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Palynology of the Jagüel Formation (Maastrichtian–Danian) in northwestern Río Negro, Neuquén Basin, Argentina: paleobiogeographic inferences

Egly Pérez Pincheira*, Mercedes di Pasquo

CONICET - Consejo Nacional de Investigaciones Científicas y Técnicas, Laboratorio de Palinoestratigrafía y Paleobotánica, CICYTTP (CONICET-ER-UADER), Dr. Materi y España, Diamante E3105BWA, Entre Ríos, Argentina

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A B S T R A C T

The palynology of the Jagüel Formation at Cerro Azul locality Río Negro province; in the Neuquén Basin, was studied. The distribution of palynomorphs (spores, pollen grains, chlorophytes, and miscellaneous forms) across the outcrops allowed the definition of three palynological associations: A1 (upper Maastrichtian), A2 and A3 (Danian). The palynological results, together with micro- and invertebrate fossils found in this locality contributed to the paleoenvironmental reconstruction of this unit. A1 is deposited in mixed (coastal) to shallow marine environments with low energy associated to freshwater bodies. Whereas it is interpreted that A2 and A3 are deposited in coastal lagoons near shallow and internal platform marine environments. The largest number of palm pollen grains of *Proxapertites* and other angiosperms *Retitrescolpites baculatus* and *Striatopollis* for the Danian of Argentina has been registered here. These associations shared species with Maastrichtian and Danian palynofloras of the Colorado and western Neuquén basins. Species with affinities from northern latitudes of South America and Africa, and a few other species distributed more widely (cosmopolitan) and from southern regions (Argentina, Chile, Antarctica, New Zealand) predominate in the Danian. Therefore, we can confirm that the palynofloras of the Jagüel Formation are part of the Mixed Floristic Realm.

1. Introduction

The study of the Cretaceous-Paleogene limit (K-Pg) and the mass extinction event that happened in this interval, its origin, and the great modifications caused in the biota have been the subject of extensive discussions worldwide (e.g., Keller et al., 2007; Keller, 2008). Palynological studies in Argentina (especially in Patagonia), southern Chile and Antarctica have increased significantly in the last five decades (see references in Ruiz et al., 1999; Melendi et al., 2003; Prámparo et al., 2007; Barreda et al., 2012; di Pasquo and Martin, 2013; Amenábar et al., 2014; Caramés et al., 2016). These studies include species from marine and continental environments that improve and substantially expand the biochronostratigraphic correlation across this boundary (*e.g.*, Dettmann and Jarzen, 1988; Papú, 1989, 2002; Askin, 1990; Baldoni and Askin, 1993; Marenssi et al., 2004; Guler et al., 2004; Prámparo and Papú, 2006; Povilauskas et al., 2008; di Pasquo and Martin, 2013). There are few palynological contributions related to the Upper Cretaceous and Paleocene from the Río Negro province (Archangelsky and Romero, 1974; Baldoni, 1991; Papú and Sepúlveda, 1995), but none of them had analyzed the Jagüel Formation.

The goal of the present work is to carry out a palynological analysis of the Jagüel Formation in the Cerro Azul locality, around Lago Pellegrini, Río Negro (Fig. 1) to document bio-events (i.e., peaks of species abundance, changes in diversity of terrestrial and marine groups), and other palynofacies data and analyze its implications.

2. Studied area

Cerro Azul is located near Lago Pellegrini, in the north-west of the Río Negro province in the Neuquén Basin. Its greatest development includes the province of Neuquén and it extends to the south of Mendoza, the west of Río Negro and La Pampa. It is bordered to the north by Sierra Pintada and to the south by the

* Corresponding author.
E-mail address: eglysauria@hotmail.com (E. Pérez Pincheira).

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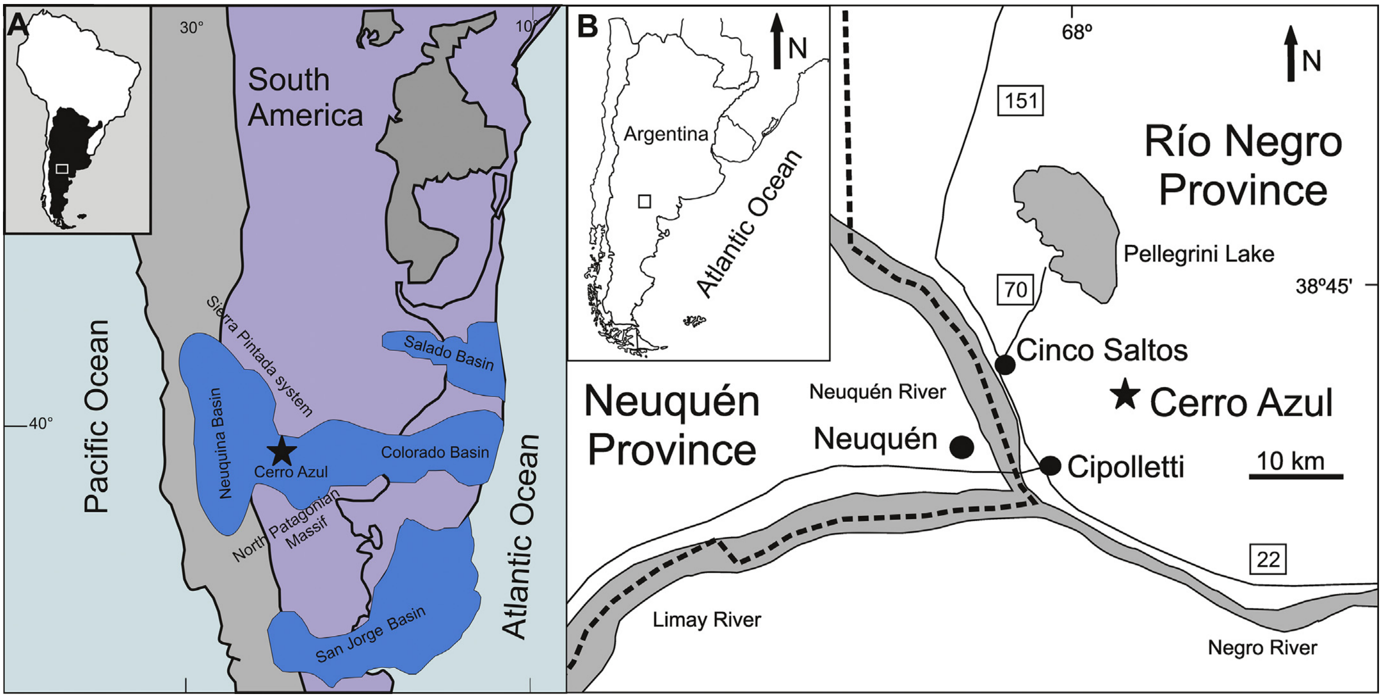


Fig. 1. A. Paleogeographic map of the Neuquén Basin and location of Cerro Azul (modified from Aguirre-Urreta et al., 2011). B. Geographic map with the Pellegrini Lake (Lago Pellegrini) and the locality of Cerro Azul.

