino et al. 2000); 6, *P. boryanum* var. *boryanum* (from Papú 2002); 7, *P. boryanum* var. *boryanum* (from Guler et al. 2002); 8, *P. boryanum* var. *boryanum* (from Tell 2004); 9, *P.* sp. aff. *boryanum* (from Quattrocchio and Volkheimer 1988); 10, *P.* sp. aff. *boryanum* (from Guerstein 1990); 11, *P.* sp. aff. *boryanum* (from Quattrocchio and Volkheimer 1990); 12, *P.* sp. aff. *boryanum* (from Papú and Sepúlveda 1997); 13, *P. boryanum* var. *longicorne* (from Starck and Anzótegui 2001); 14, *P. duplex* var. *duplex* (from Prámpano et al. 1996); 15, *P. kawraiskyi* (from Barreda and Palamarczuk 2000; Tell and Zamaloa 2004; Tell 2004); 16, *P. leonensis* (from Barreda and Palamarczuk 2000; Tell and Zamaloa 2004; Tell 2004); 17, *P. mustersii* (from Barreda 1997); 18, *P. mustersii* (from Barreda and Palamarczuk 2000; Tell 2004); 19, *P. mustersii* (from Tell and Zamaloa 2004); 20, *P. mustersii* (from Guler et al. 2002); 21, *P. mustersii* (from Tell 2004); 22, *P. simplex* (from Starck and Anzótegui 2001); 23, *P. tetras* (from Melendi et al. 2003). Scale bar = 10 μm.

Pediastrum boryanum (Turp.) Menegh. var. *boryanum* (Plate 1, figures 3–8)
Coenobia not perforated, with 4–64 cells. Cell wall finely granulated. This form is very common and widely distributed in freshwater phytoplanktonic communities. Recent records are known from the entire studied region.

Fossil specimens from sSA identified as *Pediastrum* sp. and *P.* sp. aff. *boryanum* by Fernández (1993), Ottone et al. (1998), Limarino et al. (2000), Guler et al. (2002), Papú (2002) and Barreda et al. (2003) are identified as *P. boryanum* var. *boryanum*. Those individuals figured by Tell (2004, Pl. III) come from Holocene deposits of Central East Argentina (ca. 39° S lat.).

Fossil record: This variety was found in the Late Cretaceous, the Miocene and the Holocene periods in several basins from North to Central Argentina.

Pediastrum boryanum var. *brevicorne* A. Br. (Plate 2, figures 3–5)
The presence of small, conical lobes and short horns in the external cells characterises this variety. In sSA, recent coenobia are distributed in warm and warm-temperate regions, not found in Patagonia.

Fossil record: This variety is present in low amounts in several palynological samples derived from the Miocene Pinturas and Cullen Formations. These are the first fossil records of the variety in sSA.

Pediastrum boryanum var. *longicorne* Reinsch (Plate 1, figure 13)
The lobes of the external cells deeply incised ending in long horns and the conspicuously granulated cell walls distinguish this variety from the others. In sSA, recent representatives are widely distributed from cold to warm regions.

Fossil material identified as *P. boryanum* by (Starck and Anzótegui 2001) is assigned to *P. boryanum* var. *longicorne*.

Fossil record: Found only in Late Miocene deposits from Northern Argentina.

Pediastrum duplex Meyen var. *duplex* (Plate 1, figure 14; Plate 2, figures 1–2)
This is a very well-known species largely distributed all over the world in recent phytoplankton. The species is easy to distinguish from the other species because of the regularly displaced holes between cells in the coenobia and the distinct two horns of the marginal cells in the same plane. The variety is common in eutrophic to mesotrophic lakes of temperate zones of Argentina, being absent in South Patagonia.

Fossil material identified as *Pediastrum* sp. by Prámpano et al. (1996) is assigned to *P. duplex* var. *duplex*.

Fossil record: Found in Central Argentina (Prámpano et al. 1996) in deposits of uncertain age (Late Eocene to Miocene?). Also present (and dominating several levels) in the Late Early Miocene Pinturas Formation.

Pediastrum integrum Näg var. *integrum* (Plate 2, figures 6–7)
The absence of perforations in the coenobia and the marginal cells without incisions and with 1–2 eccentrically disposed reduced horns characterise this variety. Recent representatives are rarely found in clear, oligotrophic or dystrophic swamps. In sSA this variety is distributed in temperate and warm regions, and not found in Patagonia.

Fossil record: Found in low amounts in samples of the Cullen Formation, Miocene of southern Patagonia. This is the first fossil record for the species in sSA.

