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# A Danian subtropical lacustrine palynobiota from South America (Bororó Formation, San Jorge Basin, Patagonia - Argentina)

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## ABSTRACT

New results on a lacustrine Danian palynological association in extra-andean northern Patagonia (lower member of the Cerro Bororó Formation, San Jorge Basin, Chubut province, Argentina) are presented. This is a contribution to the largely unexplored field of Paleogene freshwater environments. The palynobiota includes representatives of the kingdoms Protoctista and Plantae. Twelve of the aquatic species are Protoctista. From the nine Chlorophyta form-species, four correspond to Botryococcaceae, one to Coelastraceae and four to Zygnemataceae (*Gelasinicysta*, *Schizosporis*, *Ovoidites*, and *Pseudoschizaea*). The remaining forms are dinoflagellate cysts (*Peridinium* and dinocyst indet.) and prasinophyceans (*Leiosphaeridia*). Plants are represented by spores and pollen of Bryophytes (Sphagnaceae and Ricciaceae), Pteridophytes (Salviniaceae), and Angiosperms (Arecaceae, Araceae and Sparganiaceae/Typhaceae, the latter representing macrophytes living in or near the swampy areas). Other palynomorph groups closely related with biotopes of permanent moisture are dominated by spores of the families Selaginellaceae, Lycopodiaceae, Cyatheaceae, Schizaeaceae, Polypodiaceae and Psilotaceae. The palynological assemblage reflects a freshwater lacustrine environment that developed in a marine coastal zone nearby brackish coastal swamps. Based on the composition of the palynoflora including palm pollen and other thermophilous taxa, humid, warm climatic conditions are inferred for the area of deposition.

*KEYWORDS* **Paleogene. Patagonia. Palynology. Aquatic palynomorphs. Paleoenvironment.**

## INTRODUCTION

In paleopalynology, the algal elements constitute a problematic issue. The lack of knowledge affects the systematic work, mainly in supra-generic assignations. In pioneer works, the algal elements found in sediments were identified, but their biological affinities remained poorly known. Later, renewed interest was paid to the palynology of aquatic environments through the studies of Van Geel (1976a, b, 1978, 1979, 1986), Van Geel and Van der Hammen (1978) and Van Geel et al. (1981, 1984, 1989), among others (see Martin-Closas, 2003 and cites therein).

This paper deals with the description of a new Danian fresh lacustrine palynobiota recovered from the Bororó Formation (Fm) lower Member (San Jorge Basin, Chubut Province, Argentina; Figs. 1 and 2). This palynological assemblage was yielded by a single 15 cm thick bed of carbonaceous mudstone, and is part of a major palynologic association described in Volkheimer et al. (2007). Previous studies of the Bororó Formation include those of Romero (1968), Archangelsky et al. (1969), Petriella (1972), Andreis et al. (1973), Bertels (1973), Archangelsky (1973, 1976), Archangelsky and Romero (1974), Petriella and Archangelsky (1975), Arguijo (1979), Archangelsky and Zamaloa (1986) and Durango de Cabrera and Romero (1988).

This study is a contribution to the general knowledge of paleobiota Paleogene freshwater environments, providing a new palynologic assemblage for the Bororó Fm. Of particular importance is the investigation of the scarcely studied group of microalgae, previously unknown for this formation.

## GEOLOGICAL SETTING

The Bororó Fm crops out near the north-western border of the San Jorge Basin, which is one of the main sedimentary basins of Patagonia existing at that time (Colorado, Valdés and San Jorge basins), to the north of the Austral basin (Menichetti et al., 2008; Tassone et al., 2008; Rosello et al., 2008). The general paleogeography of Patagonia and the major lithofacies distribution within these basins during Danian times is presented on Fig. 2 (adapted from Malumián, 1999). The stratigraphic section at the sampling locality (Cerro Bororó, Puesto Fernández) is shown on Fig. 3.

The Lower Member of the Cerro Bororó Fm unconformably overlies the Late Cretaceous Chubut Group. An alternation of marginal marine strata and near-coast freshwater deposits occur in the sections.

The Danian age of the Cerro Bororó Fm at the sampling locality was established by Bertels (1973), who identified the forams *Cibicides succedens* Brotzen and *Discorbis* sp. aff. *D. newmanae* Plummer, in the Upper Member of the formation. These findings allowed a correlation with the Salamanquiano Stage of the southern part of the same San Jorge Basin (see Fig. 1 in Raigenborm et al., this issue) and also with the upper Danian of Europe.

## MATERIAL, METHODS AND TAXONOMICAL CRITERIA

The sampling locality is situated at Puesto Fernández, front of Cerro Bororó (67° 45' W; 43° 40' S), approximately 35 km to the west of Las Plumas locality, Chubut province (Fig. 1).

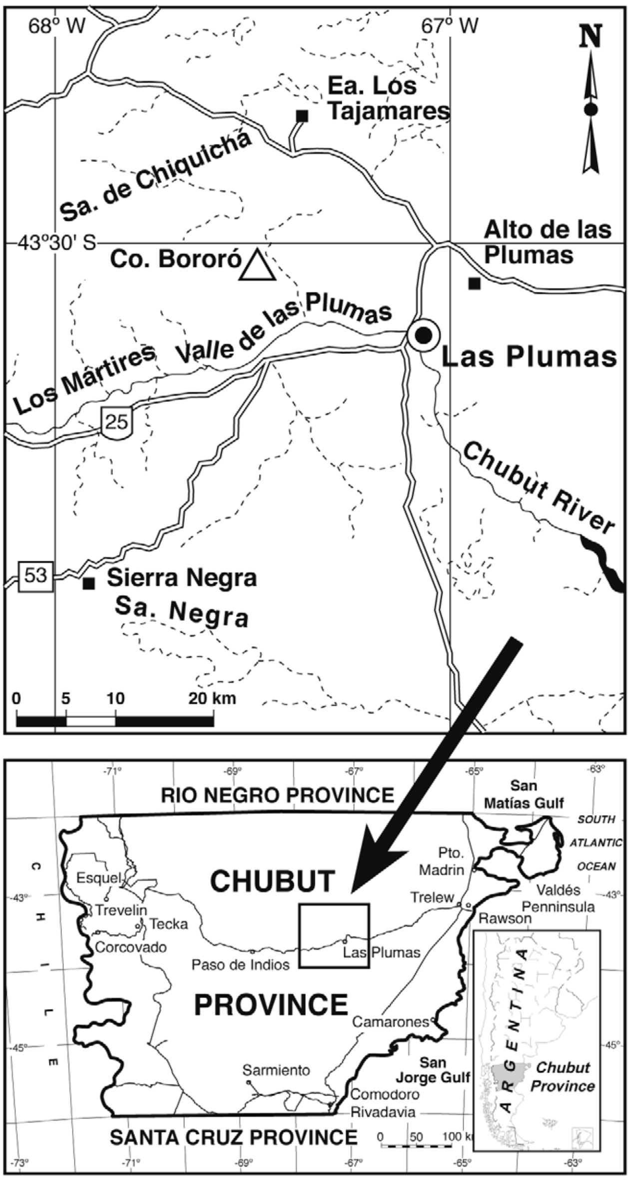

FIGURE 1 **Location map of the study area showing the position of the studied section.**

For the palynological extraction, hydrochloric acid (10%) and hydrofluoric acid (70%) were used to remove carbonates and silicates, respectively. The extracted kerogen was sieved (10 $\mu$m mesh) with sodium hexametaphosphate 0.3%. The macerated residue was oxidized with nitric acid (30%). Microscope slides were mounted in glycerine jelly and are stored in the paleopalynological repository at IANIGLA/CCT-CONICET, Mendoza province. The relative abundance of palynomorphs was based on counts of 300 palynomorph specimens.

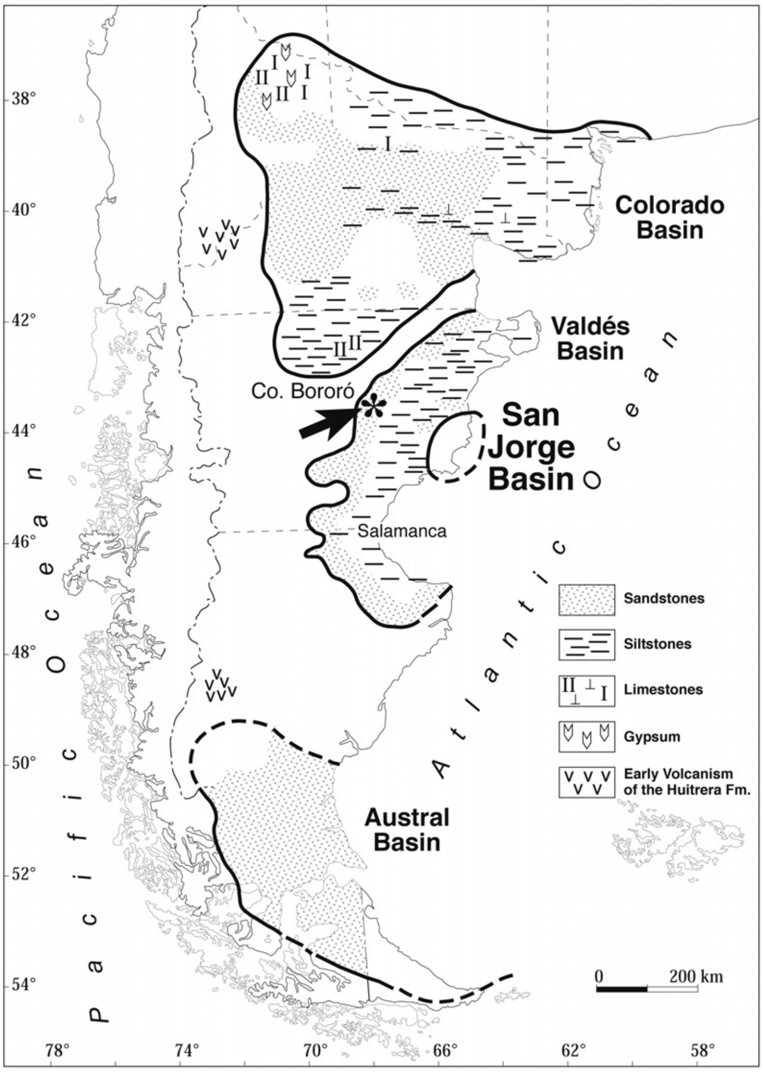

FIGURE 2 **Danian paleogeographic map of the Argentinean Atlantic continental margin showing the main sedimentary basins and their lithofacies distribution and the location of the Cerro Bororó sampling locality within the San Jorge Basin, Chubut Province (adapted from Malumián, 1999).**

Considering the diversity of this excellently preserved palynobiota, we had to make an intensive use of optical and scanning electron microscopy in order to provide a detailed taxonomic analysis of the material. The study was carried out with optical microscopes (OM) Leitz Ortholux No.762978 and Leitz Dialux 20 with interference contrast. SEM studies (Phillips XL Serie 30) were done at the Museo "B. Rivadavia." The photomicrographs were taken with Agfapan APX25 and Kodak Professional 100 TMAX film.

We follow the Whittaker classification of five kingdoms for highest taxonomic levels, considering the modifications made by Margulis and Schwartz (1998). In this classification scheme the Kingdom Plantae includes only the embryophytes, which comprise the bryophytes and tracheophytes (vascular plants). All algae belong to the very diverse Kingdom Protoctista. "Algae" is a term still in use but without taxonomic status, integrated by a heterogeneous and polyphyletic group of prokaryotic and principally eukaryotic photosynthetic organisms, traditionally included in the Kingdom Plantae (Margulis and Schwartz, 1998; Graham and Wilcox, 2000). Thus, all algae are considered here as belonging to the Kingdom Protoctista. Due to the presence of palynomorphs representing both the kingdoms Plantae and Protoctista, we refer to this assemblage as a palynobiota.

In the case of dinoflagellates the classification of Fensome et al. (1993) has been adopted. The classifications for each taxonomic group of the Kingdom Plantae follow Shaw and Goffinet eds. (2000) for bryophytes and Cronquist, Takhtajan and Zimmermann (1966) for pteridophytes and angiosperms.

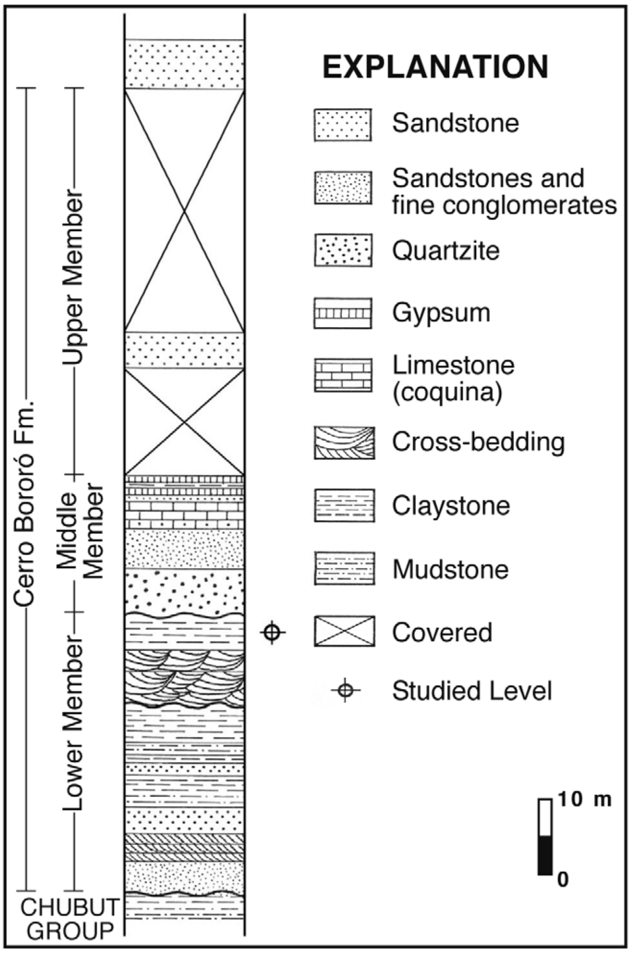

FIGURE 3 **Stratigraphic section at the sampling locality showing the Cerro Bororó Fm, which unconformably overlies the Chubut Group, and the location of the studied samples (modified from Petriella, 1972).**

# RESULTS

## Composition of the palynobiota

The composition of the palynological assemblage from the Bororó Fm in the Puesto Fernández locality is shown in Fig. 4.