Somún Curá or North Patagonian massifs (Fig. 1; see Andreis et al., 1974; Uliana and Dellapé, 1981). It has a vast, long-period sedimentary fill which, due to its richness in coal and oil, and for possessing the first dinosaur remains in South America, allowed for a wide variety of studies to be conducted in there since the beginning of the 20th century (Leanza et al., 2004). Three large sedimentary supercycles, called Jurassic (Upper Triassic–Upper Jurassic), Andicus (Upper Jurassic–Lower Cretaceous) and Riograndic (Upper Cretaceous–Paleogene), are recognized (Groeber, 1946). The latter is recorded after the intra-Cretaceous discordance determined by the Main Miranica Phase, which is part of the Patagonid Orogenic Cycle (Uliana and Dellapé, 1981), and can be homologated to the global discontinuity located in the lower Cenomanian (97 ± 3 Ma) (Rodríguez et al., 2007). This Supercycle marks the foreland stage of the basin and is divided into two subcycles represented by the Neuquén and Malargüe Groups: 1) "Neuqueniano" - middle Cenomanian to lower Campanian, and 2) "Malalhueyano" - uppermost Campanian–Paleocene, with the Huantráiquica discordance that indicates the base of the Malargüe Group. Its age was established at 74 ± 3 Ma, time in which the change in the slope towards the Atlantic would have been generated in the northern region of Patagonia, including the Neuquén Basin and the Somún Curá Massif (Leanza, 1999; Hugo and Leanza, 2001; Malumián and Náñez, 2011). In the east-southeast region, the Malargüe Group is composed upwardly by the Allen, Jagüel, Roca and El Carrizo formations and Loncoche, Jagüel, Roca and Pircala in its western portion (Barrio, 1990 a, b; Page et al., 2000). Other outcropping units in the south of the Río Negro province equivalent to the Jagüel Formation are the Los Alamitos and Coli Toro formations (see Page et al., 2000).

The studied area is part of the Lago Pellegrini region located near the Cinco Saltos town, in a natural depression of about 440 km^2 known as Cuenca Vidal. The Malargüe Group crops out variably and several geological and paleontological studies were carried out in its units (Uliana, 1979; Digregorio and Uliana, 1980; Uliana and Dellapé, 1981; Barrio, 1989, 1990 a, b; Parras et al., 1998; Parras and Casadío, 1999; Page et al., 2000; Rodríguez et al., 2007). The Vidal Basin presumably has an eolian origin (Windhausen, 1922) linked to the evolution of the Río Negro valley (Andreis et al., 1974). Cerro Azul rises 460 m above sea level and is located in the southwest of the lake (38°50'28.1′ S- 67°52′30.5″W, Fig. 1B). In 2018, it was declared site of interest and was called "Cerro Azul Geopark" (Parlament Resolution S-1411/18) to protect its varied and rich fossiliferous content present in the Roca and Jagüel formations, in which the K/Pg limit is found. Diverse fossils such as, foraminifera (Bertels, 1969, 1970, 1979, 1980; Ballent and Carignano, 2008), ostracods (Bertels, 1968, 1970, 1973, 1974, 1975; Ceolín et al., 2015), nannofossils (Musso et al., 2012), ostreids (Casadío, 1998; Del Río et al., 2007, 2011), echinoderms (Bertels, 1965; Martínez et al., 2011; Brezina et al., 2017), gastropods (Del Río et al., 2011), scallops, serpulids, corals (Parras et al., 2007), and vertebrates (Salgado, 1996; Heredia and Salgado, 1999; Gasparini et al., 2001; Cerda and Salgado, 2008; Fernández et al., 2008; de la Fuente et al., 2009; Bona et al., 2009; O'Gorman, 2016) were documented there. Although, none was about palynology up until now.

3. Materials and methods

3.1. Field-work and sampling

At the beginning of 2015, a field work to survey the outcrops of Allen and Jagüel formations around Lago Pellegrini (Cerro Azul, Cerro Gutiérrez, La Yesera) were carried out to accomplish with part of the objectives of a PhD thesis (Pérez Pincheira, 2020). A logistical support from the bentonite extraction company "Del Lago" (Cinco Saltos, Río Negro) was especially important to arrive to the localities. In 2016, a new field work to Cerro Azul that focused mainly on the sampling from the lower section of the Jagüel Formation was carried out, considering the preliminary results obtained (Pérez Pincheira and di Pasquo, 2016).

Therefore, a section of approximately 50 m thick from the Jagüel Formation was surveyed up to the first limestone bank where the

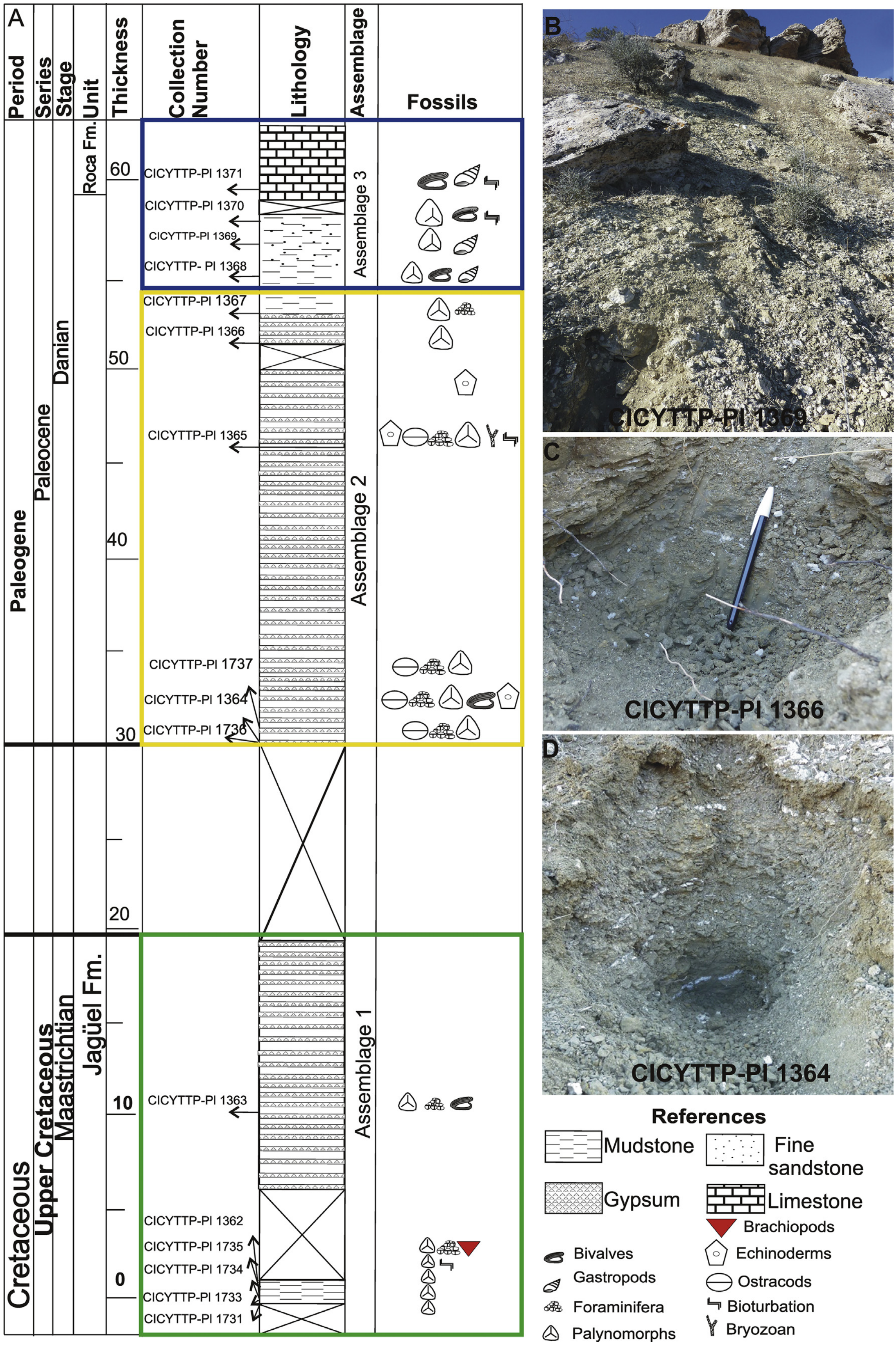


Fig. 2. A. Lithostratigraphic profile and fossil content. B–D. Field pictures of some intervals across the section.

beginning of the Roca Formation is indicated (Fig. 2A–D). Much of the outcrop is covered by a layer of debris of variable thickness between 50 cm and 1 m, which had to be removed in order to make detailed lithological observations of its layers, and to collect fresh samples for palynology and mainly *in situ* invertebrates and microfossils. At the base of the section, massive and laminated greenish gray mudstones, which were found interbedded with other yellowish green mudstone and gypsum layers, were sampled. In the upper section, the mudstone layers alternate with increasingly frequent and thicker sandstone banks until the appearance of the first limestone bank of the Roca Formation, in which limestone, marlstones, dolomites and sandstone beds predominate at its base and mid-section and evaporites at the top.