Pediastrum kawraiskyi Schmidle (Plate 1, figure 15)
This species belongs to the *Pediastrum kawraiskyi–mustersii–patagonicum–leonensis* complex, which is

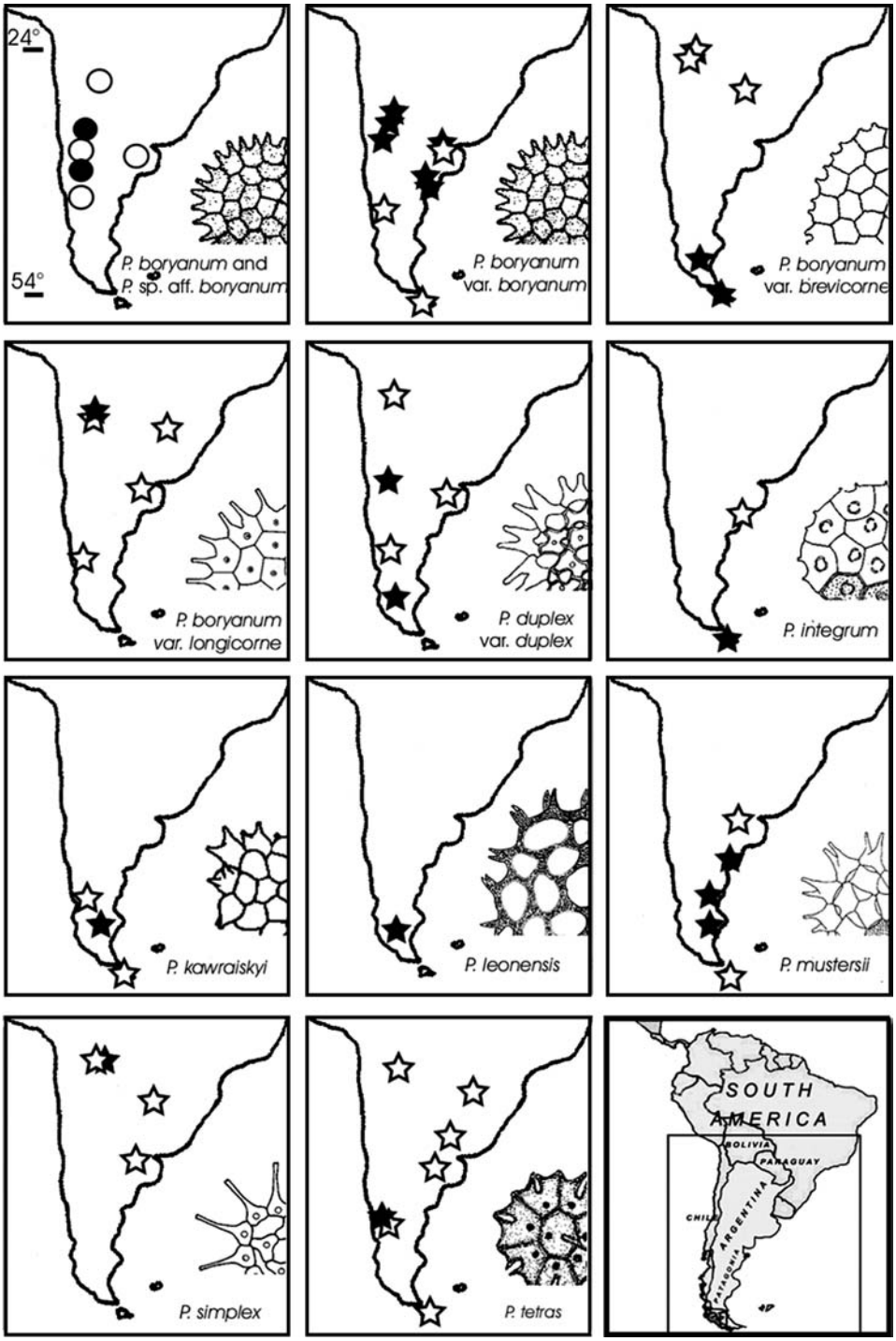

Figure 1. Fossil and present known occurrences of *Pediastrum* species and varieties in southern South America. ★ fossil record; ☆ present record; ● fossil record of *P. boryanum*; ○ fossil record of *P.* sp. aff. *boryanum*.