The aquatic forms comprise all specimens pertaining to the protoctist and a heterogeneous assemblage of unrelated aquatic plants (ferns, ferns-allies and angiosperms). Some of them are fully aquatic plants (hydrophytes), others are emergent plants rooted in a substrate below standing water (helophytes), while others may reflect stages of growth and reproduction in an aquatic environment.

The environmental characteristics of the palynobiota components allow the distinction of four groups reflecting the habitat categories and the associated algal forms.

### *Forms associated to permanently humid biotopes*

These forms correspond to bryophytes belonging to the Sphagnaceae [*Cingutriletes australis, Stereisporites antiquasporites*], and pteridophytes represented by the families Lycopodiaceae [*Retitriletes austroclavatidites, R. rosewoodensis*], Selaginellaceae [*Ceratosporites equalis, Selaginella perinata*], Cyatheaceae [*Deltoidospora minor*], Schizaeaceae [*Kuklisporites variegatus*], and Polypodiaceae? [*Laevigatosporites ovatus*, *Tuberculatosporites parvus, Polypodiisporites irregularis*] among others strongly related with this type of environments.

### *Palustrine forms*

They are represented by the aquatic angiosperms (rooted macrophytes) of the families Sparganiaceae/Typhaceae [*Sparganiaceaepollenites barungensis*], and Liliaceae [*Liliacidites regularis, L. variegatus*].

### *Floating macrophytes*

They include aquatic pteridophytes belonging to the Salviniaceae family [*Azollopsis (Azollopsis) tomentosa, Azollopsis (Spiralopsis) intermedia*], and bryophyte spores of the Ricciaceae family [probably floating forms of *Ricciocarpus natans*].

### *Halophytes and coastal forms*

They are represented by monosulcate and zonosulcate grains with affinity to the Arecaceae and Araceae; in particular to a group of palms related to the living *Nypa* (*Spinizonocolpites*-complex, *Proxapertites*-group, *Longapertites andreisii, L. patagonicus*).

### *Algal forms*

These forms are represented by chlorophytes of the families Botryococcaceae [*Botryococcus* sp.1, *B.* sp.2, *B.*

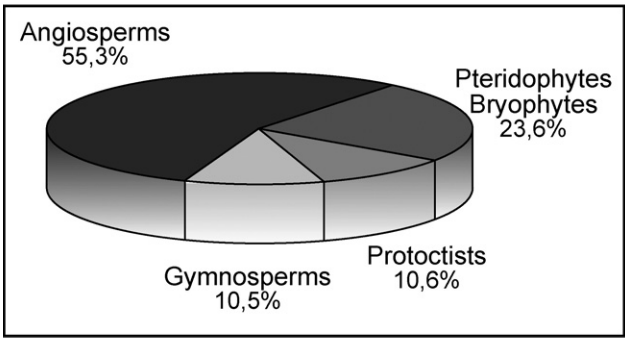

FIGURE 4 **Statistical diagram illustrating the relative abundance of the different systematic groups identified.**

sp.3, and *B.* sp.4], Coelastraceae (*Coelastrum* sp.) and Zygnemataceae [*Gelasinicysta vangeelii*, *Ovoidites* spp., *Schizosporis reticulatus* and possibly *Pseudoschizaea circula*], prasinophytes [*Leiosphaeridia hyalina*], and dinoflagellates [*Peridinium* sp. aff. *P. limbatum,* and dinocyst indet.].

## SYSTEMATIC PALYNOLOGY

Previous studies allow, with some confidence, the assignment of some fossil forms to extant families; however, in most cases form-genera are used. Notes on stratigraphic range and biological / botanical affinities are also included.

### KINGDOM PROTOCTISTA

***Algae***
**Division:** Chlorophyta PASCHER, 1914
**Class:** Chlorophyceae KÜTZING, 1843
**Order:** Chlorococcales MARCHAND orth. mut. PASCHER, 1915
**Family:** Botryococcaceae WILLE, 1909

GENUS ***Botryococcus*** KÜTZING, 1849

*Type species*: *Botryococcus braunii* KÜTZING 1849

The complicated colonial structure and the wide variability in morphologies make the taxonomic evaluation of this genus extremely difficult. In the current bibliography, *B. braunii* includes a vast spectrum of different forms. Jankovská and Komárek (2000) remark that fossil specimens commonly identified as *B. braunii* are, in most cases, a mixture of different species, adding that even in recent material species identification is relatively difficult. Furthermore, three fossil algae identified as *B. braunii* and several colonies of the modern alga *B. braunii* were studied with the light and transmission electron microscope by Burns (1982), who concluded that they represent three separate genera.

Komárek and Marvan (1992) collected populations of *Botryococcus* from different biotopes and performed a morphological analysis using light microscopy. They mention that the wide morphologic variability indicates higher species diversity within the genus. The authors identified five main groups taking into account the morphologic characters and using clustering strategies. Molecular data (Senousy et al., 2004) also support the idea that *B. braunii* should be considered as more than one species and that other species (e.g., *B. sudeticus*) should be transferred to a separate genus.

*Stratigraphic Range:* The Chlorococcales radiated and developed during the Palaeozoic. This genus has been reported from the Ordovician (or even Precambrian) to the present.

*Biological Affinity*: The specimens recovered from this palynologic assemblage are assignable to the genus *Botryococcus* and may involve several taxonomically related species. The genus is placed within the Botryococcaceae by Komárek and Fott (1983), but is assigned to the Dictyosphaeraceae by other authors.

*Habitat*: Traverse (1995) compiling data from many sources, expresses that it is highly probable that the habitat of *Botryococcus* corresponds to small, quiet, open ponds of freshwater and it is rarely found in peaty swamps, in which the water contains considerable humic matter. According to Komárek and Fott (1983), *Botryococcus* is a cosmopolitan planktonic algae, attached to benthonic plants or epiphytic on submerged plants. Zippi (1998) refers that it commonly forms water-blooms in hard waters of lakes and ponds.

*Remarks***:** Guy-Ohlson (1992) and Guy-Ohlson and Lindström (1994), considered that the comparisons between fossil and modern forms of this genus have shown to be valuable as paleoecological indicators. The variation in morphology exhibited by living *Botryococcus* may be related to environmental changes and specimens with different morphology coming from the same sample may reflect seasonal changes at the time of deposition. Batten and Grenfell (1996) indicate that fossil colonies of *Botryococcus* may be more variable in their appearance than their modern counterparts. In their opinion, the forms considered suggest a morphological continuum probably showing a single polymorphic species and perhaps reflecting different environmental conditions and/or developmental stages rather than the presence of more than one taxon. Rodríguez Amenabar and Ottone (2003) analyzed *Botryococcus* colonies from the Triassic of San Juan province (Argentina) and prefer to support an open specific assignation.

*Observations*: The morphologic features evaluated by Komárek and Marvan (1992) are linked to different parameters of the cells, colonies, mucilage and reproduction, but in the fossil material only a few of these parameters are available. Given these limitations, in our study we leave the specific assignation open and compare the colonies with the material illustrated and described by Komárek and Marvan (1992).

The vast morphologic variability of our specimens, and the excellent preservation conditions of the material, allowed performing the SEM study, showing the probable presence of four different form-species: *Botryococcus* sp.1 to *B.* sp.4. The discrimination of these different types was only possible through SEM images analysis; this situation is an evidence for the different quality of data when using different tools (SEM vs. OM) for classification.

***Botryococcus* sp. 1**
Figure 5A

*Description*: Colony circular to subcircular. Cups in groups of four, grouped in pairs, and located within discrete supporting structures. Supporting structure subcircular to oval; elaborate, massive, with a distinctive packing aspect.

*Size*: Diameter of the colonies: 35 μm. Structures bearing cups: Range of the diameter M= 8–11 μm (9,6 μm); range of the diameter m= 5–9 μm (7,6 μm); cup diameter: 2–2,5 μm

*Comparisons*: These specimens are similar to *B. fernandoi* KOMÁREK and MARVAN 1992.

*Remarks*: The habitat of *B. fernandoi* is planktonic in tropical lakes.

***Botryococcus* sp. 2**
Figure 5B

*Description*: Colony circular to subcircular. Cups single, circular, isolated and of homogeneous distribution, following an approximately orthogonal pattern. Separation between cups, generally not exceed their diameter. Borders of the cups may present folds or concentric, slightly pronounced thickenings.

*Size:* Diameter of the colonies: 45 μm. Range of the diameter of the cups: 5, 2–6, 8 μm (5,75 μm).

*Comparisons:* These specimens are similar to *B. pila* KOMÁREK and MARVAN 1992.

According to Komárek and Marvan (1992), the fossil findings assigned to *Pila*, as well as the majority of *Botryococcus* collections from Late Glacial and Postglacial peaty deposits, probably belong to this species.

*Remarks: B. pila* inhabits *Sphagnum* swamps and moors with an acid pH.

***Botryococcus* sp. 3**
Figures 5D and E

*Description*: Colony circular to subcircular. Groups of three to four cups located on bearing structures. Every bearing structure supported by a small "stem" expanding distally forming a three- or tetra-lobulate rosette, in which three or four cups are located; one of them in every lobe. These structures are very tightly distributed. The cups frequently present a striate inner wall.

*Size*: Diameter of the colonies: 45 μm. Diameter of the rosette: 7–8 μm. Diameter of the cups: 2,5 μm.

***Botryococcus* sp. 4**
Figure 5C

*Description*: Colony circular to subcircular. Cups thin walled, cylindrical to subcylindrical, wider than higher, uniformly and isolate distributed. Frequently, the marginal border of the cups is rolled inside.

*Size*: Diameter of the colonies: 47 μm. Range of the diameter of the cups: 6–7 μm (6,5 μm). Thickness of the wall of the cups: less than 1 μm.

*Comparisons*: These specimens are similar to *B. protuberans* WEST and WEST 1905 and *B. australis* KOMÁREK and MARVAN 1992.

*Remarks: B. protuberans* inhabits in clear oligo to mesotrophic or slightly eutrophic lakes. The habitat of *B. australis* is in clear ponds and lakes.

**Family:** Coelastraceae WILLE, 1909

GENUS ***Coelastrum*** NÄGELI in KÜTZING, 1849

*Type species: Coelastrum sphaericum* NÄGELI, 1849

***Coelastrum*** sp.
Figure 6A

*Description*: Coenobia of sphaeric to subsphaeric shape, wall surface scabrate and entirely conformed by polygonal to subpolygonal closely contacted packed cellular structures. Their diameters represent between 1/8 and 1/4 of the cenobial diameter. A simple, well defined circular aperture is present in each cellular structure, in a concentric disposition, whose diameter is 1/3 to 1/2 of the cell.

*Size*: Diameter of coenobium: 61 μm (one specimen measured). Diameter of the cellular structures: 8 to 14.5 μm. Diameter of the apertures: 2.8 to 7.5 μm.

*Stratigraphic Range*: This genus has been reported since the Devonian to the present.

*Biological Affinity*: The genus *Coelastrum* is placed within the Coelastraceae by Komárek and Fott (1983), but is also assigned to the Scenedesmaceae by other authors.

*Habitat*: This genus has been reported exclusively in freshwater habitats, growing in small ponds. Modern species are common in freshwater lakes and bogs. According to Jankovská and Komárek (2000), the occurrence of *Coelastrum* indicates eutrophication (data from fossil sediments).

*Remarks*: The coenobia are in most species hollow spheres composed of 4 to 128 cells.

**Class:** Charophyceae G.M. SMITH, 1938
**Order:** Zygnematales BORGE in PASCHER, 1913
**Family:** Zygnemataceae (MENEGHINI) KÜTZING, 1898

Form-GENUS ***Gelasinicysta*** HEAD, 1992

*Type species: Gelasinicysta vangeelii* HEAD, 1992

***Gelasinicysta vangeelii*** HEAD, 1992
Figures 6B, C and D

*Brief Description*: Spores composed of two convex to hemispherical halves joined by an equatorial suture. Outline circular to broadly elliptical in polar view. The wall is unstratified, with numerous large curved depressions of approximately even distribution and size over the spore.