3.2. Laboratory procedures

The material was processed following standard techniques (Traverse, 2007), with some modifications. For the disaggregation of 30 g of sample, HCl (30%) and HF (45%) were successively applied, and the washings were carried out using distilled water to neutralize the sample after each acid. In some cases, it was necessary to repeat the procedure with HF. Another set of samples was processed with HF without using HCl to avoid destroying the calcareous microfossils. A first set of slides was mounted with not sieved residues using gelly-glycerin and had its productivity defined. These slides were used to palynofacies analysis as well. After this, a treatment with hot HCl was applied to the residues to disaggregate organic matter. The residues were then filtered with 25 μm and 10 μm screens and new slides were prepared. Additional material was processed in the case of a poor recovery of some residues checked under the stereoscope. Palynomorphs were concentrated by collecting drops from residues under a stereoscope with a pipette (like picking) and more slides were prepared for microscopic study. Likewise, the processing of those sterile residues was repeated to corroborate such condition. The palynological study was performed in a Leica DM 500 light microscope, which has a fluorescent light fixture with a fluorescein filter and an AmScope 14 Mpixels video camera. Fluorescence of palynomorphs was tested in permanent slides as well as in non-permanent ones in which specimens picked from residues were mounted with water. Some of them were later mounted in stubs for SEM illustration (di Pasquo and Vilá, 2019). Most of the samples collected for palynology and microfossils were friable allowing their review under Leica S6D and Leica 58APO microscopes bearing Leica S3 and DFC 295 video cameras. The observed microfossils were separated from the sediment by means of the hand "Picking" method, cleaned with a brush and distilled water, and photographed. Subsequently, a selection of those microfossils was mounted in stubs for study in the Phenom Pro (Jenck) SEM at the CICYTTP (CONICET-ENTRE RIOS-UADER), Diamante, Entre Ríos. The processing and optical analyses performed in the Laboratory of Palynology and Paleobotany (LPP) and the material studied has been deposited in the collections of Paleopalynology (CICYTTP-Pl), Invertebrates (CICYTTP-In) and Microfossils (CICYTTP-Mic) of said laboratory.

The taxonomic classification and botanical affinities of terrestrial and aquatic palynomorphs are based on the literature concerning fossil studies of the region and numerous Jurassic to Paleogene works (e.g., Wilson, 1988; Backhouse, 1988; Williams et al., 1993; Jaramillo and Dilcher, 2001; Pardo-Trujillo et al., 2003; Slimani et al., 2010; Raine et al., 2011; Jaramillo, 2014; Williams et al., 2017).

The palynofacies components used to characterize the palynoassemblages are palynomorphs, unstructured (amorphous organic matter) and structured organic matter (i.e., phytoclasts (cuticles, tracheids, brown and black particles), zooclasts) (Batten, 1996). Palynomorphs were gathered in morphogroups after having their biological affinities and percentages calculated based on the counting of c. 250–350 specimens per sample. Palynofacies percentages are calculated as an average of the number of particles of those components in at least 10 campus under 10× magnification in the microscope.

4. Results

Out of the 17 samples taken from the Jagüel Formation (Fig. 2A), 15 were productive for palynology, 6 for microfossils and 6 for invertebrates.

4.1. Palynology

The palynofacies of the assemblages in the Jagüel Formation are characterized by low frequency of cuticles, tracheids, and amorphous organic matter (AOM) which, in part, comes from the internal filling of some of the microfossils observed in the palynological preparations of the samples not treated with HCl. A variable frequency of palynomorphs is represented by ferns (3 species), Gymnospermae (3), Angiospermae (14), Chlorophyte (20), dinoflagellate cysts (22) and Acritarch (1). The sporomorphs are in fairly good condition, but, unlike prasinophytes and most of the *Proxapertites* pollen grains that are complete and well-preserved (yellow color), dinoflagellates and some zygospores tend to be more deteriorated (almost transparent in color) and fragmented.

The stratigraphic distribution of the identified species allows the characterization of three palynological associations described below. A selection of most relevant species included (Figs. 3-11, Tables 1–4).

4.1.1. Association 1 (A1)

This assemblage is mainly composed of AOM (70%), subordinated palynomorphs (20%), and phytoclasts (10%). The AOM is brown in color and presents granular and spongy types with low yellow fluorescence, and scarce and poorly preserved small and equidimensional brown-black particles. A low diversity of palynomorphs derived from pteridophytes, angiosperms, dinoflagellates and spheroidal forms of probable algal affinities constitute the main groups (Fig. 10A, D). Among the angiosperms, scarce specimens of *Tricolpites* sp., *Psilatricolpites* sp., and *Liliacidites variegatus*, and chlorophytes (*Palambages* form A, *Cymatiosphaera* cf. *conopa*, *Zygnema*) were recorded through all the assemblages, whereas the acritarch *Baltisphaeridium angulosum* and the dinoflagellate *Nummus similis* were restricted to the basal samples. The dinoflagellates *Fromea fragilis* and *Senoniasphaera inornata* occurred at the top of this section (Fig. 11).

4.1.2. Association 2 (A2)

It is integrated by spongy-type light brown AOM (25%) and brownish-yellow phytoclasts (5%). A major diversity and abundance of well-preserved palynomorphs (70%) characterize this assemblage. The total diversity of these palynomorphs (100%) is composed of chlorophycean algae (22%), gymnosperm pollen grains (2%), and angiosperms (40%), dinoflagellates (14%), and indeterminate algal and other remains (Fig. 10B, D).

The sample CICYTTP-Pl 1365 presents terrestrial species and phytoplankton in a similar percentage. Among the former predominates the pollen grains of *Proxapertites*, composing c. 75% of the total of angiosperms. The remaining percentage is represented by monocotyledon (*Liliacidites* spp., *Longapertites patagonicus*,