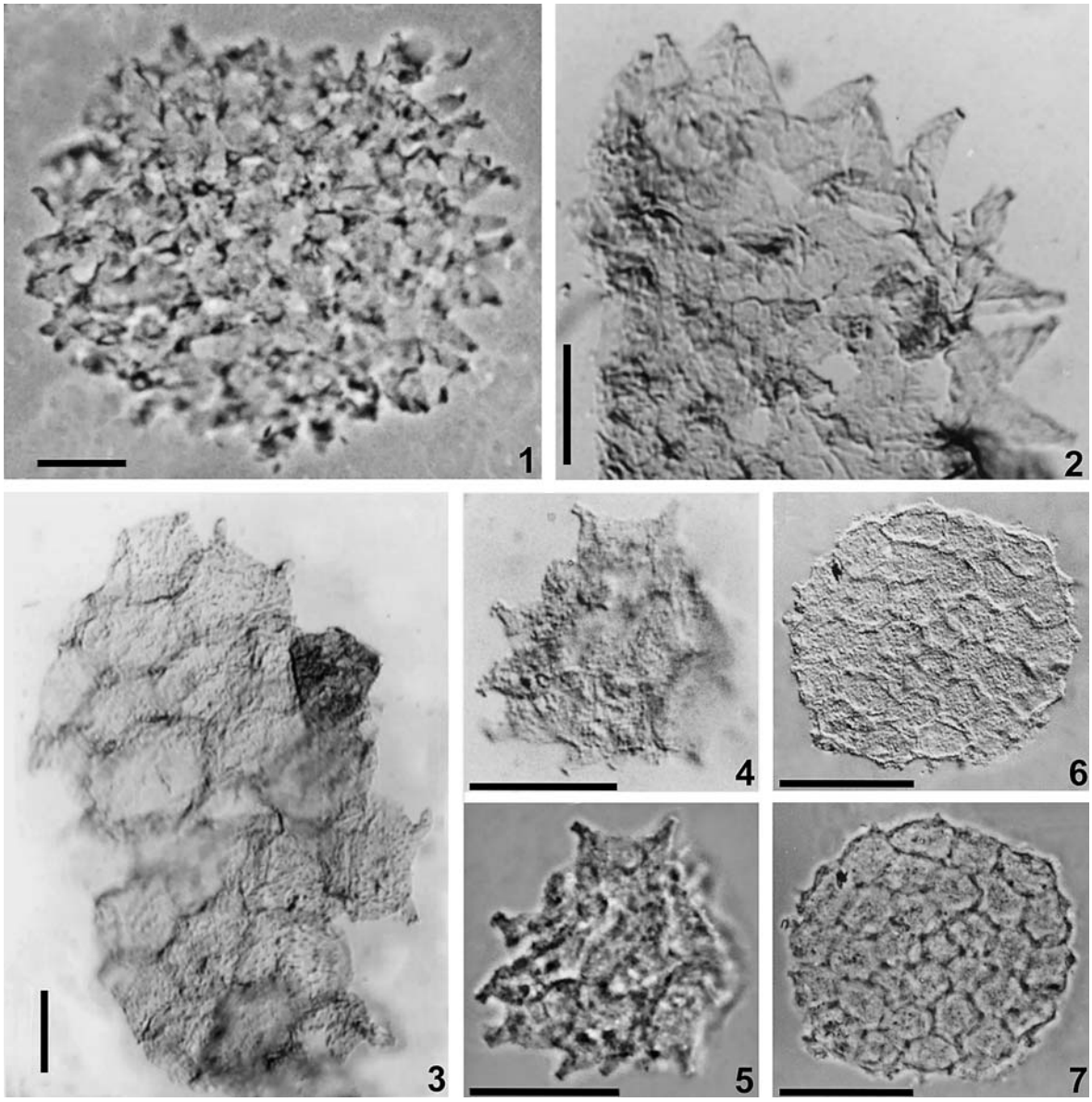

Plate 2. 1–2, *Pediastrum duplex* var. *duplex* (from the Miocene Pinturas Formation); 3–5, *P. boryanum* var. *brevicorne* (3, from the Miocene Pinturas Formation; 4–5, from the Cullen Formation). 6–7, *P. integrum* var. *integrum* (from the Cullen Formation). 2, 3, 4 and 6 in phase contrast. Scale bar = 20 μm.

characterised by the lobes of the external cells oriented in different planes (Tell and Mataloni 1990; Tell and Zamaloa 2004). *P. kawraiskyi* and *P. mustersii* are known from recent and fossil materials; *P. patagonicum* was recorded only from South Patagonia recent freshwater phytoplankton, and *P. leonensis* is only known from fossil samples (Tell and Zamaloa 2004).

Pediastrum kawraiskyi is characterised by the flat or frequently twisted coenobia, without holes, showing the lobes of the marginal cells in different planes. It is a well-known species, with a recent distribution restricted to colder regions, in clear stenotherm oligo- or meso-trophic water bodies, or linked to peaty habitats. We agree with Komárek and Jankovská's (2001) hypothesis that suggests it

is a relictual in its present distribution. Recent representatives in sSA were found in the cold and mountainous region of Central and South Patagonia.