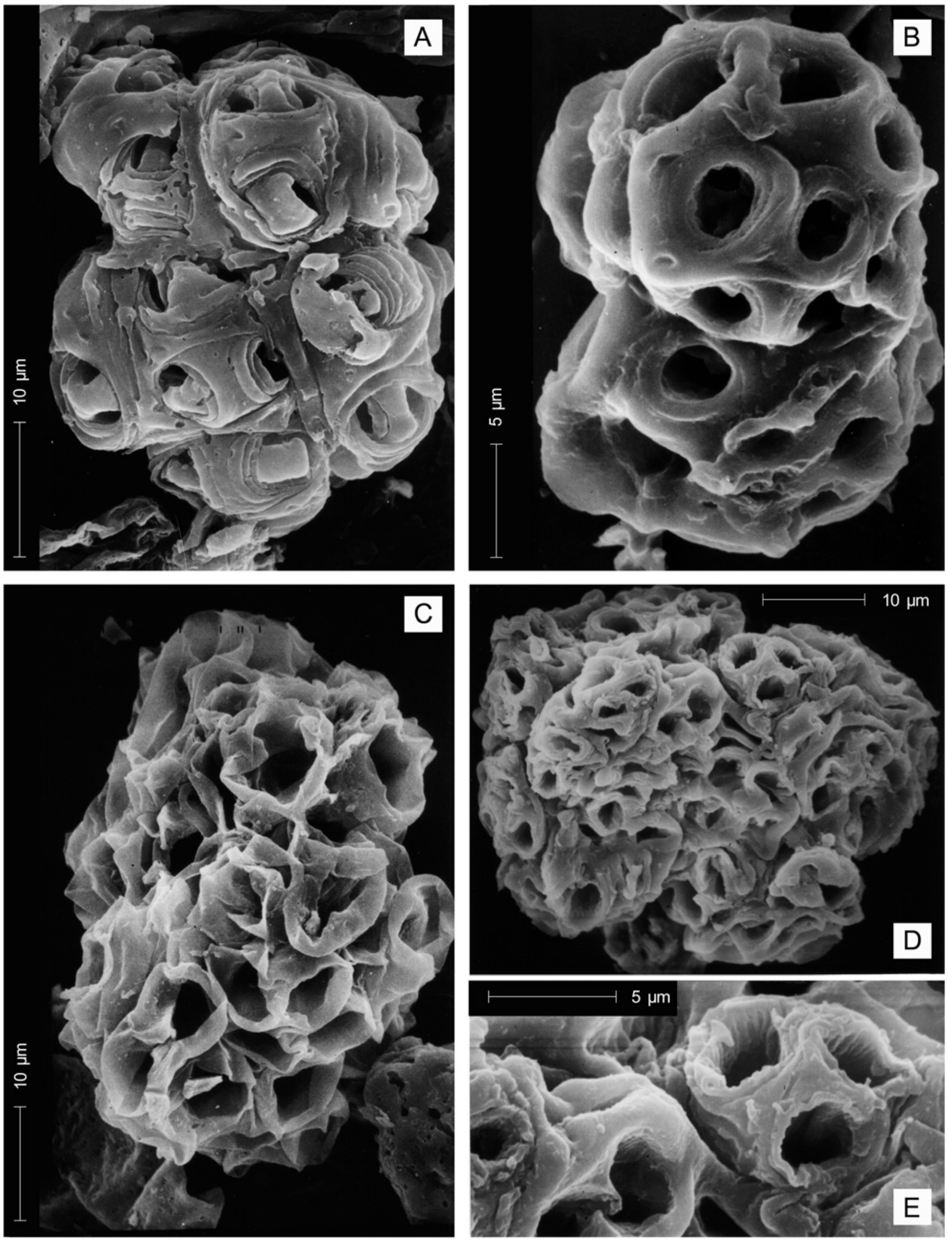

FIGURE 5 **A) *Botryococcus* sp. 1 [SEM]; B) *B.* sp. 2 [SEM]; C) *B.* sp. 4 [SEM]; D) B. sp. 3 [SEM]; E) *B.* sp. 3 detail [SEM].**

Wall surface is smooth or faintly granulate. Equatorial diameter: 65 to 73 μm.

*Stratigraphic Range: T*he Zygnemataceae range from the Carboniferous to the present. Zygnematales radiated and developed during the Palaeozoic and diversified during the Jurassic and Early Cretaceous; Mougeotia is recorded from this time. According with Head (1992), spores possibly assignable to *Gelasinicysta* have a range that probably extends downwards at least into the Paleogene (Eocene?).

*Biological Affinity: Zygnema*-type. The specimens resemble zygospores that occur in several extant genera of the Zygnemataceae, especially *Zygnema* but also *Mougeotia.* According to Van Geel and Van der Hammen (1978) this type of spores is also known in the family Oedogoniaceae.

*Habitat*: Zygnematalean algae are almost exclusively found in freshwater habitats and especially in bogs and mildly acidic, nutrient-poor streams (Graham and Wilcox, 2000). The modern genera have a wide distribution, preferring slowly flowing freshwater streams or stagnant ponds and exhibit tolerance of a wide range of pH (3-9). According to Van Geel and Van der Hammen (1978), optimal growth conditions for *Zygnema* are temperatures between 15 and 20°C.

*Remarks*: Microfossils with similar characteristics have been previously assigned to the Zygnemataceae Type 58 (Van Geel, 1978), *Zygnema*-type (Van Geel 1986; Van Geel et al., 1989; Van Geel and Van der Hammen, 1978; Van Geel et al., 1981); *Zygnema* sp. (Melendi, Scafati and Volkheimer, 2003), *Zygnema*? sp. Tipo B (Zamaloa, 1996), and *Catinipollis geiseltalensis* (Frederiksen, 1983; Archangelsky and Zamaloa, 1986; Zamaloa and Romero, 1990; Báez et al., 1991), among other records, some of them in Head (1992).

Form-GENUS ***Ovoidites*** POTONIÉ, 1951 ex THOMSON and PFLUG, 1953 emend. KRUTZSCH, 1959

*Ovoidites* POTONIÉ 1951 (nomen nudum)
*Ovoidites* POTONIÉ ex THOMSON and PFLUG 1953
*Ovoidites* POTONIÉ emend. KRUTZSCH 1959
*Schizosporis* COOKSON and DETTMANN 1959
*Ovoidites* POTONIÉ *ex* POTONIÉ 1966
*Brazilea* TIWARI and NATALE 1967
*Psiloschizosporis* JAIN 1968
*Pilospora* VENKATACHALA and KAR 1968
*Schizophacus* PIERCE 1976
*Schizosporis* (COOKSON and DETTMANN) TAKAHASHI and JUX 1982

*Type species: Ovoidites ligneolus* POTONIÉ ex KRUTZSCH, 1959

***Ovoidites*** spp.
Figures 6E and F; Figure 7A

*Brief Description:* Spores typically ovoid. However, the shapes of individuals vary considerably from subspherical to elliptical, with a dehiscence suture extended around the equator along which the specimens split. Specimens frequently occurs gaping open at the ends. Sculpturing is variable; specimens seen in transmitted light appear smooth or reticulate. Equatorial diameter: 35 to 48 μm.

*Stratigraphic Range: Ovoidites* range extends back to the Cretaceous; the range of the genus *Spirogyra* extends from the Carboniferous to the present.

*Biological Affinity*: All the morphological features of this genus are comparable with zygospores of modern zygnematacean genera such as *Spirogyra* and *Sirogonium* (Zippi, 1998).

*Habitat*: Among living *Ovoidites*-producing algae habitat preferences include stagnant, shallow and more or less mesotrophic freshwater habitats (Van Geel and Van der Hammen, 1978). According to Rich et al. (1982), *Ovoidites* occurs preferentially in open, freshwater marsh habitats having an apparently narrow range of habitat preferences. Following Zippi (1998), in situ *Ovoidites* can be used to infer freshwater paleoenvironments where the water depth is shallow lacustrine, paludal or low gradient fluvial; the waters may be ephemeral. According to Graham and Wilcox (2000) optimal growth conditions for *Spirogya* are at temperatures over 20°C.

*Remarks*: Although the studies made by Van Geel (1976b, 1978), and Van Geel and Van der Hammen (1978) revealed the relation between *Ovoidites* and *Spirogyra* or related algae, certain taxonomic confusion seems to persist, specially in their separation from *Schizosporis.*

According to Rich et al. (1982), the original description of *Ovoidites* was broad enough so that later authors could associate *Ovoidites* with fossil types morphologically quite different, and thus heavily reticulate forms (*Schizosporis*) have been included into *Ovoidites*. They also comment that the form genus *Ovoidites* probably consists of several biologic species. In Zippi (1998) this issue is extensively analysed and it is stated that all *Schizosporis* species having non-cellular wall are clearly encompassed by Krutzsch's emended generic diagnosis of *Ovoidites*. Living counterparts of these fossil zygospores reveal that, above the species level, the nature of the dehiscence suture and the overall shape are more important features for classification.

Moreover, our knowledge of the different spore-wall ornamentation of these fossil and modern algae is still insufficient.

Form-GENUS ***Schizosporis*** (COOKSON and DETTMANN) PIERCE, 1976

*Type species: Schizosporis reticulatus* COOKSON and DETTMANN, 1959

***Schizosporis reticulatus*** (COOKSON and DETTMANN) PIERCE, 1976
Figure 7B

*Brief Description*: Specimens spherical to slightly ellipsoidal, with a dehiscence suture extended around the

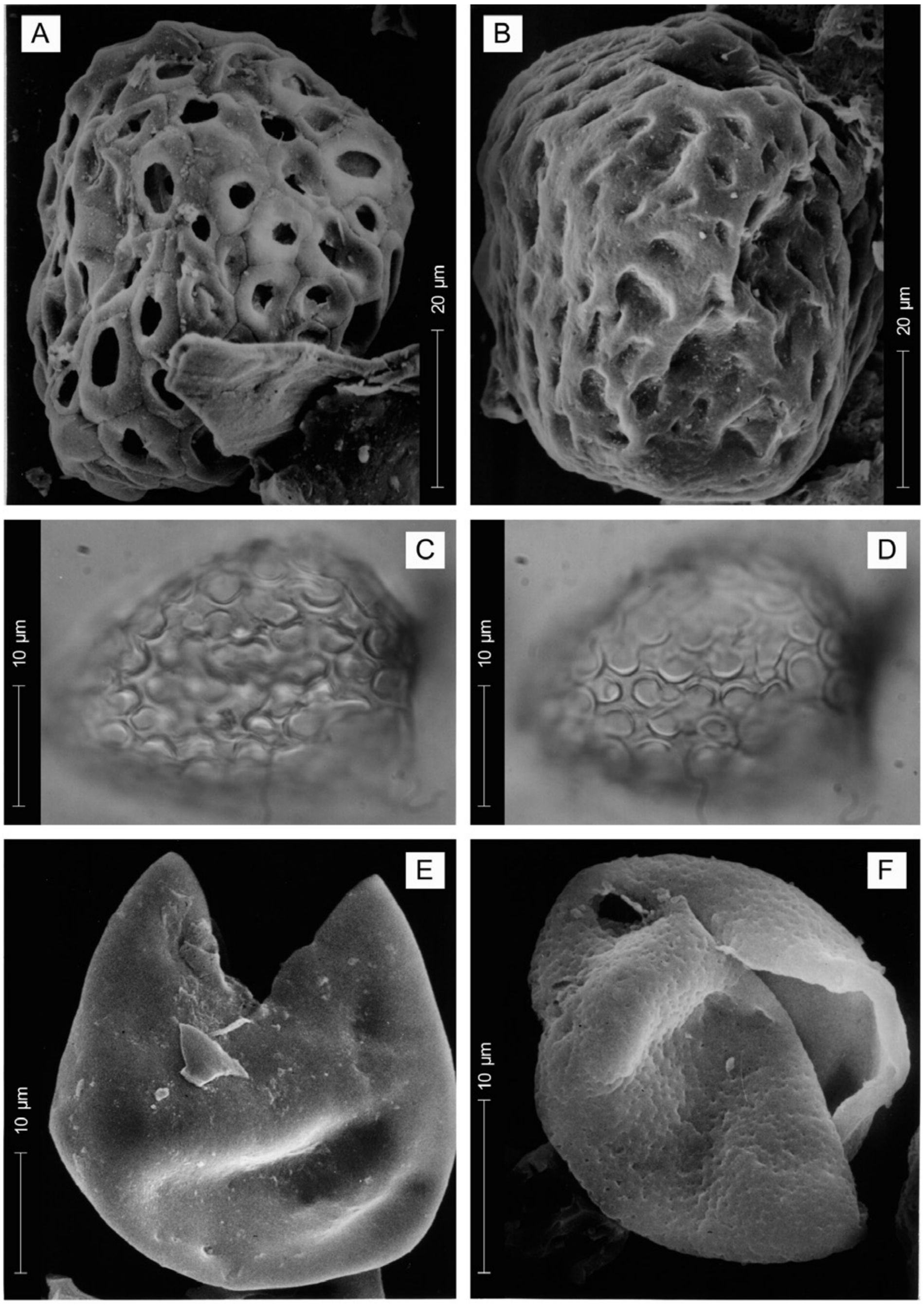

FIGURE 6 **A) *Coelastrum* sp. [SEM]; B) *Gelasinicista vangeelii* HEAD, 1992 [SEM]; C,D) *G. vangeelii* HEAD, 1992 [OM]; E,F) *Ovoidites* spp. [SEM].**

equator where they often split. Inner wall smooth; outer surface with a reticulate appearance. Equatorial diameter: 85 to 93 μm.