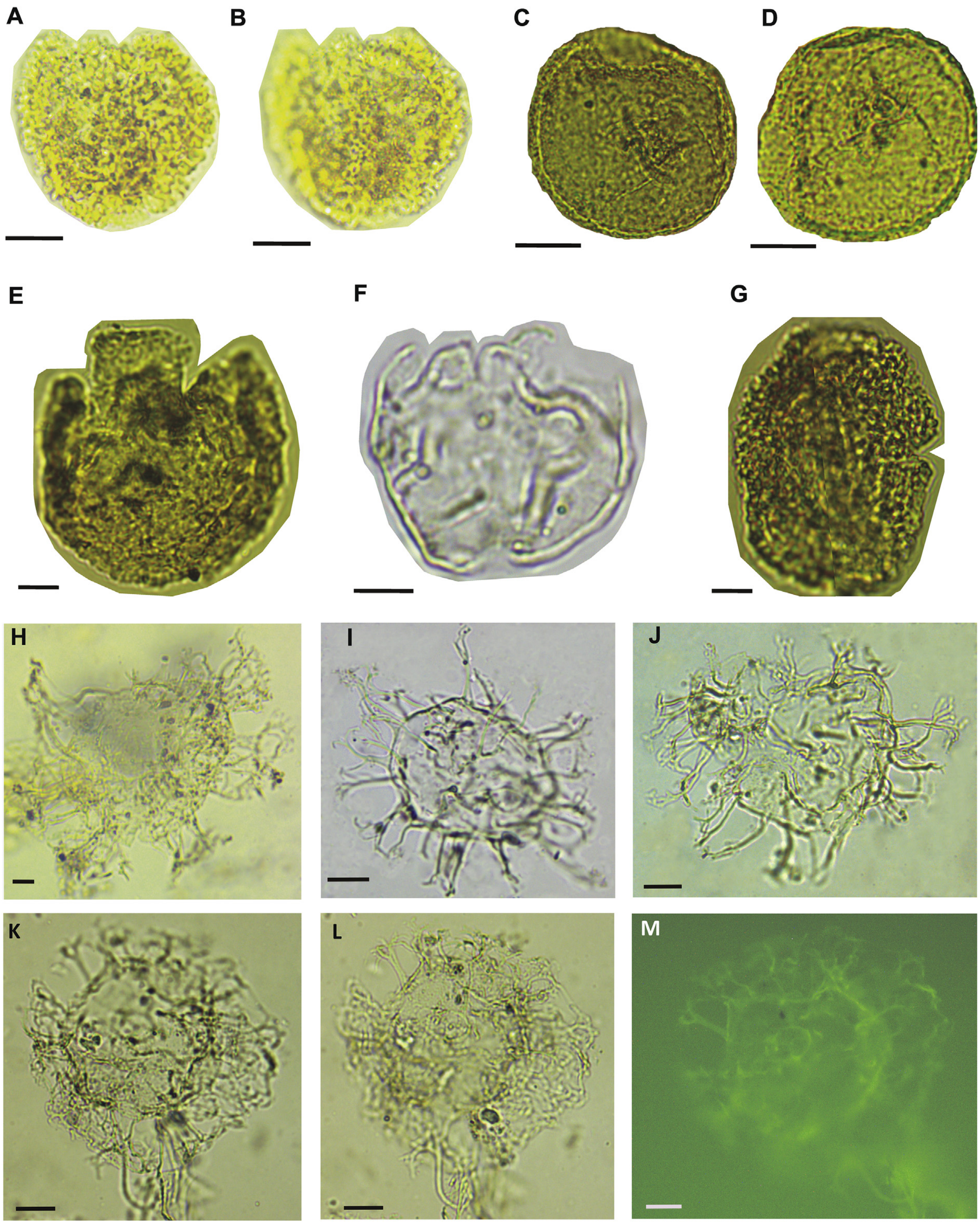


Fig. 3. Selected palynomorphs from the Jagüel Formation. **A—B**. *Batiacasphaera cassicula* CICYTTP-Pl 1365-1HF2 K35/3, **C—D**. *Batiacasphaera cassicula*, CICYTTP-Pl 1365-2HF H31/3. **E.** *Trithyrodinium suspectum*, CICYTTP-Pl 1365-1HF2 G33. **F.** *Kallosphaeridium parvus*, CICYTTP-Pl 1369-1HF2 L28/1. **G.** *Cerebrocysta* cf. *C. waipawaensis*, CICYTTP-Pl 1365-2HF2 N34/4. **H.** *Glaphyrocysta ordinata*, CICYTTP-Pl 1365-1HF2 Q18. **I.** *Achomosphaera danica*, CICYTTP-Pl 1369-1HF2 Q32. **J.** *Achomosphaera danica*, CICYTTP-Pl 1369-1HF Z51/2. **K.** *Glaphyrocysta retiintexta*, CICYTTP-Pl 1369-1HF P4/2. **L.** *Glaphyrocysta retiintexta*, CICYTTP-Pl 1369-1HF P4/2. **M.** *Glaphyrocysta retiintexta*, CICYTTP-Pl 1369-1HF P4/2. **Scale bars** 10 μm. England Finder coordinates.

Longapertites andreisi, Sparganiaceae) and dicotyledonean species (*Ulmoideipites patagonicus* Archangelsky (= *Verrustephanoporites simplex* Leidelmeyer), *Retitrescolpites baculatus*). Gymnosperms are also present with *Araucariacites australis,* algal groups like Zygnemataceae (*Paralecaniella, Lecaniella, Ovoidites*), prasinophytes (*Pterospermella* spp., *Cymatiosphaera* sp.) and dinoflagellates (*Glaphyrocysta ordinata*, *Manumiella rotunda*, *Batiacasphaera cassicula*, *Kallosphaeridium parvum*, *Nummus similis*).