Barreda and Palamarczuk (2000) illustrated two fossil coenobia under the name *Pediastrum* spp. Tell (2004) considered that the individuals shown in these photographs belong to *P. kawraiskyi*.

Fossil record: Only recorded in the Early Miocene of South Patagonia.

Pediastrum leonensis Tell et Zamaloa (Plate 1, figure 16)
This species is distinguished by the large perforations of the coenobia, the Y-shaped inner cells with pronounced concave margins and the almost X-shaped outer cells with two long external horns. This species was not found at present.

Fossil record: Only recorded in the Early Miocene in southern Patagonia.

Pediastrum mustersii Tell et Mataloni (Plate 1, figures 17–21)
Coenobia flat or twisted with regular convex-sided perforations. The species occurs rarely in recent freshwater plankton of mesotrophic or oligotrophic lakes, in temperate and cold regions of Argentina.

Some of the fossil specimens illustrated by Barreda and Palamarczuk (2000) and Guler et al. (2002) under the name *Pediastrum* spp. are here identified as *P. mustersii*. Those coenobia illustrated by Tell (2004, Pl. III) have been found in Holocene deposits of Central East Argentina (ca. 39° S lat.).

Fossil record: Found in Patagonia in the Miocene age and in Central Argentina in the Holocene age.

Pediastrum simplex Meyen (Plate 1, figure 22)
This species presents only one lobe in each marginal cell. According to Komárek and Jankovská (2001) perforations in the coenobia may or may not be present. This is a variable species with many recent infraspecific taxa and many described ecomorphs. The main features for the characterisation of the infraspecific taxa are the morphology of the coenobia and the pattern of the cell wall ornamentation. *P. simplex* is common in freshwater plankton of eutrophic or oligotrophic reservoirs with neutral to alkaline waters (Tell 2004). Komárek and Jankovská (2001) point out that this species occurs in recent temperate and warm regions, and is absent in cold waters. The geographical distribution in South America is consistent with these data.

Fossil record: Late Miocene of Northern Argentina.

Pediastrum tetras (Ehrenb.) Ralfs (Plate 1, figure 23)
Coenobia usually small composed by 4–16(–32) cells, always without holes. This is a very common and widely distributed species, probably represented by different morphotypes. It occurs in plankton of mesotrophic and eutrophic waters of ponds, swamps and shallow lakes. *P. tetras* is distributed throughout sSA.

Fossil record: Early Eocene of North-West Patagonia.

Cretaceous record

The earliest fossil record of *Pediastrum* in sSA is from the Late Cretaceous. In the Maastrichtian age, only *P. boryanum* var. *boryanum* is recognised from the illustrated material. Coenobia were illustrated and identified as *Pediastrum* sp. and as *Pediastrum* sp. aff. *P. boryanum* in a few papers dealing with palynology of several West Central Argentina deposits. Limarino et al. (2000) found the coenobia as the dominant element in the upper levels of the Maastrichtian Ciénaga del Río Huaco Formation.

Paleogene record

Poorly illustrated records demonstrate that representatives of *P.* sp. aff. *boryanum* were present in Patagonia (45° S lat.) during the Paleogene (Papú and Sepúlveda 1997) and in North Argentina (25° S lat.) in the Paleocene (Quattrocchio and Volkheimer 1988, 1990). Abundant mentions of *Pediastrum* sp., lacking illustrations, come from Paleocene and Eocene deposits of Northern Argentina (del Papa 1999; del Papa et al. 2002). The only record of *P. tetras* for the region is registered in the Early Eocene of North-West Patagonia (41° S lat.) (Melendi et al. 2003).

Neogene record

The fossil record of *P. boryanum* var. *boryanum* continues through the Miocene age being reported in few basins from 29° to 41° S lat. It was found in the Chinches, Barranca Final and Cerro Morado Formations (Ottone et al. 1998; Guler et al. 2002; Barreda et al. 2003). Eight species/varieties have their oldest records in the Early Neogene. Representatives of *P. mustersii* have been first recorded in Patagonia (45–50° S lat.) during the Early Miocene age in the Chenque and Monte León Formations (Barreda 1997; Barreda and Palamarczuk 2000). In the latter formation, a mass occurrence of *P. mustersii, P. kawraiskyi* and *P. leonensis* was recognised (Tell and Zamaloa 2004). *P. mustersii* and *P. boryanum* var. *boryanum* were also reported in the Middle to Late Miocene at about 41° S lat. (Guler et al. 2002).