*Stratigraphic* Range: Forms assigned to *Schizosporis* are recorded from the Jurassic and Early Cretaceous (Zippi, 1998). According to Segroves (1967), *Schizosporis* has been reported since the Permian.

*Biological Affinity:* The zygospores of the modern Zygnemataceae are the most important characteristic utilised to identify the species. Although the morphologic features are conservative within a species, above the species level the dehiscence suture and overall shape are more important for classification.

Frederiksen (1983), Brenner and Foster (1994), and Martín-Closas (2003) compared the spores of the recent freshwater alga *Spirogyra* with the form-genus *Schizosporis* and with *Ovoidites*. Although, according to Zippi (1998), zygospores of the Zygnemataceae do not have cellular walls, they often have strongly sculptured multi-layer walls. Zippi also explains that such a cellular wall fits well with a hydrodictyacean affinity.

*Habitat*: *S. reticulatus* is a positive indicator of freshwater environments and seems to prefer shallow, ephemeral waters (Zippi, 1998).

*Remarks*: Pierce in 1976 emended the genus to include only the type species, based on the different nature of the wall structure (spores with a complex wall consisting of cell-like units).

**Family:** Zygnemataceae?

Form-GENUS ***Pseudoschizaea*** THIERGART and FRANTZ *ex* R.POTONIÉ emend.CHRISTOPHER, 1976

*Sporites* H. POTONIÉ 1893 (*partim.*)

*Concentricystes* ROSSIGNOL 1962 (*nomen nudum*)

*Pseudoschizaea* THIERGART and FRANTZ 1962 (*nomen nudum*)

*Pseudoschizaea* THIERGART and FRANTZ *ex* POTONIÉ 1966

*Type species: Pseudoschizaea circula* (WOLFF) CHRISTOPHER, 1976

We include here all subcircular forms which split along the equatorial plane; ornamented with finger-print like concentric or spiral ribs in at least one hemisphere, subjected to a variety of systematic treatments. In the bibliography, similar forms are assigned to a diversity of form-genera, including *Circulisporites* DE JERSEY *1*962 emend. NORRI*S* 1965 and *Chomotriletes* NAUMOVA 1939 ex Naumova 1953.

*Stratigraphic Range:* Recent studies reveal the presence of *Concentricystes* in sediments as old as Devonian (Milanesi et al., 2006). Circulisporites has been reported from Permian sediments (Segroves, 1967) and from the Triassic (Brenner and Foster, 1994). *Chomotriletes minor* is known from the Jurassic to the Eocene (Zippi, 1998). Deposits containing *Pseudoschizaea* are Pleistocene or Quaternary in age (Christopher, 1976). A detailed taxonomic study of the genus *Pseudoschizaea* is necessary in order to obtain a closer definition of its stratigraphic distribution.

*Biological Affinity:* These forms are considered as cysts of freshwater algae. The form-genus is placed within the Zygnemataceae but also as Oedogoniaceae(?). According to Grenfell (in Van Geel and Grenfell, 1996), *Concentricystes*, and also *Circulisporites*, are possible zygnematacean genera. Zippi (1998) reports that ornamented oospores of Oedogoniaceae are similar to *Chomotriletes minor.*

*Habitat:* The form-genus occurs occasionally in sediments of subtropical shallow-water sites (Davis, 1992). Carrión and Navarro (2002) referred that *Pseudoschizaea* cysts inhabit relatively warm climatic areas with desiccation phases or enhanced summer drought (local seasonal drying). According to Milanesi et al. (2006) *Concentricystes* lives in freshwater marshes.

*Remarks:* Segroves (1967) pointed out a possible future recombination of *Circulisporites parvus* as *Concentricystes*. In addition, Brenner and Foster (1994) remark that forms similar to *Circulisporites* have been assigned to *Chomotriletes*, *Concentricystes* and *Pseudoschizaea*, but also possibly include some species of *Ephedripites*.

Christopher (1976) made the revision of the genus *Pseudoschizaea* and suggested a solution to the nomenclatural problems associated with these forms. Following this author, the correct citation of the generic name is *Pseudoschizaea*. In Christopher (1976) this genus is also compared with *Chomotriletes* and *Circulisporites*. *Chomotriletes* lacks the characteristic polar ornamentation of *Pseudoschizaea* and *Circulisporites* is ornamented with a thickened disc in each polar area rather than with a complex of muri. The former author also observed that the forms assigned by Hekel (1972) as *Circulisporites* most likely belong to the genus *Pseudoschizaea*. However, Zippi (1998) continues using the generic name *Chomotriletes* (incertae sedis).

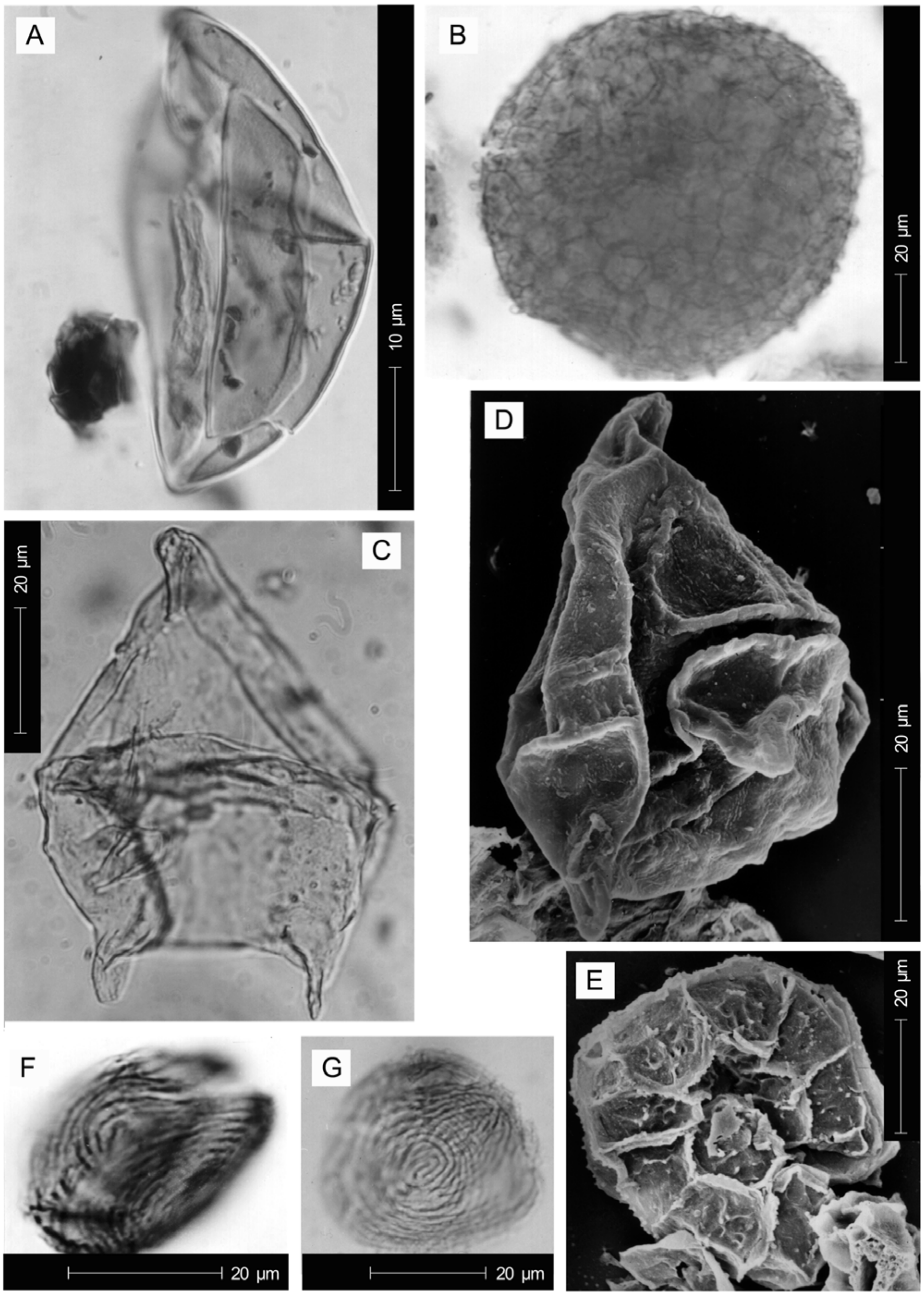

FIGURE 7 **A) *Ovoidites* spp. [OM]; B) *Schizosporis reticulatus* (Cookson and Dettman) Pierce, 1976 [OM]; C) *Peridinium* sp. aff. *P. limbatum* (Stokes) Lemmermann, 1899 [OM]; D) *P.* sp. aff. *P. limbatum* (Stokes) Lemmermann, 1899 [SEM]; E) dinocyst indet. [SEM]; F,G) *Pseudoschizaea circula* (Wolf) Christopher, 1976 [OM].**

***Pseudoschizaea circula*** (WOLFF) CHRISTOPHER, 1976

*Sporites circulus* WOLFF 1934

*Concentricystes rubinus* ROSSIGNOL 1962 (*partim.*) (*nomen nudum*)

*Pseudoschizaea ozeanica* THIERGART and FRANTZ 1962 (*nomen nudum*)

*Sporites circulus* WOLFF 1934 (*partim.*) - ROSSIGNOL 1964

Figures 7F and G

*Brief Description*: Body subcircular in polar view, biconvex in equatorial view. Inaperturate, although the test occasionally splits into two equal hemispheres along the equatorial plane. Polar area in each hemisphere ornamented with a series of muri which form a pattern of loops, curls, spirals or bars. A series of concentric ribs surround the polar area. Equatorial diameter: 30 to 38 $\mu$m.

*Stratigraphic Range:* This species is reported from Pliocene to Holocene deposits (Christopher, 1976).

*Remarks:* According to Christopher (1976) the cysts belong to freshwater algae, based on the fact that they occur in abundance in river terrace deposits, and due to their difficulty to get stained. This view agrees with Rossignol (1962, 1964) and Hekel (1972).

**Class:** Prasinophyceae CHRISTENSEN ex MOESTRUP and THRONDSEN, 1988
**Order:** Prasinophyceae incertae sedis
**Family:** Prasinophyceae incertae sedis

Form-GENUS ***Leiosphaeridia*** (EISENACK) DOWNIE and SARJEANT, 1963

*Type species: Leiosphaeridia baltica* EISENACK, 1958

***Leiosphaeridia hyalina*** (DEFLANDRE) DOWNIE, 1957
Not illustrated

*Brief Description*: Subspherical cysts often collapsed or folded, without processes and with thin, smooth or faintly microgranulate walls. Equatorial diameter: 20 to 50 $\mu$m.

*Stratigraphic Range*: Prasinophytes have been reported since Precambrian to present day sediments.

*Biological Affinity*: Evidences from the past few decades (morphological, biochemical, molecular, and life-history studies) indicate that the Division Chlorophyta includes four classes (monophyletic lineages) of green algae: Ulvophyceae, Trebouxiophyceae, Chlorophyceae, and Charophyceae. The prasinophyceans, a basal group, are not regarded as a monophyletic, although as Sym and Pienaar (1993) suggest, they are often included in the class Prasinophyceae (Graham and Wilcox, 2000).

*Habitat*: Prasinophyceans are mostly marine, and a few inhabit tidepools, brackish or even freshwater environments (Tappan, 1980; Graham and Wilcox, 2000).

**Division:** Dinoflagellata (Dinomastigota) (BÜTSCHLI) FENSOME et al., 1993
**Class:** Dinophyceae PASCHER, 1914
**Order:** Peridiniales HAECKEL, 1894
**Family:** Peridiniaceae EHRENBERG, 1831

GENUS ***Peridinium*** EHRENBERG, 1830

*Type species: Peridinium limbatum* (STOKES) LEMMERMANN, 1899

***Peridinium* sp. aff. *P. limbatum*** (STOKES) LEMMERMANN, 1899
*Protoperidinium limbatum* STOKES 1887
Figures 7C and D

*Brief Description:* Peridinioid cyst, with a blunt hollow apical horn which is distinguished by a characteristic left-lateral inclination when the cyst is viewed from the dorsal side. Cingulum defined by two parallel rows of granules separated by a smooth area. Two antapical horns often somewhat unequal and conspicuously chisel-shaped in lateral view, with their distal extremities inclined towards the ventral surface. Ornamentation variable in strength and character, but is almost psilate. Maximum diameter: 86 $\mu$m.

*Stratigraphic Range*: Freshwater dinoflagellates have been reported from the Upper Jurassic to the present.

*Habitat: P. limbatum* is a freshwater dinoflagellate found in ponds with *Sphagnum* and other mosses (Popovský and Pfiester, 1990). Most *Peridinium* species occur in lakes, lagoons, swamps and brackish water bodies. Extant peridinioideans are predominantly freshwater dinoflagellates (Fensome et al., 1993).