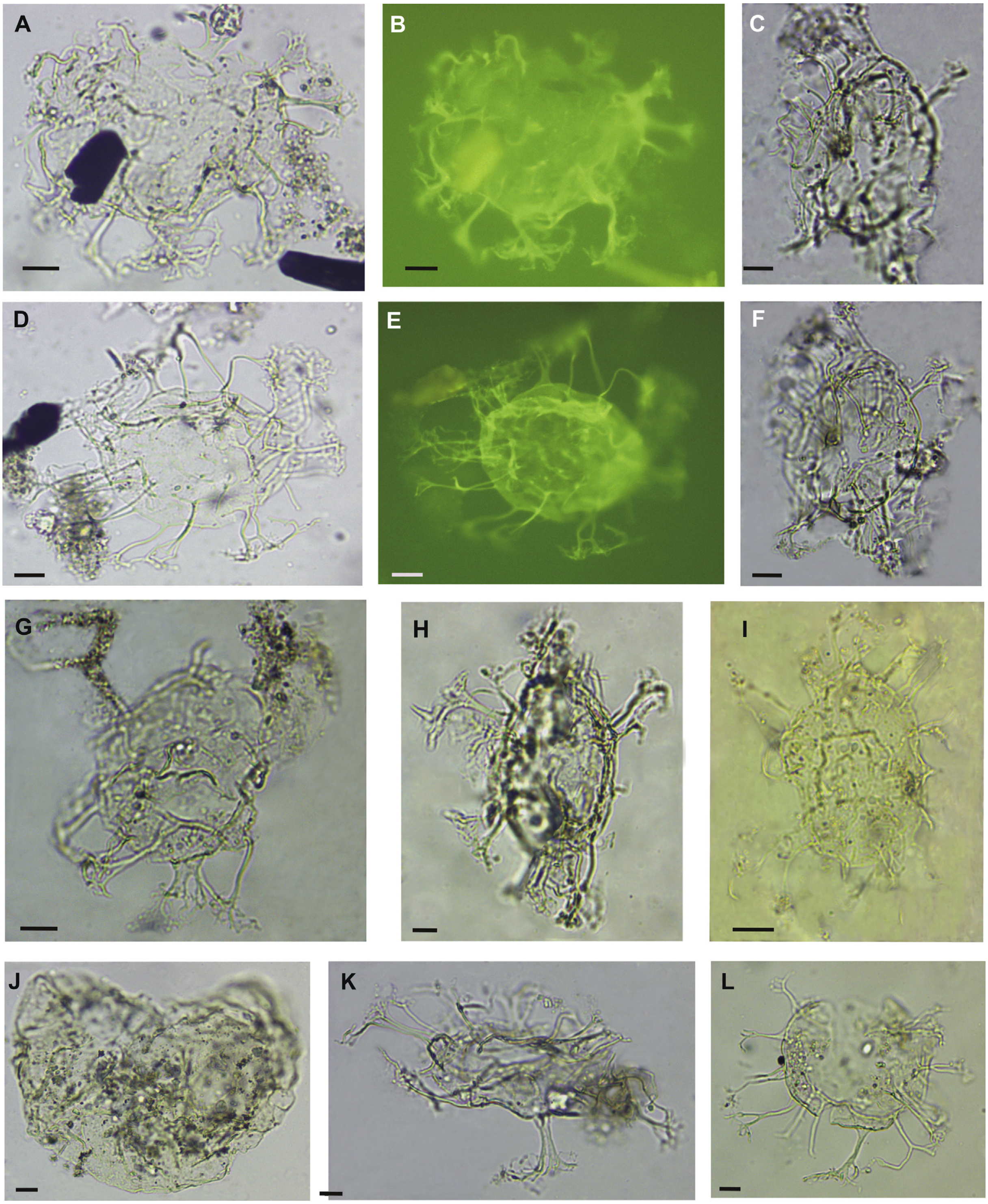


Fig. 4. Selected palynomorphs from the Jagüel Formation. **A—B.** *Glaphyrocysta retiintexta*, CICYTTP-Pl 1369-1HF O45/3 (B. under fluorescence). **C.** *Glaphyrocysta delicata*, CICYTTP-Pl 1369-1HF2 L43/1. **D—E.** *Glaphyrocysta delicata*, CICYTTP-Pl 1369-1HF P30/2 (E. under fluorescence). **F.** *Glaphyrocysta delicata*, CICYTTP-Pl 1369-1HF2 M43/1. **G.** *Achomosphaera heterostyla*, CICYTTP-Pl 1369-2HF W59/2. **H.** *Spiniferella* cf. *cornuta*, CICYTTP-Pl 1369-2HF D30/3. **I.** *Spiniferites multibrevis*, CICYTTP-Pl 1365-2HF N54/4. **J.** *Senoniasphaera inornata*, CICYTTP-Pl 1368-1HF2 D22/0. **K.** *Achomosphaera heterostyla*, CICYTTP-Pl 1369-1HF R24/3. **L.** Chorate cyst cf. *Glaphyrocysta*, CICYTTP-Pl 1369-2HF O59/3. **Scale bars** 10 μm.

4.1.3. Association 3 (A3)

Samples of the upper part of the Jagüel Formation yielded low percentage of AOM (c. 20%) and phytoclasts (10%), with small fragments of tracheids. The remaining 70% corresponds to well-preserved and diverse terrestrial and marine palynomorphs (Fig. 10C, D). The total diversity of these palynomorphs is composed of Chlorophycean (14%), and other algal and indeterminate forms. Ferns (0.5%), gymnosperms (2%), and angiosperms (2%) are subordinated to the abundance of dinoflagellates (71%). Among the latter, *Glaphyrocysta ordinata* predominates in the A3, whereas it is low in

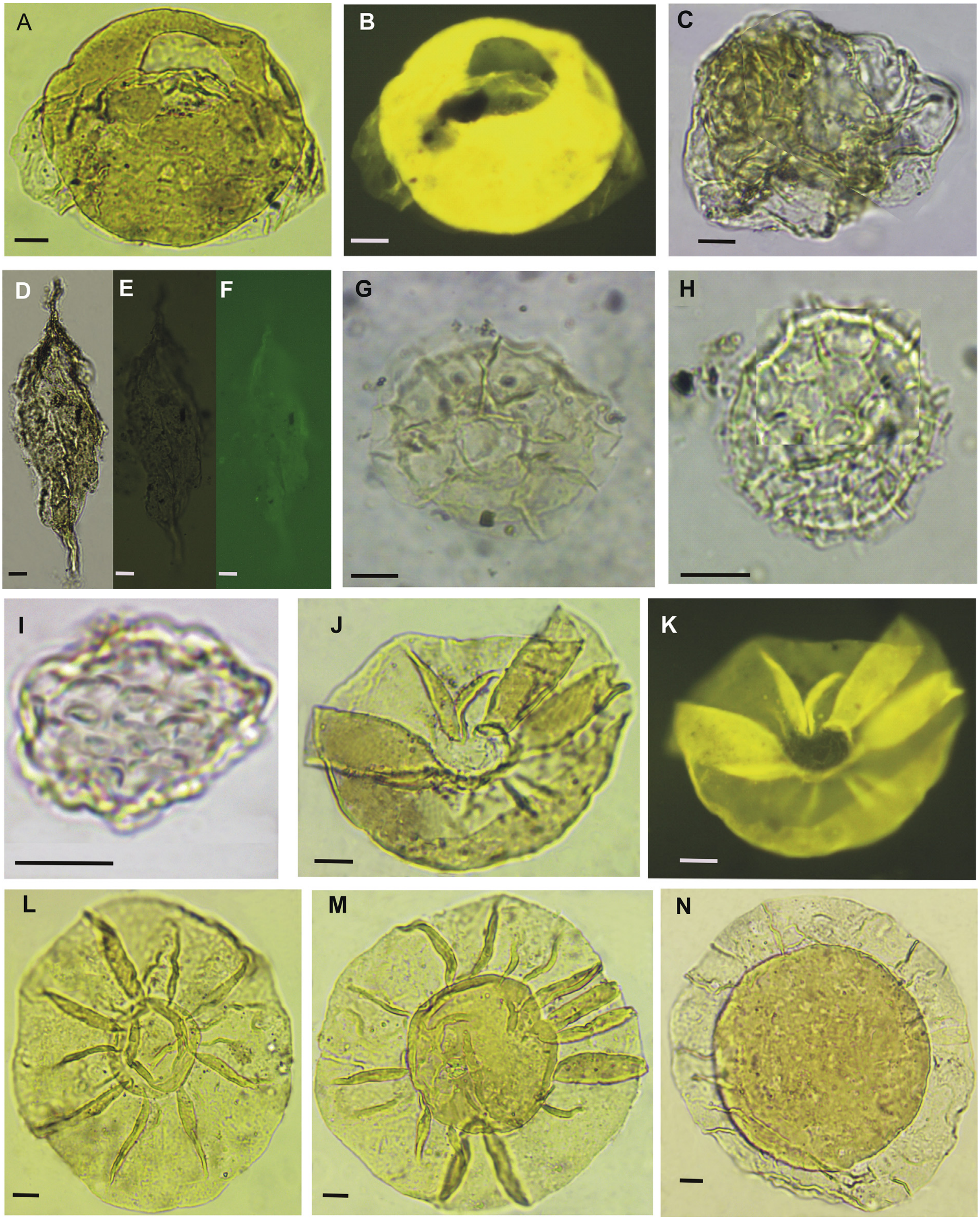


Fig. 5. Selected palynomorphs from the Jagüel Formation. **A—B.** *Manumiella rotunda*, CICYTTP-Pl 1365-1HF2 D24/0 (B. under fluorescence). **C.** *Senoniasphaera inornata*, CICYTTP-Pl 1368-1HF2 V28/0. **D—F.** *Paleocystodinium australinum*, CICYTTP-Pl 1366-1HF2 P22/2 (E-F. under fluorescence). **G.** *Cymatiosphaera* sp., CICYTTP-Pl 1368-1HF G32/0. **H.** *Cymatiosphaera* cf. *conopa*, CICYTTP-Pl 1335-2HF2 O48/0. **I.** *Oedogonium cretaceum*, CICYTTP-Pl 1363-1HF2 M31/3. **J—K.** *Pterospermella australiensis*, CICYTTP-Pl 1365-1HF2 G21/0, (K. under fluorescence). **L.** *Pterospermella australiensis*, CICYTTP-Pl 1365-1HF2 R22/0. **M.** *Pterospermella* aff. *harti*, CICYTTP-Pl 1365-2HF R46/3. **N.** *Pterospermella aureolata*, CICYTTP-Pl 1365-2HF2 J22/0. **Scale bars** 10 μm.

the A2. *G. delicata* and *G. retiintexta* are more frequent in sample CICYTTP-Pl 1369, in which *Achomosphaera* (*A. heterostila*, *A. danica*) and *Spiniferella* cf. *cornuta* occurred together with dispersed opercula.