Scarce specimens of *P. integrum* and *P. boryanum* var. *brevicorne* are present in the Early or Middle Miocene Cullen Formation (ca. 52° S lat.). Some levels of the Late Early Miocene Pinturas Formation (ca. 46° S lat.) are completely dominated by *P. duplex* var. *duplex* with a minor proportion of *P. boryanum* var. *brevicorne*. *P. duplex* var. *duplex* also occurs in deposits of uncertain age of the Pachaco Formation from West Central Argentina (ca. 32° S lat.).

Pediastrum simplex has the earliest regional record in the Late Miocene Palo Pintado Formation (26° S lat.) from Northern Argentina (Starck and Anzótegui 2001), where it has been found associated with *P. boryanum* var. *longicorne*. Both species dominate the palynological assemblage in several levels of the outcrop. Acevedo and Anzótegui (1998) referred to such events as "*Pediastrum* episodes".

Quaternary record

Quaternary reports are scarce and most of them lack microphotographs. We can confirm the presence of *P. boryanum* var. *boryanum* and *P. mustersii* in Holocene lakes bottom sediments at 35° and 37° S lat. (Fernandez 1993; Tell 2004).

Discussion

Coenobia of *Pediastrum* are frequently mentioned as part of the Cretaceous and Cenozoic palynological assemblages from sSA. Nevertheless, species identification was only attempted in a few works, whereas well-documented fossil records including descriptions and good quality photographs are uncommon in the literature. All illustrated fossil records for the studied region come from Argentina. There is only one mention of *Pediastrum* sp. in the Late Pliocene of Paraguay (Lovera 1998) and another in the Miocene? of Central Chile (Doubinger 1972).

Several fossil associations, among different species and varieties, occurred since the Miocene age. These are: *P. mustersii* + *P. kawraiskyi* + *P. leonensis*; *P. boryanum* var. *brevicorne* + *P. duplex*; *P. boryanum* var. *brevicorne* + *P. integrum*; *P. boryanum* var. *longicorne* + *P. simplex* and *P. boryanum* var. *boryanum* + *P. mustersii*. Similar assemblages can be found in freshwater phytoplankton at present (except for *P. leonensis*, which is only known as a fossil).

Likewise, mass occurrence episodes can be detected since the earliest record of the genus in Late Cretaceous age. At least four palynological assemblages with abundant and dominant *Pediastrum* are evident: (1) in the Maastrichtian, dominated by *P. boryanum* var. *boryanum* (Limarino et al. 2000); (2) in the Early Miocene, with *P. kawraiskyi, P. mustersii* and *P. leonensis* (Barreda and Palamarczuk 2000; Tell and Zamaloa 2004); (3) in the Late Early Miocene, with *P. duplex* var. *duplex* and *P. boryanum* var. *brevicorne*; and (4) in the Middle to Late Miocene, with *P. simplex* and *P. boryanum* var. *longicorne* (Acevedo and Anzótegui 1998; Starck and Anzótegui 2001).

Assuming that the past ecological requirements of the species/varieties were similar to those of the extant representatives, we can use the fossil record to interpret environmental changes. For most sSA representatives of *Pediastrum*, the fossil and living ranges of geographical distribution are coincident. Nevertheless, the Early Miocene high southern latitude records (ca. 46° and 52° S lat.) of *P. integrum* and *P. boryanum* var. *brevicorne*, two species that are today restricted to lower latitudes (ca. 28° and 39° S lat.), are remarkable. These findings are evidence of the existence of warm-temperate temperatures at high latitudes during this interval of time, and they denote that at least part of the Cullen and Pinturas floras developed under mild climate. Sedimentology, palynology and terrestrial and marine fauna indicate similar

climatic conditions (Bown and Larriestra 1990; Bellosi 1995; Barreda 1996; Zamaloa 1996, 2000). A subsequent retreat in the distribution of warm demanding taxa to lower latitudes could occur as a response to the post Middle Miocene climate cooling.

Since the Late Cretaceous to the Paleogene, most records are sporadic, and mainly represented by *P. boryanum*, while an increase in diversity is apparent during the Miocene. Both observations can be interpreted as a consequence of the tectonic and sedimentary characteristics of the studied region during the Cenozoic and a probable lack of paleoenvironments appropriate for the development of *Pediastrum* as will be discussed below. On the other hand, the scarcity may be reflecting a still incomplete palynostratigraphic knowledge of that interval of time. Likewise, taphonomic and diagenetic processes must not be discarded as being partially responsible for the paucity of the fossil record.