## KINGDOM PLANTAE

### *Bryophytes*

Division: Bryophyta A.BRAWN in ASCHERSON, 1860
Class: Sphagnopsida (ENGL.) OCHYRA, 2006
Order: Sphagnales LIMPR., 1877
Family: Sphagnaceae DUMORT., 1829

Form-GENUS ***Cingutriletes*** (PIERCE) DETTMANN, 1963

*Type species: Cingutriletes congruens* PIERCE, 1961

***Cingutriletes australis*** (COOKSON) ARCHANGELSKY, 1972
Not illustrated

*Brief Description*: Trilete spores with cingulum, amb subcircular; exine thick and smooth. Equatorial diameter: 22 to 35 $\mu$m.

*Stratigraphic Range:* The species have been reported from the Upper Cretaceous to the present.

*Botanical Affinity*: It has affinities with *Sphagnum* spores.

*Habitat*: According to Hutchinson (1975) these spores belong to aquatic mosses living in a variety of calcium-poor habitats ranging from damp clearings in woodland to the infralittoral zone of lakes.

Form-GENUS ***Stereisporites*** PFLUG, 1953

*Type species: Stereisporites steroides* (POTONIÉ and VENITZ) PFLUG, 1953 (in THOMSON and PFLUG, 1953)

***Stereisporites antiquasporites*** (WILSON and WEBSTER) DETTMANN, 1963
Figure 8C

*Brief Description*: Trilete spores, amb subcircular to subtriangular with convex sides and broadly rounded angles. Laesurae long, extending almost to the equator. Exine smooth with a not clearly discernible distal polar thickening; without cingulum. Equatorial diameter: 20 a 36 μm.

*Stratigraphic Range:* It has been reported from the Triassic to the present.

*Botanical Affinity***:** This form-genus includes *Sphagnum*-like spores.

*Habitat*: All *Sphagnum* species tend to be acidophilic.

**Division:** Marchantiophyta (Hepatophyta) STOTLER and CRAND.-STOTL., 2000
**Class:** Marchantiopsida CRONQUIST, TAKHT. and W. ZIMM., 1966
**Order**: Ricciales (SCHLJAKOV) STOTLER and STOTL.-CRAND., 2000
**Family:** Ricciaceae REICHENB., 1828

GENUS ***Ricciocarpus*** CORDA, 1829

*Type species: Ricciocarpus natans* (L.) CORDA, 1829

***Ricciocarpus natans*** (L.) CORDA, 1829
Figure 8B

*Brief Description*: Trilete spores, amb subcircular to subtriangular. Laesurae straight with elevated lips, extending almost to equator. Proximal face with interradial areas ornamented with a low reticulum. Lumina subcircular to polygonal. Equatorial diameter: 48 to 70 μm.

*Stratigraphic Range:* Aquatic bryophytes assigned to Ricciaceae have been described from the Jurassic (or even Triassic) to the present.

*Habitat*: *R. natans* grows in lagoons and ditches, or on land, when these are dried, forming rosettes (Hässel de Menéndez, 1962). This species is a semi-aquatic plant which produces a floating form, but can also grow as a rooting liverwort (Mahabalé, 1968). According to Hutchinson (1975), this aquatic species inhabits the surface of standing waters in tropical environments, living pleustonically in the protected marginal parts; it occurs only in eutrophic waters.

### *Pteridophytes*

**Division:** Lycopodiophyta (Lycophyta) D.H. SCOTT, 1909
**Class:** Lycopodiopsida BARTL., 1830
**Order:** Lycopodiales DUMORT., 1829
**Family:** Lycopodiaceae P.BEAUV. ex MIRBEL in LAM. and MIRB., 1802

Form-GENUS ***Retitriletes*** VAN DER HAMMEN ex PIERCE emend. DÖRING, KRUTZSCH, MAI and SCHULZ, 1963

*Type species: Retitriletes globosus* PIERCE, 1961

***Retitriletes austroclavatidites*** (COOKSON) DÖRING, KRUTZSCH, MAI and SCHULZ, 1963
Not illustrated

*Brief Description*: Trilete spores, amb subcircular to convexly subtriangular. Laesurae straight, length about 3/4 of the spore radius, enclosed within membranous, elevated lips. Exine smooth proximally and reticulate both distally and equatorially. Regular coarse-meshed reticulum which simulate a membranous flange at the equator. Lumina hexagonal to pentagonal in outline. Equatorial diameter: 34 to 58 μm.

*Stratigraphic Range:* It has been reported widely from the Jurassic to the present.

*Botanical Affinity*: This form-species closely resemble the spores of *Lycopodium clavatum.*

*Habitat*: It inhabits mainly humid and swampy environments.

***Retitriletes rosewoodensis*** (DE JERSEY) DE JERSEY 1963
NOT ILLUSTRATED

*Brief Description*: Trilete spores, amb subcircular to subtriangular. Laesurae straight extending almost to equator. Exine with proximal and distal reticulum. Lumina polygonal to subcircular in outline. Muri stout of irregular height. Equatorial diameter: 25 to 40 μm.

*Stratigraphic Range:* It has been reported widely from Mesozoic sediments.

*Botanical Affinity*: This form-species is similar to some spores of *Lycopodium.*

*Habitat*: They inhabit mainly humid and swampy environments.

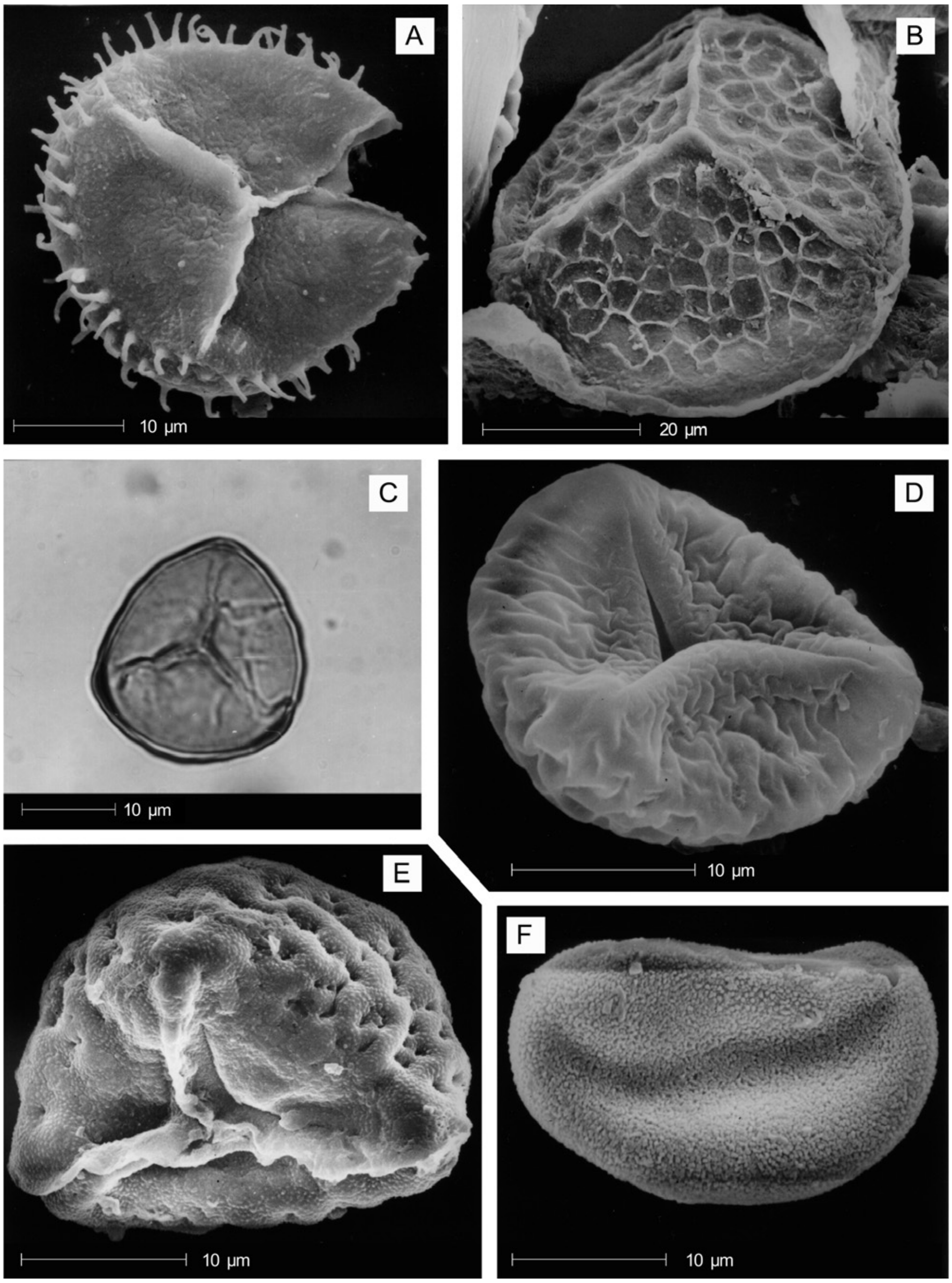

FIGURE 8 **A) *Ceratosporites equalis* COOKSON AND DETTMANN, 1958 [SEM]; B) *Ricciocarpus natans* (L.) CORDA, 1829 [SEM]; C) *Stereisporites antiquasporites* (WILSON AND WEBSTER) Dettmann, 1963 [OM]; D) *Selaginella perinata* (KRUTZSCH et al.) FREDERIKSEN, 1980 [SEM]; E) *Klukisporites variegatus* COUPER, 1958 [SEM]; F) *Polypodiisporites irregularis* POCKNAL and MILDENHALL, 1984 [SEM].**

**Order:** Selaginellales PRANTL, 1874
**Family:** Selaginellaceae WILLK., 1861

Form-GENUS ***Ceratosporites*** COOKSON and DETTMANN, 1958

*Type species: Ceratosporites equalis* COOKSON and DETTMANN, 1958

***Ceratosporites equalis*** COOKSON and DETTMANN, 1958
Figure 8A

*Brief Description*: Trilete spores, amb subcircular to subtriangular. Laesurae extending almost to equator, with membranous elevated lips. Exine smooth to scabrate proximally. Distal surface sculptured with slender clavate to capillate, and occasionally spinulate to setulate elements. Equatorial diameter (including sculpture): 34 a 56 $\mu$m

*Stratigraphic Range*: It has been widely reported from Cretaceous sediments.

*Botanical Affinity*: This form shows a striking resemblance with *Selaginella tenuispinulosa*.

*Habitat*: It inhabits mainly humid and shadowy environments and also swamps.

GENUS ***Selaginella*** BEAUVOIS, 1804

*Type species: Selaginella* perinata (KRUTZSCH et al.) FREDERIKSEN, 1980

***Selaginella perinata*** (KRUTZSCH et al.) FREDERIKSEN, 1980
Figure 8D

*Brief Description*: Trilete spores, outline rounded triangular. Laesurae wavy, margo wrinkled giving the appearance of a sinuous ribbon. Equatorial diameter: 20 to 48 $\mu$m.

*Stratigraphic Range*: It has been reported from the middle Eocene (USA) by Frederiksen et al. (1983).

*Botanical Affinity*: According to Frederiksen et al. (1983), *S. perinata* is very similar to spores of *Selaginella rupestris* and *S. sellowii;* also Martin and Rouse (1966) reported a strong similarity of the fossil species to spores of *Selaginella wallacei* and *S. oregona*.

*Habitat*: They inhabit mainly humid and shadowy environments and also swamps. Most species of *Selaginella* are found in wetland tropical regions.

**Division:** Polypodiophyta (Filicophyta) CRONQUIST, 1966
**Class**: Polypodiopsida CRONQUIST, 1966
**Order**: Cyatheales (Filicales) A.B. FRANK in LEUNIS, 1977
**Family:** Cyatheaceae KAULFUSS, 1827

Form-GENUS ***Deltoidospora*** MINER, 1935 emend. POTONIÉ, 1956

*Type species: Deltoidospora hallii* MINER, 1935

***Deltoidospora minor*** (COUPER) POCOCK, 1970
Not illustrated

*Brief Description*: Trilete spores, outline in polar view triangular with straight to slightly convex sides and rounded angles. Laesure straight and clearly defined. Exine smooth and thin-walled. Small size; equatorial diameter: 25 - 38 $\mu$m.

*Stratigraphic Range:* It has been reported widely from Jurassic and Cretaceous sediments.

*Botanical Affinity*: Probably attributed or related to Cyatheaceae.

*Habitat*: It inhabits mainly humid and swampy environments.

**Order**: Schizaeales (Filicales) A.B. FRANK in LEUNIS, 1877
**Family:** Schizaeaceae KAULFUSS, 1827

Form-GENUS ***Klukisporites*** COUPER, 1958

*Type species: Klukisporites variegatus* COUPER, 1958

***Klukisporites variegatus*** COUPER, 1958
Figure 8E

*Brief Description*: Trilete spores, amb rounded-triangular in polar view, margins irregular from the projecting sculptural elements. Lesurae extend to equator, flanked by a margo and a smooth area. Distal surface and sectors of the proximal face ornamented by a coarse reticulum with polygonal to subcircular lumina. The rounded muri usually anastomose. Equatorial diameter: 25 to 47 $\mu$m.

*Stratigraphic Range*: It has been reported widely from the Jurassic to Recent.

*Botanical Affinity*: The spores of *Klukisporites* resemble the spores of some species of *Lygodium,* however this affinity is controversial.

*Habitat*: They inhabit mainly humid and swampy environments.