4.2. Micro- and megafossils

The foraminifers *Guembelitria cretacea*, *Polymorphina* and *Guadripina boltoskoyi*, and inarticulate brachiopods (*Lingula*) were

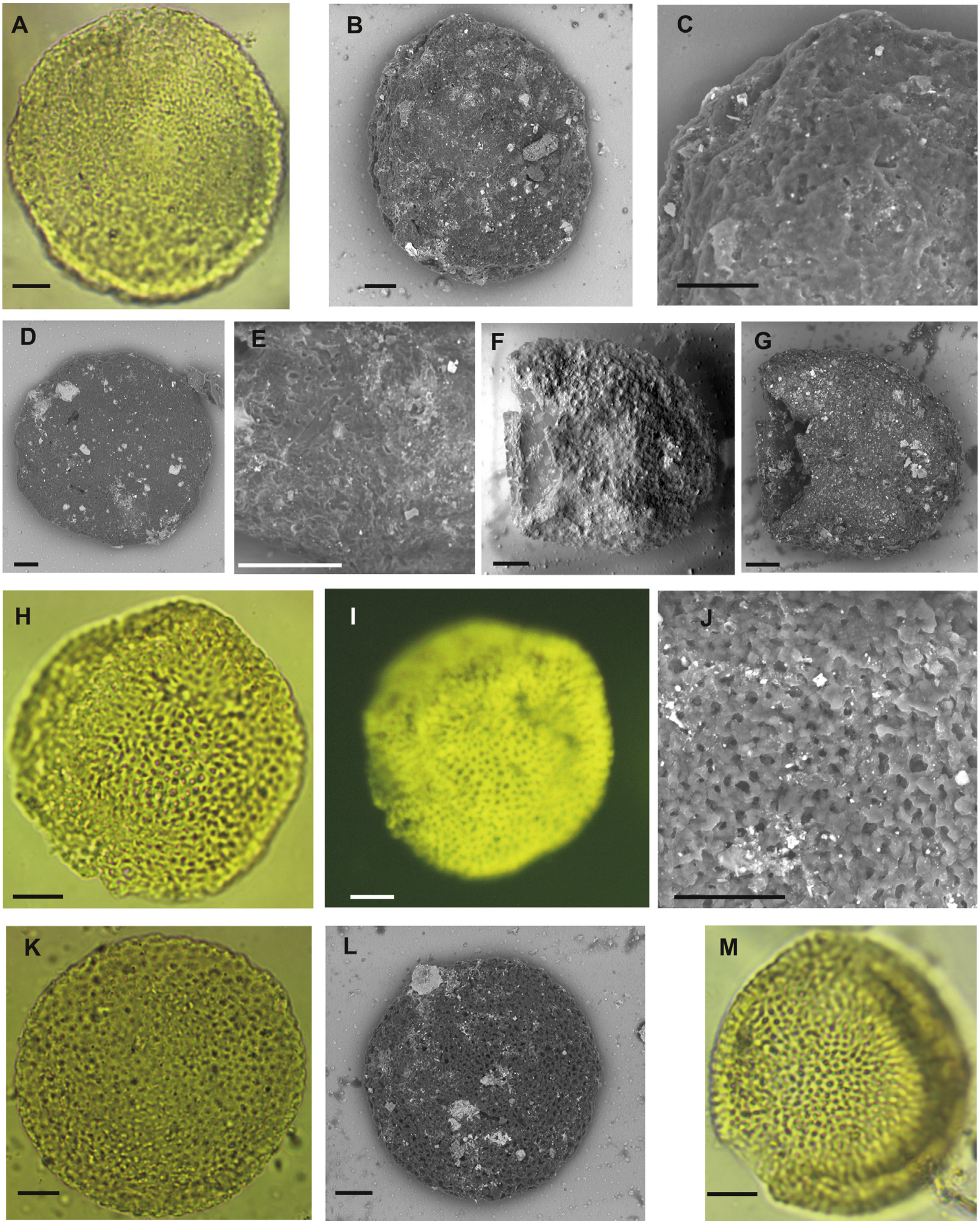
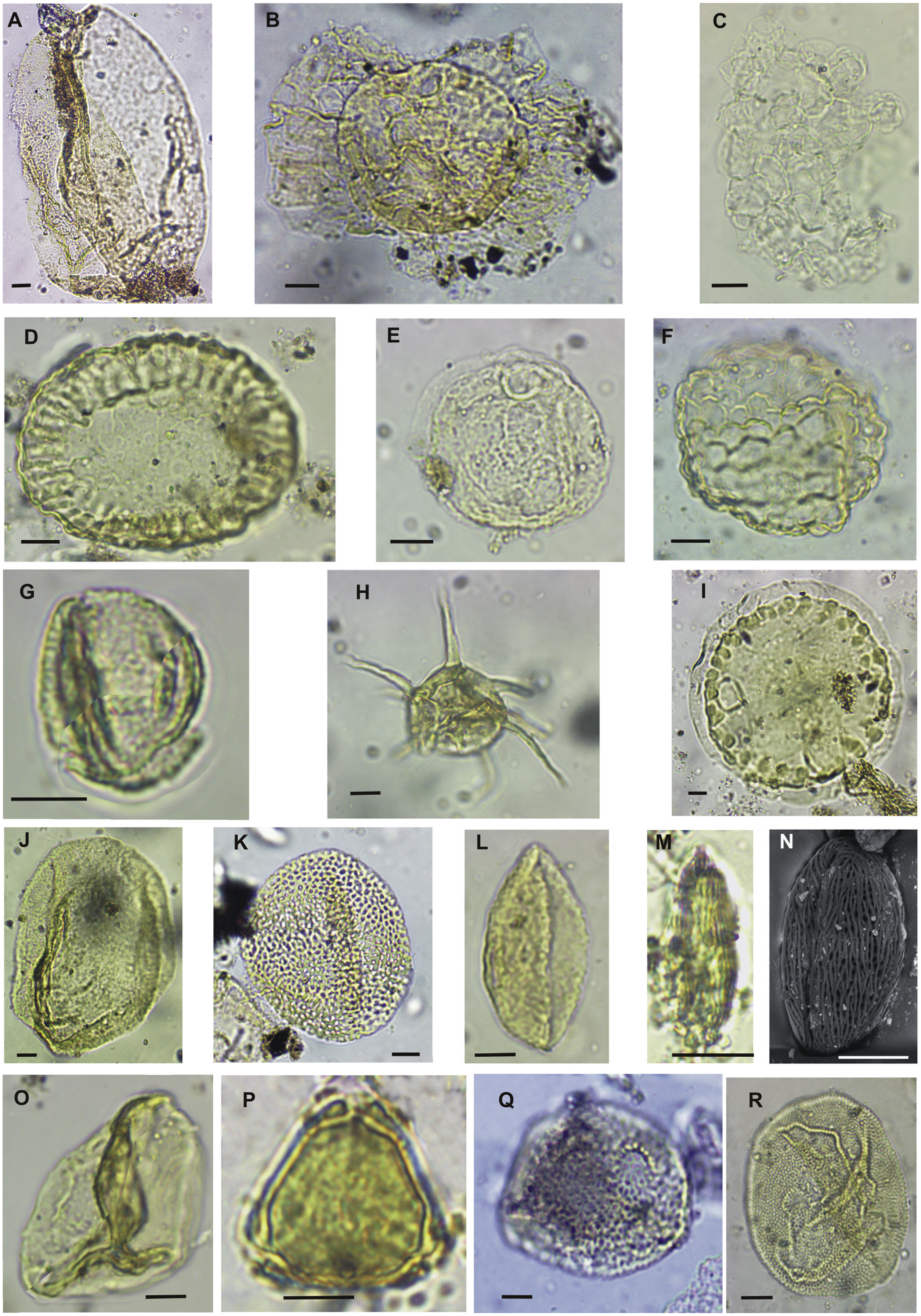