During the Maastrichtian and most of the Paleogene, extensive emergent landmasses, reduced areas of active sedimentation and low sedimentation rates prevailed in sSA. Continental deposits for this interval are sparse (Malumián 1999), while stratal discontinuities (Legarreta and Uliana 1994) providing evidence of widespread erosion are frequent (Bellosi 1995). Major marine successions were deposited during the Late Maastrichtian-Early Paleocene and Late Oligocene, as a consequence of transgressive episodes, when shallow waters coming from the Atlantic Ocean covered lower areas of Patagonia (Malumián 1999).

By the Early Neogene, pronounced paleoenvironmental changes took place. Several extensive Atlantic transgressions influenced Patagonia and few continental deposits accumulated under cool temperate conditions. A brief warmer and humid period was proposed for the Late Early to Middle Miocene when at least part of the Pinturas (and probably the Cullen) Formation accumulated. By the Middle Miocene, the Atlantic waters retreated definitively from mainland Patagonia (Bellosi 1995) coincidentally with the climate cooling.

From the Middle to Late Miocene, in Central and North-East Argentina, the most extended Cenozoic Atlantic transgression flooded the region reaching as far as southern Bolivia and Paraguay, and numerous lacustrine environments were formed close to the Andean and Patagonian borders (Aceñolaza 2000).

As a consequence of the above summarised Neogene regional events, associated to the uplift of the Andes Mountains and to deep climatic global changes, new habitats were created. These seem to have consisted of more or less permanent water bodies, some of them with little marine influence, and in which *Pediastrum* could develop. Further on, in this new scenario, numerous areas of active sedimentation could be established, and a relatively more abundant palynological record was left for this interval.

Conclusions

The present study compiles the fossil sSA record of *Pediastrum*, including species and varieties identifications when possible. Likewise, the importance of accurate species identifications as useful palynological tools to improve paleoenvironmental interpretations is demonstrated.

A total of 10 species/varieties of *Pediastrum* are recognised since the Late Cretaceous to the Quaternary age in sSA. All the taxa but one, *P. leonensis*, are known from present lakes. The oldest record of *Pediastrum* in the studied region comes from the Late Cretaceous age and since that time to the present an almost uninterrupted fossil record is preserved, although records for the Quaternary age are sporadic.

The genus has a wide geographical distribution that includes different basins from North Argentina to Southern Patagonia. *P. boryanum* var. *boryanum* is the oldest and most widespread variety in sSA. Since the Late Cretaceous to the Early Eocene, only *P. boryanum* var. *boryanum* was found. In the Early Eocene *P. tetras* appears. In the Miocene eight different taxa are recognised: *P. boryanum* var. *brevicorne*, *P. boryanum* var. *longicorne*, *P. duplex*, *P. integrum*, *P. kawraiskyi*, *P. leonensis*, *P. mustersii* and *P. simplex*.

The fossil record shows a paucity during the Late Cretaceous-Paleogene and an apparent increase in the diversity in the Miocene. These observations may be a reflection of the geological history and depositional conditions of the studied region (including the existence of appropriate habitats for the growth of *Pediastrum*) otherwise than a representation of the evolutionary history of the genus.

Acknowledgements

We thank Dr. Inés O'Farrell (Universidad de Buenos Aires) and Dr. Eduardo Bellosi (Museo Argentino de Ciencias Naturales B. Rivadavia) for the critical reading of the manuscript.

Plate 1, figures 1, 2, 6, 7, 14, 15, 16, 17, 18 and 20 were reprinted from Ameghiniana with permission from Asociación Paleontológica Argentina; figures 13 and 22 were reprinted from J. S. Am. Earth Sci. with permission from Elsevier; figures 4 and 10 were reprinted from Rev. Esp. Micropaleontol. With permission from Instituto Geológico y Minero de España; figures 11 and 23 were reprinted from N. Jb. Geol. Paläont. with permission from Schweizerbart-Publishers http://www.schweizerbart.de; figures 8 and 21 were reprinted from Arch. Hydrobiol./Algol.Stud. with permission from Schweizerbart-Publishers http://www.schweizerbart.de; figure 3 was reprinted from Palynology with permission from American Association of Stratigraphic Palynologists; figure 5 was reprinted from Rev. Asoc. Geol. Argen. with permission from Asociación Geológica Argentina; figure 12 was reprinted from Geociències with permission from Instituto de Geociências Universidade Guarulhos. The original Plate/figure numbers and full references are indicated in Table 1 and in References.

References

Aceñolaza F. 2000. La Formación Paraná (Mioceno Medio): estratigrafía, distribución regional y medidas equivalentes. In: Aceñolaza F. and Herbst R. (eds), El Neógeno de Argentina. Instituto Superior de Correlación Geológica, Tucumán, Argentina, Serie Correlación Geológica 14, pp. 9–27.