**Order**: Polypodiales (Filicales) METT. ex. A.B. FRANK in LEUNIS, 1877
**Family:** Polypodiaceae BERCHT. and J. PRESL, 1820

Form-GENUS ***Laevigatosporites*** (IBRAHIM) ALPERN and DOUBINGER, 1973

*Type species: Laevigatosporites vulgaris* IBRAHIM, 1933

***Laevigatosporites ovatus*** WILSON and WEBSTER, 1946
Not illustrated

*Brief Description*: Monolete spores with distinct and comparatively long laesurae. Amb oval. Exine smooth. Maximum diameter: 31 to 50 $\mu$m.

*Stratigraphic Range*: It has been reported widely from the Devonian to Recent.

*Botanical Affinity:* This species could be related or assigned to Polypodiaceae.

*Habitat*: They inhabit moist-humid environments. Nearly all species of Polypodiaceae are today epiphytic ferns.

Form-GENUS ***Tuberculatosporites*** IMGRUND ex POTONIÉ and KREMP, 1954

*Type species: Tuberculatosporites anicystoides* IMGRUND, 1952

***Tuberculatosporites parvus*** ARCHANGELSKY, 1972
Not illustrated

*Brief Description*: Monolete spores, apiculate, with a comprehensively developed conate to spinulose sculpture. Maximum diameter: 28 to 40 μm.

*Stratigraphic Range*: The species have been recorded from the Paleocene of Chubut (Bororó and Salamanca Formations).

*Botanical Affinity*: This species could be attributed or related to Polypodiaceae.

*Habitat*: They inhabit moist-humid environments.

Form-GENUS ***Polypodiisporites*** POTONIÉ (in POTONIÉ and GELLETICH, 1933) ex POTONIÉ, 1956

*Type species*: *Polypodiisporites favus* POTONIÉ 1931 ex POTONIÉ, 1956

***Polypodiisporites irregularis*** POCKNAL and MILDENHALL, 1984
Figure 8F

*Brief Description*: Monolete spores, laesura from 1/2 to 2/3 spore length. Amb reniform elongate, plano-convex to concavo-convex. Exine thick, covered with small verrucae interspersed with granules or scabrae; some verrucae are fused. Maximum diameter: 27 to 74 μm**.**

*Stratigraphic Range*: This species has been recorded from the early Miocene. Similar forms assigned to this genus have been reported from the Triassic.

*Botanical Affinity*: Generally attributed to Polypodiaceae, but also to Schizaeaceae and Psilotaceae (some spores are very similar to those of *Tmesipteris tannensi).*

*Habitat*: This species was found in flood basin marsh and temporary pond environments. Psilotaceae and nearly all species of Polypodiaceae are today epiphytic ferns.

**Order:** Salviniales BRITT., 1901
**Family:** Salviniaceae T. LESTIB., 1826

Form-GENUS ***Azollopsis*** HALL, 1968 emend. SWEET and HILLS, 1974
**Subgenus:** *Azollopsis* SWEET and HILLS, 1974

*Type species*: *Azollopsis coccoides* HALL, 1968

*Observations*: Major differences are found in the morphology of the massula and glochidium than in the morphology of the megaspore complex. Consequently, two subgenera were defined (Sweet and Hills, 1974). Both subgenera were identified in this palynobiota.

***Azollopsis (Azollopsis) tomentosa*** HALL, 1968
Figures 9A and B

*Brief Description*: Massulae fragment with multibarbed glochidia. Glochidia 50–70 μm long, with alternate barbs and single-barbed tips.

*Stratigraphic Range*: They have been reported from Maastrichtian to Paleocene or even Eocene sediments.

*Habitat*: These ferns inhabit freshwater bodies of low energy; mainly tropical to subtropical. Modern forms are lacustrine or pond ferns.

**Subgenus:** *Spiralopsis* SWEET and HILLS, 1974

*Type species*: *Azollopsis intermedia* SWEET and HILLS, 1974

***Azollopsis (Spiralopsis) intermedia*** SWEET and HILLS, 1974
Figures 9C and D

*Brief Description*: Massulae ovate to subrectangular in shape, with relatively numerous, small circinate glochidia. Glochidial stalk 30–60 μm long, with expanded terminations and spiral appearance (coiled tips).

*Stratigraphic Range*: It has been reported from Campanian to Paleocene sediments.

*Habitat*: These ferns inhabit freshwater bodies of low energy; mainly tropical to subtropical. Modern forms are lacustrine or pond ferns

***Angiosperms***
**Division:** Magnoliophyta (Angiospermophyta) CRONQUIST in TAKHT and ZIMMERMANN,1996

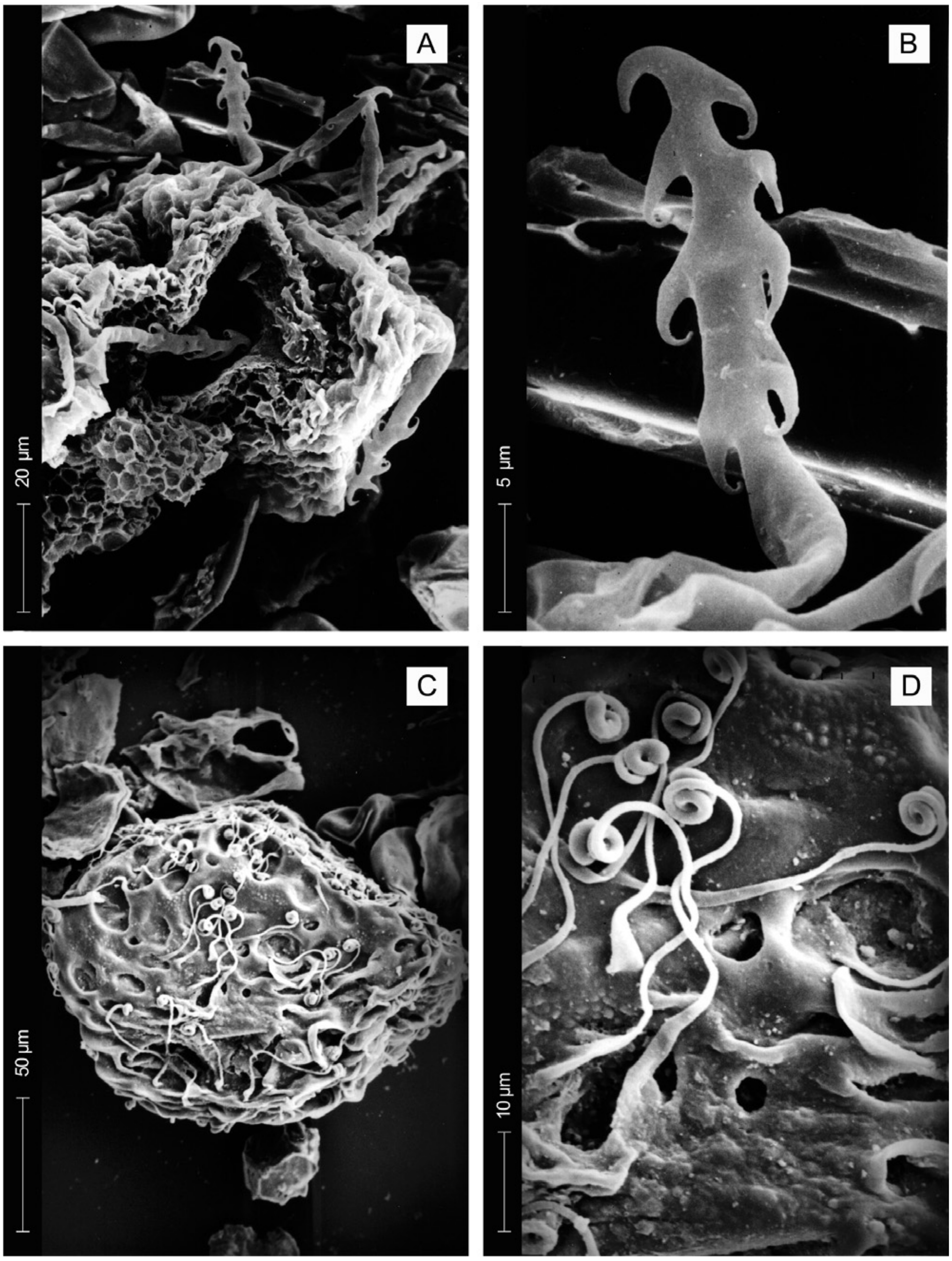

FIGURE 9 **A,B) *Azollopsis (Azollopsis) tomentosa* Hall, 1968, A: massula and glochidia, B: detail of glochidium [SEM]; C,D) *Azollopsis (Spiralopsis) intermedia* Sweet and Hills, 1974, C: massula and glochidia, D: glochidia [SEM].**

**Class:** Liliopsida (monocots) Brongn., 1843
**Order:** Liliales Perleb, 1826
**Family:** Liliaceae Jussieu, 1789

Form-GENUS ***Liliacidites*** Couper, 1953

*Type species*: *Liliacidites kaitangataensis* Couper, 1953

***Liliacidites variegatus*** Couper, 1953
Not illustrated

*Brief Description*: Monosulcate pollen grains, sulcus long. Grain usually elongate to subcircular. Exine very thin, sexine finely baculate to clavate, forming a fine reticulum. Lumen of reticulum up to 2 µm across at centre of grain and less than 1 µm at ends of grain. Size: 26–36 µm long and 16–26 µm wide.

*Stratigraphic Range*: It has been reported since the Aptian to Recent.

*Botanical Affinity*: This form-genus was proposed to include the fossil pollen of liliaceous affinities. According to Frederiksen (1983), probably includes mainly Palmae, although other monocot families such as Liliaceae could also be involved.

*Habitat*: Usually considered as plants living in a moist marsh or paludal environment.

***Liliacidites regularis*** ARCHANGELSKY, 1973
Not illustrated

*Brief Description*: Monosulcate pollen grains; outline oval to subcircular with rounded angles. Sulcus extends 3/4 to 4/5 length of the grain; edges smooth. Exine semitectate, reticulate; reticulum with thin muri and polygonal lumens. Mesh of reticulum generally larger on the proximal face and reduced in the extremes. Size: 27–43 $\mu$m long and 17–25 $\mu$m wide.

*Stratigraphic Range*: It has been reported from the Paleocene of Chubut (Salamanca Formation).

*Botanical Affinity*: These forms could be related with pollen of liliaceous affinities.

*Habitat*: Usually considered as plants living in a moist marsh or paludal environment.

**Order:** Arecales BROMHEAD, 1840
**Family:** Arecaceae SCHULTZ-SCHULTZENSTEIN, 1832

Form-GENUS ***Longapertites*** VAN HOEKEN-KLINKENBERG, 1964

*Type species: Longapertites marginatus* VAN HOEKEN-KLINKENBERG, 1964

***Longapertites andreisii*** ARCHANGELSKY, 1973
Figure 10A

*Brief Description*: Monosulcate pollen grains, shape oval. Sulcus extends the full length of the distal face. In polar view, the sulcus usually gapes open. Exine tectate. Columelae forming thin, irregular and sinuous muri. Size: 64–76 $\mu$m long and 28–45 $\mu$m wide.

*Stratigraphic Range*: It has been reported from Paleocene sediments.

*Habitat*: It corresponds to the typical coastal tropical palm species.

*Remarks*: Extended monosulcate ellipsoid pollen grain (aperture type 3 in Harley and Baker, 2001).

***Longapertites patagonicus*** ARCHANGELSKY, 1973
Figure 10B

*Brief Description*: Monosulcate pollen grains; outline oval in equatorial view. The sulcus has a length greater than the medial width of the grain. Exine tectate and collumelae densely packed. The tectum is psilate. Size: 37–50 $\mu$m long and 22–36 $\mu$m wide.

*Stratigraphic Range*: It has been reported from Late Cretaceous and Paleocene sediments.

*Botanical Affinity*: This form-genus has a *Calamus*-type pollen.

*Habitat*: Typical tropical coastal palm species. *Calamus* species today inhabit swamp perimeters beyond saline influence (Playford, 1982) and according to Frederiksen (1985) they may have lived in the same habitats in the Paleogene.

*Remarks*: Extended monosulcate ellipsoid pollen grain (aperture type 3 in Harley and Baker, 2001). The grains are finely perforate-reticulate and often separate into two halves.

Form-GENUS ***Spinizonocolpites*** MÜLLER, 1968 emend. MÜLLER et al., 1987

*Type species*: *Spinizonocolpites echinatus* MÜLLER, 1968

***Spinizonocolpites*-**complex
For complete synonymy, see Frederiksen (1994)
Figures 11B to F

Müller (1968) described two forms, *S. echinatus* (= *S. prominatus*) and *S. baculatus*, differenced by the spine shape. Frederiksen (1994) refers to four species, and synonymised the species listed by Singh, 1990 resulting in five species of *Spinizonocolpites*. According to Zetter and Hoffmann (2001), an assemblage of fossil *Nypa* pollen always represents a mixture of mature, immature and aberrant forms, thus displaying the whole pollen grain variation of the *Nypa*-population. A comparable degree in variability has been recognised in different fossil *Nypa* fruits from London Clay and in pollen assemblages from late Paleocene-early Eocene units from India and Pakistan (Tripathi et al, this issue). Considering these criteria and the diversity of forms found in our material, we appoint the term "complex" (used by Frederiksen, 1994) to name them.