Fig. 6. Optical and SEM pictures of *Proxapertites* from the CICYTTP-Pl 1365 and 1369 samples. **A—G.** *Proxapertites* group with thicker and homogenous exine. **A**. CICYTTP-Pl 1365-2HF2 B34. (**B—G.** SEM picture) **H—M**. *Proxapertites* group with wider reticulum of exine. **H–I.** Specimen illustrated under white and fluorescent light, CICYTTP-Pl 1365-1HF2 K36/4. **J, L**. SEM pictures of same specimen. **K**. CICYTTP-Pl 1365-2HF H54. **M.** *Proxapertites* sp. CICYTTP-Pl 1365-2HF2 Q48. **Scale bars** 10 μm.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documented in the lower part of the outcrop; *Rugotruncana subpennyi*, *Cibicides succedens*, *Amonolinoides acuta,* along with ostreids and echinoderms, in the middle; and gasteropods, pectinids, serpulids, corals, echinoderms, foraminifers, ostracods, and bryozoans at the top (Fig. 2 and Tables 3 and 4).

5. Discussion

5.1. Paleoenvironmental interpretation

The sedimentologic and palynofacies features and paleoecology of mega- and microfossils, and palynomorphs allowed us to characterize the paleoenvironmental changes across the Jagüel Formation at Cerro Azul.

5.1.1. Association 1

The lower portion of the profile is characterized by a predominance of greenish-green, yellowish-green and grayish-green mudstones with iron oxide patina. At its base, massive layers have internal molds of inarticulate brachiopods (*Lingula*); and upwardly, it presents a section of laminated mudstones with gypsum intercalations and banks of ostreids on its uppermost part. The samples, preserved inside microfossils, are characterized by abundant dark-brown AOM in lumps of granular type and fine particles. Planktonic foraminifera (*Guembelitria cretacea*, *Guadripina boltoskoyi*) and less frequent species of angiosperms, likely of herbaceous plants (*Tricolpites, Liliacidites*), together with aquatic freshwater algal (*Lecaniella, Oedogonium*, Zygospora *Zygnema* type) and marine species (*Baltisphaeridium angulosum*, *Cymatiosphaera* cf. *conopa*, *Palambages*) are also documented (Tables 1–4).

Zygnemataceae is better represented in ponds and shallow water bodies with slight euxinic conditions poor in nutrients (Graham and Wilcox, 2000; Mautino, 2007; Scafati et al., 2009). Zippi (1998) related the presence of zygospores with repeated cycles of arid conditions as well as moderate to higher warm temperatures that triggered their germination (Zavattieri and Prámparo, 2006; Mautino, 2007). The marine phytoplankton is characteristic of shallow waters (Wrenn and Hart, 1988; van Geel and Grenfell, 1996; Guy-Ohlson, 1996). The low frequency of the latter forms suggests deposition in a shallow brackish to marginal marine environment with low energy and terrestrial input from lowlands and freshwater bodies. The presence of *Lingula*, ostreids, and foraminifers, such as *Guembelitria cretacea,* which thrived in environments that are generally toxic to other species (presumably due to eutrophic conditions during the upper Maastrichtian in the Neuquén Basin (Keller et al., 2007)), reveals high-stress conditions confirming our interpretation. The zygnemataceae suggest the alternation of wet and dry periods in this interval, also supported by the registration of gypsum sheets, which are formed from waters rich in sulfates and chlorides in shallow marine environments subjected to a warm and dry climate (periods of higher evaporation). This interpretation agrees with Musso et al. (2012), whose work is based mainly on lithological studies of clay, and with the paleoecologic analyses of ostracods by Ceolín et al. (2015); both carried out in our profile.

5.1.2. Association 2

The middle section, characterized by presenting yellowish-green to yellowish-brown mudstones, presents *Skolithos*-type bioturbation in its basal part (CICYTTP-Pl 1365), which are associated with shallow, near the coast areas of the marine platform (Droser, 1991), and indicate moderate to high energy conditions with tidal influence (Alpert, 1974; Cónsole Gonella and Aceñolaza, 2009; Buatois and Mángano, 2011).

In addition, complete, articulated and non-articulated shells of ostracods and complete foraminifera are found. Among the determined foraminifera species, agglutinated benthic (*Migros hanseni, Pseudonodosaria conica*) and calcareous forms (*Planulina camachoi*, *Lenticulina rivadariensis*, Type cf. *Pullenia cretacea*, *Discorbinella castellaroae*, *Guembelitria cretacea*, *Rugotruncana subpennyi*), and the ostracods *Cytherella saraballentae*, *Paracypris imaguncula* and *Bairdoppilata* sp. are present. This suggests the existence of shallow marine environments (Ceolín et al., 2015 and their references) Tables 1–4.

Among the pollen elements, low frequent angiosperm grains derived from herbaceous (*Liliacidites* spp.), arboreal (*Ulmoideipites patagonicus*), and water plants of Sparganiaceae are present together with species of *Longapertites* associated with Arecaceae (*Nypa* type), which preferentially lives in coastal and halophyte environments (Volkheimer et al., 2007; Scafati et al., 2009). Species of *Proxapertites* of affinity Araceae (Herngreen et al., 1996; Zetter et al., 2001; Vajda and Bercovici, 2012) were, in high proportion, likely well-adapted to the warm and humid environmental conditions. The morphological and structural characteristics of pollen grains of *Araucariacites*, such as the large size and structure of the exine (Caccavari, 2003), suggest that their dispersion is more likely by runoff and not anemophylous (Olivera et al., 2015). Hence, groups of plants were distributed in the surrounding lands relatively near to the depocenter, similar to the environmental reconstruction of the Danian Cerro Bororó Formation proposed by Volkheimer et al. (2007).

Spheroidal structures and *Leiosphaeridia*, possibly assignable to arthropod eggs and euryhaline prasinophytes (*Pterospermella aureolata, P. australiensis*) and, to a lesser extent, dinoflagellates such as *Senoniasphaera inornata, Trithyrodinium evittii,* and *Fromea fragilis*, are groups best represented in the shallow inner platform (Skupien and Mohamed, 2008). On the contrary, *Batiacasphaera cassicula*, *Kallosphaeridium parvum,* and *Nummus similis* come from more distal marine environments (Figs. 3-9).

According to Quattrocchio (2018), the presence of neritic and oceanic taxa in the same association is evidence that shallow water associations have moved to deeper marine environments. However, A2 is interpreted as being deposited in a shallow marine setting with tidal influence supported by paleontological evidence such as *Skolithos*-type bioturbation and shallow water ostracods (Fig. 2). Marginal environments and freshwater bodies, swamps, and coastal vegetation under warm and seasonal humid paleoclimatic conditions were part of the terrestrial landscape. Species of the genus *Glaphyrocysta* and *Manumiella* are indicators of a shallow marine environment, relatively close to the shore (Askin, 1988; Thorn et al., 2009; Slimani et al., 2010).