Acevedo L. and Anzótegui L. 1998. El rol de *Pediastrum* en la Formación Palo Pintado (Mioceno superior), Salta, Argentina. Resúmenes VII Congreso Argentino de Paleontología y Bioestratigrafía, Bahía Blanca, Argentina, 1998, pp. 13.

Barreda V. 1996. Bioestratigrafía de polen y esporas de la Formación Chenque, Oligoceno Tardío?-Mioceno de las provincias de Chubut y Santa Cruz, Patagonia, Argentina Ameghiniana 33: 33–56.

Barreda V. 1997. Palynomorph assemblage of the Chenque formation, Late Oligocene?-Miocene from Golfo San Jorge Basin, Patagonia, Argentina. Part 1: terrestrial algae, trilete and monolete spores Ameghiniana 34: 69–80.

Barreda V. and Bellosi E. 2003. Ecosistemas terrestres del Mioceno Temprano de la Patagonia central, Argentina: primeros avances. Rev. Mus. Argen. Cienc. Nat., n.s. 5: 125–134.

Barreda V. and Palamarczuk S. 2000. Palinomorfos continentales y marinos de la Formación Monte León en su área tipo, provincia de Santa Cruz, Argentina. Ameghiniana 37: 3–12.

Barreda V., Limarino C., Fauqué L., Tripaldi A. and Net L. 2003. Primer registro palinológico del miembro inferior de la Formación Cerro Morado (Mioceno), Precordillera de La Rioja. Ameghiniana 40: 81–87.

Batten D. 1996. Colonial Chlorococcales. In: Jansonius J. and McGregor D.C. (eds), Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation, Dallas, Texas, USA, pp. 191–203.

Bellosi E. 1995. Paleogeografía y cambios ambientales de la Patagonia central durante el Terciario medio. Bol. Inform. Petrol. 44: 50–83.

Bown T. and Larriestra C. 1990. Sedimentary paleoenvironments of fossil platyrrhine localities, Miocene Pinturas Formation, Santa Cruz Province, Argentina. In: Fleagle J. and Rosenberger A. (eds), The Platyrrhine Fossil Record. Academic Press Ltd, London, pp. 87–119.

del Papa C. 1999. Sedimentation on a ramp type lake margin: Paleocene-Eocene Maíz Gordo Formation, northwestern Argentina. J. S. Am. Earth Sci. 12: 389–400.

del Papa C., García V. and Quattrocchio M. 2002. Sedimentary facies and palynofacies assemblages in an Eocene perennial lake, Lumbrera formation, northwest Argentina. J. S. Am. Earth Sci. 15: 553–569.

Doubinger M. 1972. Evolution de la flore (pollens et spores) au Chili central (Arauco), du Crétacé supérieur au Miocéne. C. R. Soc. Biogéogr. 427: 17–25.

Evitt W. 1963. Occurrence of freshwater alga *Pediastrum* in Cretaceous marine sediments. Am. J. Sci. 261: 890–893.

Fleagle J., Bown T., Swisher C. and Buckley G. 1995. Age of the Pinturas and Santa Cruz Formations. Actas VI Congreso Argentino de Paleontología y Bioestratigrafía, Trelew, Argentina, 1994, pp. 129–135.

Fernández C. 1993. Fungal palynomorphs and algae from Holocene bottom sediments of Chascomús Lake, Buenos Aires province, Argentina. Palynology 17: 187–200.

Guerstein G. 1990. Palinología estratigráfica del Terciario de la Cuenca del Colorado, Republica Argentina. Parte I: Especies terrestres de la perforación Nadir N° 1. Rev. Esp. Micropaleontol. 22: 33–61.

Guler M., Guerstein G. and Malumián N. 2002. Bioestratigrafía de la Formación Barranca Final, Neógeno de la Cuenca del Colorado, Argentina. Ameghiniana 39: 103–110.

Komárek J. and Jankovská V. 2001. Review of the green algal genus *Pediastrum*; implication for pollen-analytical research. Biblioth. Phycol. 108: 1–127.

Legarreta L. and Uliana M. 1994. Asociaciones de fósiles y hiatos en el Supracretácico-Neogeno de Patagonia: una perspectiva estratigráfico-secuencial. Ameghiniana 31: 257–281.

Limarino C., Net L., Gutiérrez P., Barreda V., Caselli A. and Ballent S. 2000. Definición litoestratigráfica de la Formación Ciénaga del Río Huaco (Cretácico Superior), Precordillera central, San Juan, Argentina. Rev. Asoc. Geol. Argen. 55: 83–99.