*Brief Description*: This complex has a great variety of zonosulcate, spiny pollen grains, 40–50 $\mu$m in diameter, ornamented with processes of variable shape, ranging

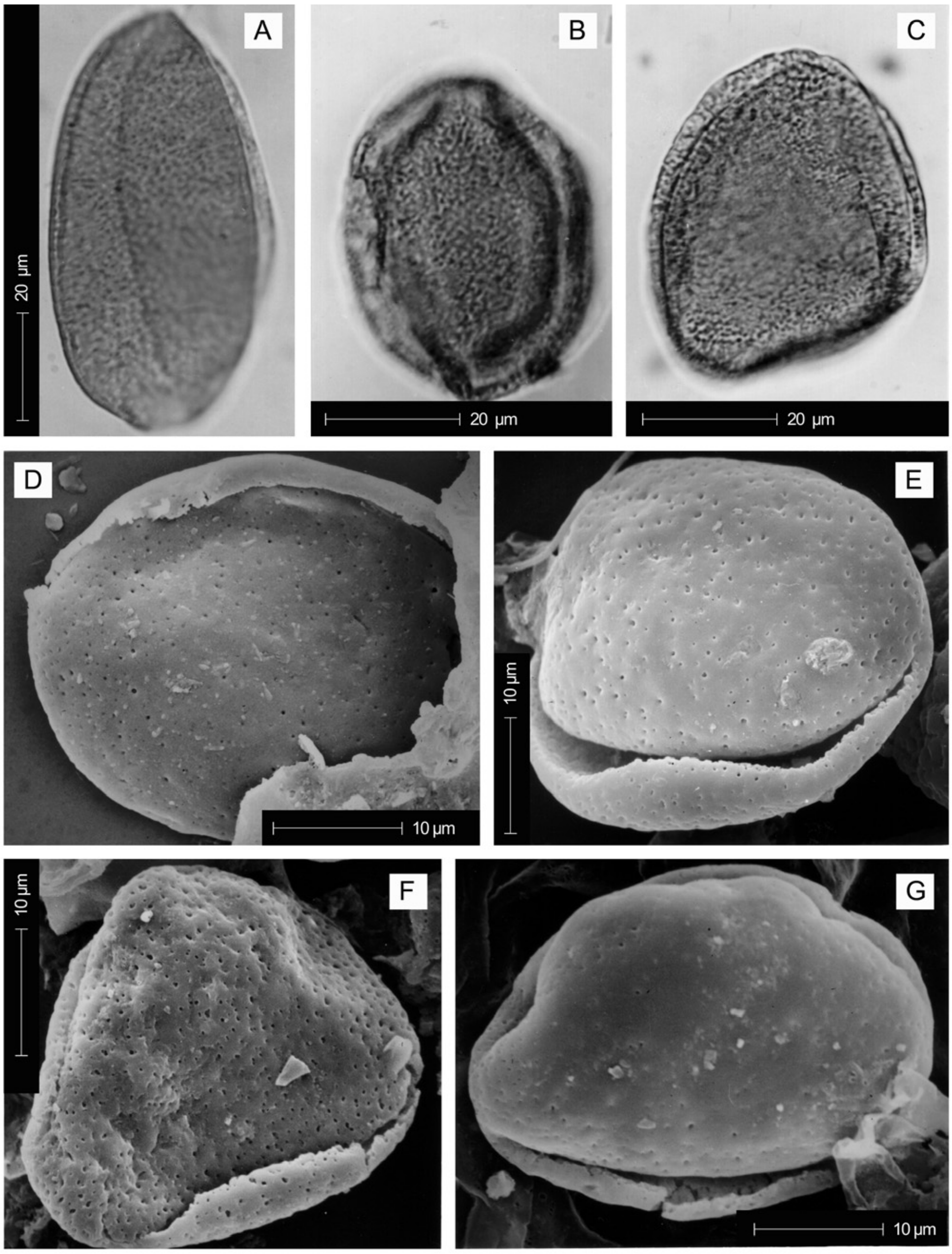

FIGURE 10 **A) *Longapertites andreisii* Archangelsky, 1973 [OM]; B) *L. patagonicus* Archangelsky, 1973 [OM]; C-G) *Proxapertites*-group, C: [OM], D-G: [SEM].**

from thin spines, low coni, rounded coni or verrucae and baculae also bulbous at the base, scattered over the whole surface. The grains are mostly separated into two halves. The exine is tectate, perforate to microreticulate.

*Stratigraphic Range*: It has been reported since the Late Cretaceous to Recent.

*Botanical Affinity*: *Nypa*-type; related to the modern *Nypa* palm. Following Müller (1968), *S. echinatus* is identical with the pollen of the recent *Nypa fruticans*. Harley et al. (1991) suggested that the extant *Nypa fruticans* might be a relict species of an ancient, more diverse genus, because the morphology of recent *Nypa* pollen is notably more uniform than the morphology of dispersed *Spinizonocolpites*. According to Harley and Baker (2001) the recent findings from the Eocene of Tasmania of numerous fossil *Nypa* fruits in close association with quantities of *Spinizonocolpites* pollen, add convincing evidence in support of the ancestral relationship between the fossils and the recent species.

*Habitat*: Following Frederiksen (1985), the presence of *Nypa* pollen would suggest but would not prove that the sample formed in a brackish-water to marine coastal environment. *Nypa fruticans* prefers tidally influenced brackish waters and grows in small belts along estuarine channels, rivers and lagoons, or produce extensive monotypic stands in the SE Asia and Pacific regions (Zetter and Hoffmann, 2001). Parts of Africa and South America were covered by the Senonian Palmae Province of Herngreen and Chlonova (1981). Arecaceae palms are abundant in Asian mangroves (Germeraad et al., 1968). The genus is widely distributed in tropical and subtropical regions, as well as ranging into more temperate latitudes.

*Remarks*: Zonosulcate spheroidal pollen grain (aperture type 16 in Harley and Baker, 2001), often separated into two halves.

**Order:** Arales (Alismatales) Dumortier, 1829
**Family** Araceae Jussieu, 1789

Form-GENUS ***Proxapertites*** van der Hammen, 1956

*Type species: Proxapertites operculatus* (van der Hammen) van der Hammen, 1956

***Proxapertites*-group**
Figures 10C to G

Considering the diversity of forms encountered in our material, and the probability that pollen grains belonging to other genera and also families were included, we appoint the category “group” to name them.

*Brief Description*: This group comprise a great variety of zonoaperturate/ zonosulcate pollen grains with a somewhat irregular circular to elliptic outline. The diameter ranges from 30 to 45 µm however, smaller grains were also found. Because of the aperture configuration, the grains often appear as two slightly different sized halves. There is also a considerable variation in ornamentation. The exine is perforate to foveolate. In some cases the halves show relatively few perforations and appear more or less psilate. In other cases perforations increase in number and often the individual perforations are connected to form narrow “grooves,” which may give rise to a finely perforate or even foveolate/microreticulate ornamentation.

*Stratigraphic Range*: Several species of *Proxapertites* have been reported from Cretaceous to Eocene deposits; only few records exist up to recent times.

*Botanical Affinity*: According to Zetter and Hoffmann (2001), the fossil morpho-type *P. operculatus* has been recognised as an Araceae; comparison of SEM images with modern Araceae points towards the outer subfamily Zamioculcadeae, particularly the endemic genera *Gonatopus*. According to Hesse et al. (2001), pollen grains remain intact in both mentioned genera, while in the subfamily Monsteroideae-Monstereae (*Monstera*-type) the pollen grains split. Moreover, Zetter et al (2001) indicate that *P. cursus* is related to another family, perhaps to the Arecaceae.

Harley and Baker (2001) attributed this type of pollen to a few species of *Areca* (Arecaceae), extinct *Nypa* relative. The zonosulcus in *Areca* pollen may be equatorial and the exine is tectate-perforate or finely reticulate; in *Nypa* pollen (Arecaceae) the zonosulcus has been demonstrated to be meridional (parallel with the polar axis) and the exine is tectate-perforate and spiny (Harley and Dransfield, 2003).

*Habitat*: Almost all extant Araceae require abundant water and generally high humidity. The occurrence of abundant pollen of this type could be an indicator of deposition near coastal areas. Müller (1968) showed that *Proxapertites* had a pantropical distribution similar to that of *Nypa*. Araceae and Arecaceae are both tropical to subtropical families. Particular morphologies could be indicative of lacustrine or fluvial environment instead of the deltaic to mangrove environment. Frederiksen (1985) expressed that *Proxapertites* is an interesting taxon whose parent plants probably lived mainly in coastal environments, but the genus is worth further paleoecological investigation.

*Remarks*: Incomplete zonosulcate spheroidal pollen grain, simple tectate or reticulate (aperture type 15 in Harley and Baker, 2001).

**Order:** Typhales Dumortier, 1829
**Family:** Sparganiaceae Hanin, 1811 / Typhaceae Jussieu, 1789

Form-GENUS ***Sparganiaceaepollenites*** Thiergart, 1937 ex Potonié, 1960

*Type species: Sparganiaceaepollenites polygonalis* Thiergart (designed by Potonié, 1960)

***Sparganiaceaepollenites barungensis*** Harris, 1972
Figure 11A

*Brief Description*: Monoporate pollen grains; pore 5–7 µm in diameter with slightly irregular edges. Outline oval with broadly rounded ends. Exine reticulate, muri simplibaculate, lumina rather uniform in size, about 2 µm over the entire grain. Length: 28–40 µm.

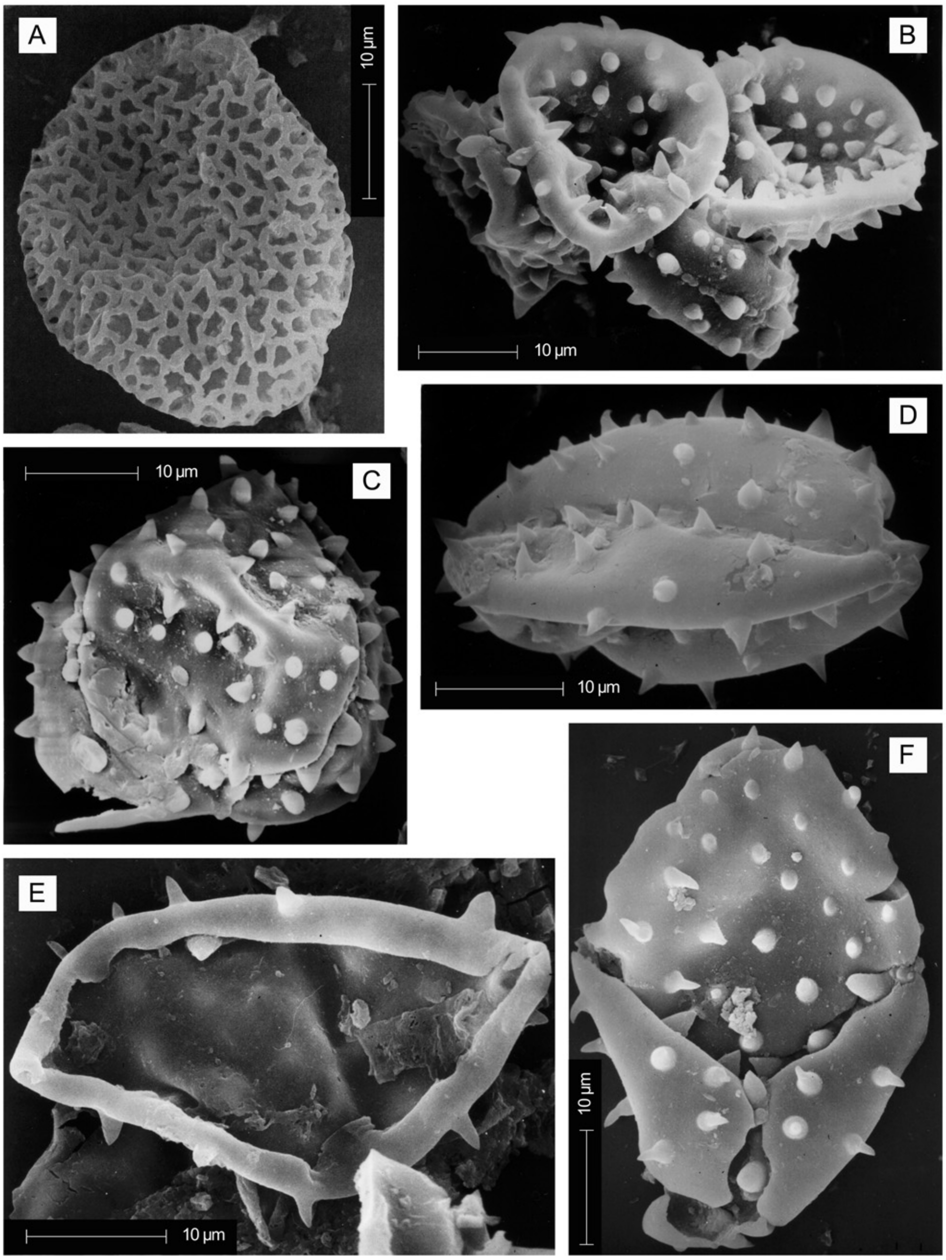

FIGURE 11 **A) *Sparganiaceaepollenites barungensis* Harris, 1972 [SEM]; B-F) *Spinizonocolpites*-complex [SEM].**

*Stratigraphic Range*: The genus has been recorded from the Cretaceous-Paleogene boundary. The fossil record of *Typha* extends to the Maastrichtian and younger sediments, while *Sparganiaceaepollenites* is known to extend to the Paleocene.

*Botanical Affinity*: This form-genus is similar to *Sparganium*-type or *Typha*-type*;* probably *Typha angustifolia.*

*Habitat*: Modern *Typha* occurs worldwide in tropical and temperate regions confined largely to freshwater swamps and ponds; however some species prefer brackish coastal waters. *Sparganium* is indicative of similar ecological niches but occurs also in temperate, arctic and high altitudinal regions.

## DISCUSSION

### Paleoenvironmental interpretation

The palynobiota from the Bororó Fm has been used to assess the paleoenvironment. Based on the thermophilic taxa of miospores (e.g. palm pollen) together with the diverse freshwater algal assemblage, a warm, humid, probably lagoonal, depositional environment is proposed. A similar, coeval assemblage described for Bolivia (Vajda, 1999; Vajda and McLoughlin, 2005) also supports this interpretation.

Dispersal mechanisms, pollination modes and plant ecological requirements have been considered. We had in mind that tropical to subtropical floras contain high percentages of animal-pollinated species with water dispersed forms (*Nypa*, *Calamus*-type, Araceae, and Sparganiaceae, among others). The presence of these zoophilous types indicates very high dominance of plant producers in those particular habitats. Moreover, studies of recent tropical sediments by Müller (1959) show that in a humid environment, water transport may have greater quantitative importance than wind transport (Germeraad et al., 1968).

Other evidences supporting our interpretations are shown below.

### Evidence for freshwater conditions

The presence of certain protoctists demonstrates the existence of a shallow freshwater body. Unicellular and filamentous green algae are significant components of freshwater planktonic and periphytic (benthonic) communities. The colonial algae *Botryococcus* spp. are important planktonic components in the assemblage studied herein indicating a freshwater (also brackish) paleoenvironment such as lakes, ponds, and bogs. According to Hutchinson (1975), the genus appears to require fairly high concentrations of nutrients for optimal growth.

The absence of *Pediastrum* is striking and interesting as it is a characteristic form of this kind of environments and in contrast with palynobiotas corresponding to similar, coeval environments in the Patagonian region, where the genus *Pediastrum* has been identified.

*Coelastrum* is a planktonic algae restricted to freshwater habitats. The occurrence of fossil *Coelastrum* in sediments indicates eutrophication although this is not exactly the case in present forms (Jankovská and Komárek, 2000).

Most zygnemataceans live in freshwater environments and represent the filamentous periphyton in ponds, growing associated to aquatic plants. Their zygospores are particularly characteristic of oxygen-rich, shallow, stagnant, mesotrophic waters, where temperature can increase quickly and they reflect strictly local habitats (Van Geel, 1978; Head, 1992). The presence of fossil zygnemataceous zygospores has been linked to seasonal warming and desiccation of the habitat. Zygnemataceae are also known to be associated with coastal dune pools (Head, 1992).

*Gelasinicysta* represents particularly *Zygnema*-type spores, but also *Mougeotia* spores. Optimal growth conditions for *Zygnema* are considered between 15º–20º C. *Mougeotia* exhibit tolerance of a wide pH range, allowing growth in acidified environments.

*Ovoidites*-producing organisms are assumed to be species of *Spirogyra,* which are typically attached to stable substrates, but can also occur as free-floating mats that originate from benthic zygotes or filaments. Filamentous *Spirogyra* forms conspicuous springtime blooms that may cover the surface of freshwater ponds. Taking into account that *Spirogyra* species are also characteristic of the low pH waters of *Sphagnum* bogs (Graham and Wilcox, 2000), *Ovoidites* can be used to infer freshwater marsh habitats.

The equatorial dehiscence suture present in *Schizosporis reticulatus* is considered a diagnostic feature of the Zygnemataceae; thus *Pseudoschizaea* can probably be included into this green algal family. Their presence in the palynobiota confirms as well the occurrence of a freshwater environment. Carrión and Navarro (2002) mentioned that *Pseudoschizaea* cysts inhabit relatively warm climate with desiccation phases or enhanced summer drought (local seasonal drying).

*Leiosphaeridia* includes smooth cysts belonging to ancestral prasinophytes. These green algae grow in freshwater, but also in brackish and marine environments.

Within the dinoflagellates, *Peridinium* is one of the most characteristic freshwater genera. It inhabits waters characterized by high calcium-ion concentration, low nutrient, and low pH.

### Evidence for low energy water body

*Azollopsis (Azollopsis) tomentosa* and *A. (Spiralopsis) intermedia* are free floating macrophytes (Salviniaceae) indicating a low energy freshwater body.

Another important plant of still, eutrophic waters is *Ricciocarpus natans*. Aquatic bryophytes assigned to *Ricciocarpus* often occur in facies attributed to shallow lakes or taxodiaceous swamps.

The coenobia of *Coelastrum* are also most likely to be found in shallow low energy freshwater bodies.

### Evidence for subtropical-tropical paleoclimate

The abundance of zonosulcate and monosulcate pollen grains probably belonging to the Arecaceae and Araceae, indicate marshy and brackish biotopes near the marine coast. A similar spatial distribution of biotopes is found today, for example, along thousands of kilometres of the North American Atlantic and the Gulf of Mexico coasts at latitudes between 38º and 26º N.

Some of the mentioned forms correspond to *Nypa*, whose modern distribution is in brackish environments (the extant *Nypa fruticans* grows in mangrove environments). Both *Proxapertites* and *Spinizonocolpites* have a definite pantropical distribution. Palm pollen is reflecting a warm, subtropical to tropical paleoclimate.

The high relative frequency and diversity of pteridophyte spores belonging to Schizaceae (*Klukisporites variegatus*), Cyatheaceae (*Deltoidospora minor*), Selaginellaceae (*Ceratosporites equalis*, *Selaginella perinata*), Lycopodiaceae (*Retitriletes austroclavatidites*, *R. rosewoodensis*) and probably Polypodiaceae (*Laevigatosporites ovatus, Tuberculatosporites parvus* and *Polypodiisporites irregularis*) among others, characterise an ecotonal community typical of warm and humid environments (palm pollen even more so). According to Frederiksen (1985), the Paleocene understorey vegetation (represented here by the families Sparganiaceae / Typhaceae and possibly Liliaceae) was, in many communities, dominated by a great variety of ferns. Bog mosses (hydrophytes*)* with *Sphagnum* affinities, like *Cingutriletes australis* and *Stereisporites antiquasporites* producers, inhabit acid environments (pH 4.5–3.0). According to Frederiksen (1985), the different producing plants were probably particularly sensitive with respect to pH and availability of nutrients in the environments they lived in.

The angiosperm *Sparganiaceaepollenites barungensis* (*Sparganium*-type/ probably *Typha angustifolia*) indicate the presence of emerged and rooted macrophytes; they

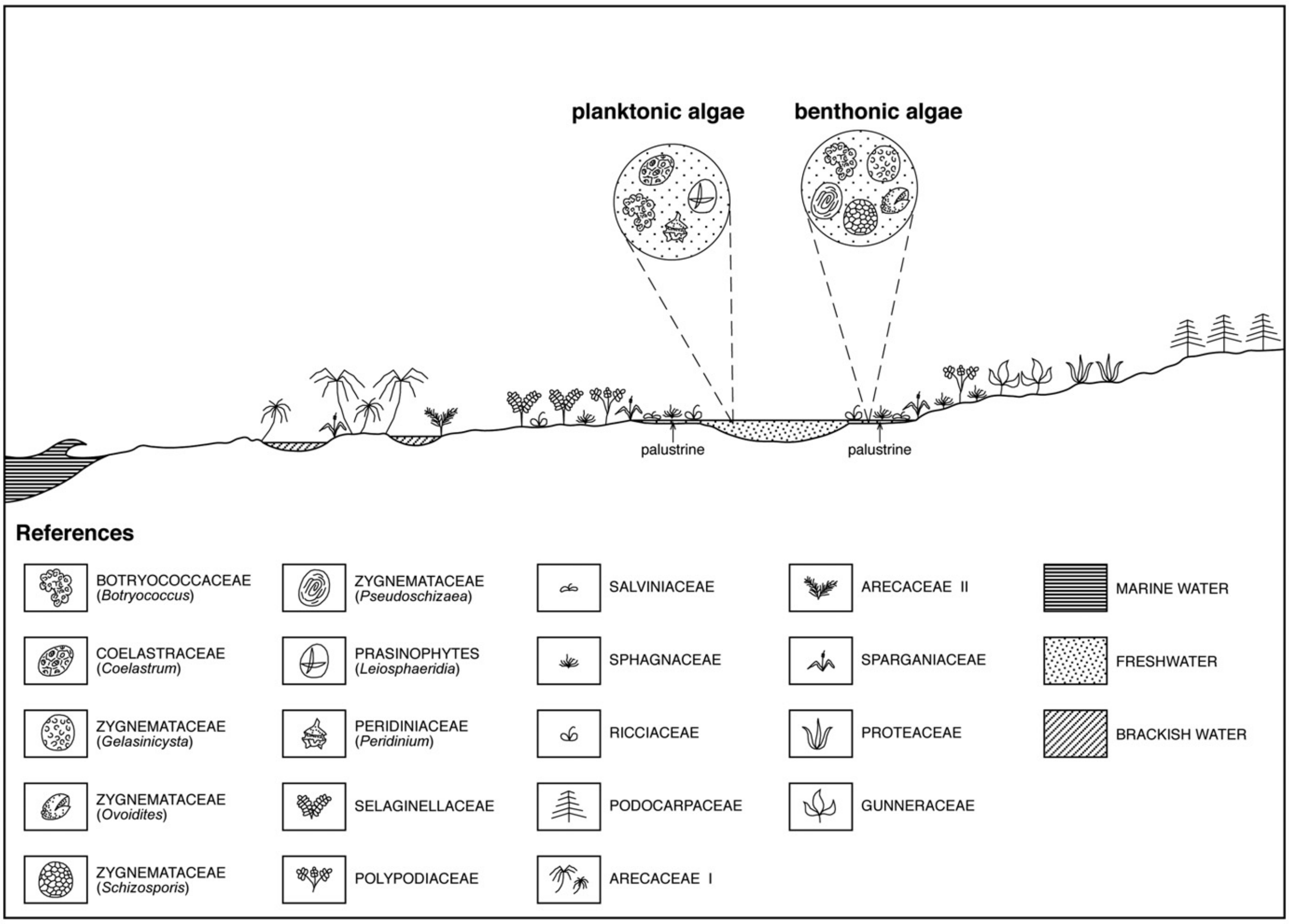

FIGURE 12 **Depositional environmental model deduced from the studied Danian palynobiota, showing the sequence of changing humidity and water salinity along the environmental profile. Brackish palm swamps with Arecaceae and Araceae developed along the back-shore, fringing the shoreline. Swampy zones with a hygrophile ecotonal community of Lycopodiaceae, Selaginellaceae, Schizaeacea and Polypodiaceae (among others published in Volkheimer et al., 2007) and associated moss (Sphagnaceae) occupied a landward position. In its turn this assemblage surrounded a shallow low energy freshwater body, dwelled by abundant microalgae (principally Botryococcaceae, Zygnemataceae and Peridiniaceae) and fringed by a wetland (freshwater palustrine zone) inhabited by Sparganiaceae / Typhaceae, Liliaceae, aquatic pteridophytes (Salviniaceae) and Ricciaceae.**

conform paludal herbs which grow in sites of shallow and protected waters, tolerating a certain rank of salinity.

The presence of a 1 m thick bed of coarse sandstone containing shark teeth, 3 m above the palynobiota horizon, supports the proximity to the marine shoreline and may represent a storm deposit.

This paleoenvironmental interpretation agree with the results on calcareous microfossils by Bertels (1973), who pointed out that intermixed terrestrial and marine sediments occurred in the study area, corresponding to transgressive and regressive facies.

Palynologic assemblages presented in Volkheimer et al. (2007) characterise the larger scale environmental setting of these water bodies. Combining the data from that previous investigation with the new results presented here we propose the depositional environmental model shown in Fig. 12.

## CONCLUSIONS

The new subtropical lacustrine palynobiota recorded from the Cerro Bororó Fm (San Jorge Basin, Chubut province, Argentina) shows a high diversity and improves significantly our knowledge on the largely unexplored field of Paleogene freshwater environments.

The excellent preservation of the scarcely studied group of aquatic species, which had been unknown for this Formation, allows extending considerably the knowledge on the coeval Danian coastal paleoenvironments that developed in the studied area of Patagonia.

The studied assemblage developed in situ and records the local depositional environments. It is peculiarly characterised by the relatively high amount of pollen masses (monospecific agglomerates) and the abundance of algal forms belonging to the autochthonous water body community.

The palynobiota records a shallow low energy freshwater lacustrine environment that developed in a marine littoral setting behind the coastal line, where neighbouring brackish coastal swamps were present. A diversified hygrophile ecotonal community of ferns with a palustrine zone also surrounded the freshwater body (Fig. 12). These environments developed under subtropical, warm and moist climatic conditions.

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