Lovera C. 1998. Palinología y ambiente de la Formación Ituzaingó (Plioceno Superior) del Departamento Itapúa, República del Paraguay. Resúmenes VII Congreso Argentino de Paleontología y Bioestratigrafía, Bahía Blanca, Argentina, 1998, pp. 23.

Malumián N. 1999. La sedimentación y el volcanismo terciarios en la Patagonia Extraandina. La sedimentación en la Patagonia Extraandina. In: Caminos R. (ed.), Geología Argentina, Anales del Instituto de Geología y Recursos Minerales 29, pp. 557–612.

Melendi D., Scafati L. and Volkheimer W. 2003. Palynostratigraphy of the Paleogene Huitrera formation in N-W Patagonia, Argentina. N. Jb. Geol. Paläont. Abh. 228: 205–273.

Ottone E., Barreda V. and López D. 1998. Basin evolution as reflected by Miocene palynomorphs from the Chinches formation, Frontal Cordillera (32°S), San Juan province, Argentina. Rev. Esp. Micropaleontol. 30: 35–47.

Papú O. 1990. Contribución a la palinología estratigráfica de la Formación Malargüe, Cretácico Superior, sur de la provincia de Mendoza, Argentina. Parte I: Especies terrestres y de aguas continentales. Ameghiniana 27: 289–303.

Papú O. 2002. Nueva microflora de edad maastrichtiana en la localidad de Calmu-Co, sur de Mendoza, Argentina. Ameghiniana 39: 415–426.

Papú O. and Sepúlveda E. 1997. Nuevos datos sobre la presencia de *Azolla* Lamarck (Salviniaceae) en el Paleógeno de la Patagonia, Argentina. Algunos aspectos paleoambientales y paleoclimáticos. Geociências 2 (n° especial): 107–111.

Prámpano M., Papú O. and Milana J. 1996. Estudio palinológico del miembro inferior de la Formación Pachaco, Terciario de la Provincia de San Juan. Descripciones sistemáticas. Ameghiniana 33: 397–407.

Quattrocchio M. and Volkheimer W. 1988. Microflora de los estratos limítrofes entre Cretácico y Terciario en las localidades de Tilián y Corralito, Cuenca del Grupo Salta. Descripciones sistemáticas. Actas IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza, Argentina, 1986, pp. 109–120.

Quattrocchio M. and Volkheimer W. 1990. Paleogene paleoenvironmental trends as reflected by palynological assemblage types, Salta Basin, NW Argentina. N. Jb. Geol. Paläont. Abh. 181: 377–396.

Singh H. and Khanna A. 1978. Some fossil species of *Pediastrum* and their palaeoecological significance in the Subathu Formation of Himachal Pradesh. Paleobot. 25: 466–474.

Starck D. and Anzótegui L. 2001. The late miocene climatic change-persistence of a climatic signal through the orogenic stratigraphic record in northwestern Argentina. J. S. Am. Earth Sci. 14: 763–774.

Tell G. 2004. Recent and fossil species of the genus *Pediastrum* Meyen (Chlorococcales) from Argentina and their geographical distribution. Arch. Hydrobiol./Algol. Stud. 112: 49–71.

Tell G. and Mataloni G. 1990. Systematic studies on the *Pediastrum kawraiskyi–musterii–patagonicum* complex (Chlorophyta): two new species and morphological variations in two Patagonian lakes (Argentina). Nova Hedwigia 50: 159–180.

Tell G. and Zamaloa M.C. 2004. A Miocene algal assemblage dominated *by Pediastrum leonensis* n. sp. (Chlorophyceae) from Patagonia, Argentina: paleoenvironmental implications. J. Paleolimnol. 32: 247–254.

Wilson L. and Hoffmeister W. 1953. Four new species of fossil *Pediastrum*. Am. J. Sci. 251: 753–760.

Zamaloa M.C. 1993. Hallazgos palinológicos en la Formación Pinturas, Sección Cerro de los Monos (Mioceno inferior), Provincia de Santa Cruz, Argentina. Ameghiniana 30: 353.

Zamaloa M.C. 1996. Asociación de zigósporas de Zygnemataceae (Chlorophyta) en el Terciario Medio de Tierra del Fuego, Argentina. Ameghiniana 33: 179–184.

Zamaloa M.C. 2000. Palinoflora y ambiente en el Terciario medio del noroeste de Tierra del Fuego, Argentina. Rev. Mus. Argen. Cienc. Nat., n.s. 2: 43–51.

Zamaloa M.C. 2004. Miocene algae and spores from Tierra del Fuego, Argentina. Alcheringa 28: 205–227.