Fig. 7. Selected palynomorphs from the Jagüel Formation. **A.** *Fromea fragilis*, CICYTTP-Pl 1363-2HF J37. **B.** *Thalassiphora patula*, CICYTTP-Pl 1365-1HF R55. **C.** *Palambages* sp. form A Manum and Cookson, CICYTTP-Pl 1733-1HF O21/3. **D.** Zygospore *Derbarya*-type, CICYTTP-Pl 1737-1HF R16/3. **E.** *Nummus similis,* CICYTTP-Pl 17332-HF Z16/4. **F.** Cf. *Gelanicista vangeelii* in Scafati et al. (Zygospore), CICYTTP-Pl 17372-HF2 D47/4. **G.** *Tricolpites* sp., CICYTTP-Pl 1734-2HF2-HClcte D58/4. **H.** *Baltisphaeridium angulosum*, CICYTTP-Pl 1733-1HF C38/1. **I.** Indeterminate form. CICYTTP-Pl 1369-1HF2 D27/1. **J.** *Araucariacites australis*, 1736-2HF2-HClcte Y18. **K.** *Liliacidites* cf. *variegatus*, CICYTTP-Pl 1365-1HF2 S51. **L.** *Longapertites andreisii*, CICYTTP-Pl 1365 X47/3. **M**—**N.** *Striatopollis bellus*. **M.** CICYTTP-Pl 1369-1HF2 Z55/3. **N.** SEM picture. **O.** *Birretisporites potoniaei*, CICYTTP-Pl 1367-2HF2 W27/4. **P.** *Myrtaceidites* cf. *mesonesus*, CICYTTP-Pl 1369-2HF2 G19. **Q.** *Sparganiaceapollenites* sp., CICYTTP-Pl 1365-1HF2 M32/4. **R.** *Sparganiaceapollenites*? CICYTTP-Pl 1737-1HF Q39/3. **Scale bars** 10 μm.

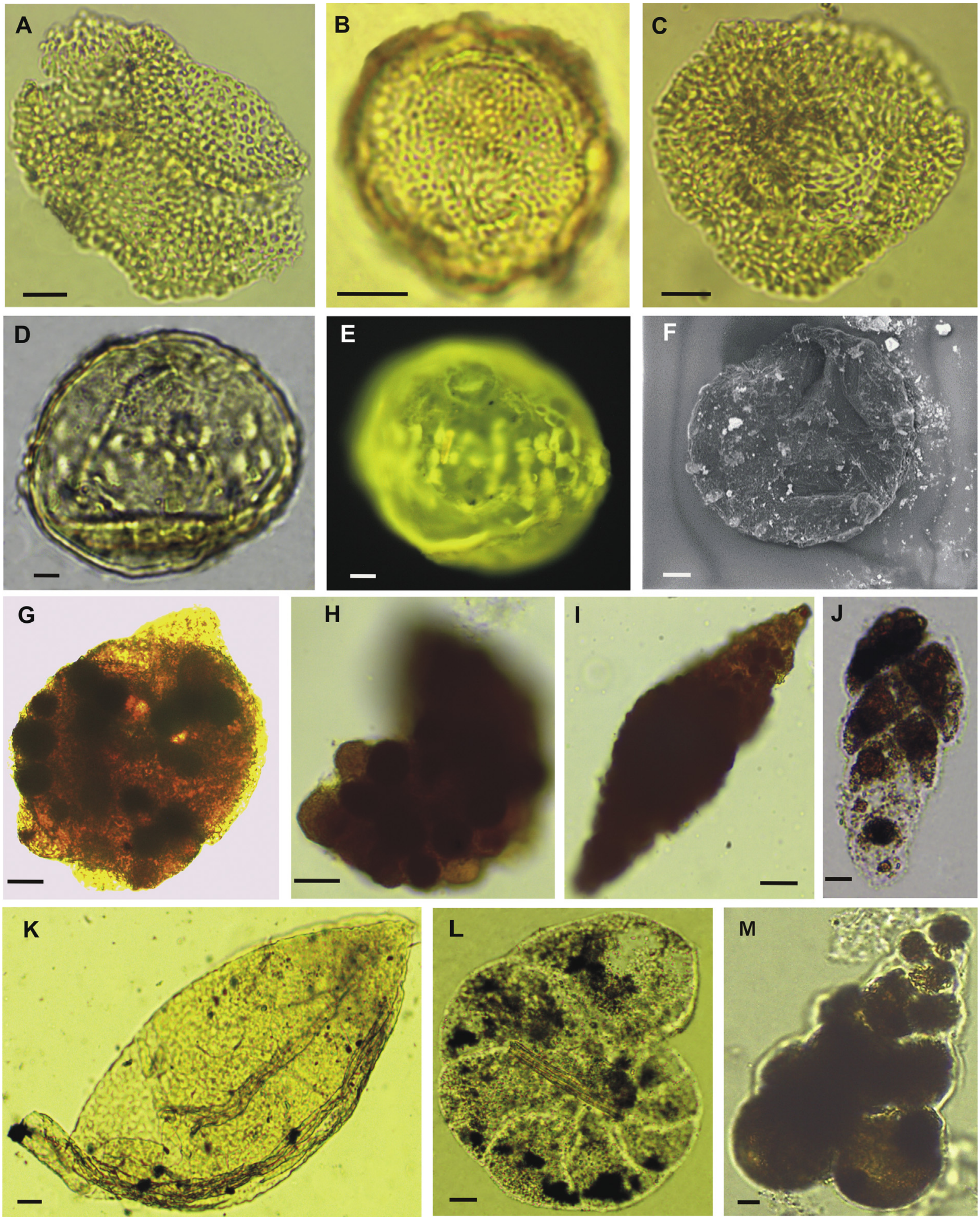


Fig. 8. Selected palynomorphs from the Jagüel Formation. **A.** *Liliacidites* sp., CICYTTP-Pl 1365-1HF2 S45/0. **B.** *Ulmoideipites patagonicus* (= *Verrustephanoporites simplex* Leidelmeyer), CICYTTP-Pl 1365-2HF2 L22/0. **C.** *Retitrescolpites baculatus*, CICYTTP-Pl 1365-1HF2 G53/2. **D**—**F.** Same specimen of indetermined form, CICYTTP-Pl 1369-1HF2 G25/2 (E. under fluorescence, F. SEM). **G.** Indetermined dinoflagellate filled with AOM, CICYTTP-Pl 1362-1HF H30/0. **H.** Specimen filled with AOM, CICYTTP-Pl 1362-1HF N28/0. **I.** Specimen filled with AOM. CICYTTP-Pl 1362-1HF O37/0. **J.** Foraminifer filled with AOM, CICYTTP-Pl 1362-2HF M28/2. **K.** Arthropod egg, CICYTTP-Pl 1365-1HF2 Q53/0. **L.** *Cibicides succedens*, CICYTTP-Pl 1365-2HF R42/0. **M.** *Guembelitria cretacea*, specimen filled with AOM, CICYTTP-Pl 1362-1HF J27/0. **Scale bars:** A—J 10 μm; K—M 30 μm.

Ballent and Carignano (2008) and indicated hypersalinity anomalies and/or fluctuations in salinity based on the record of benthic foraminifera at the Maastrichtian (A1) and Danian limits in this region.

5.1.3. Association 3

The upper section of the Jagüel Formation at Cerro Azul is composed of massive and compact yellowish-green mudstones with discontinuous gypsum sheets, and sandstone deposits. The

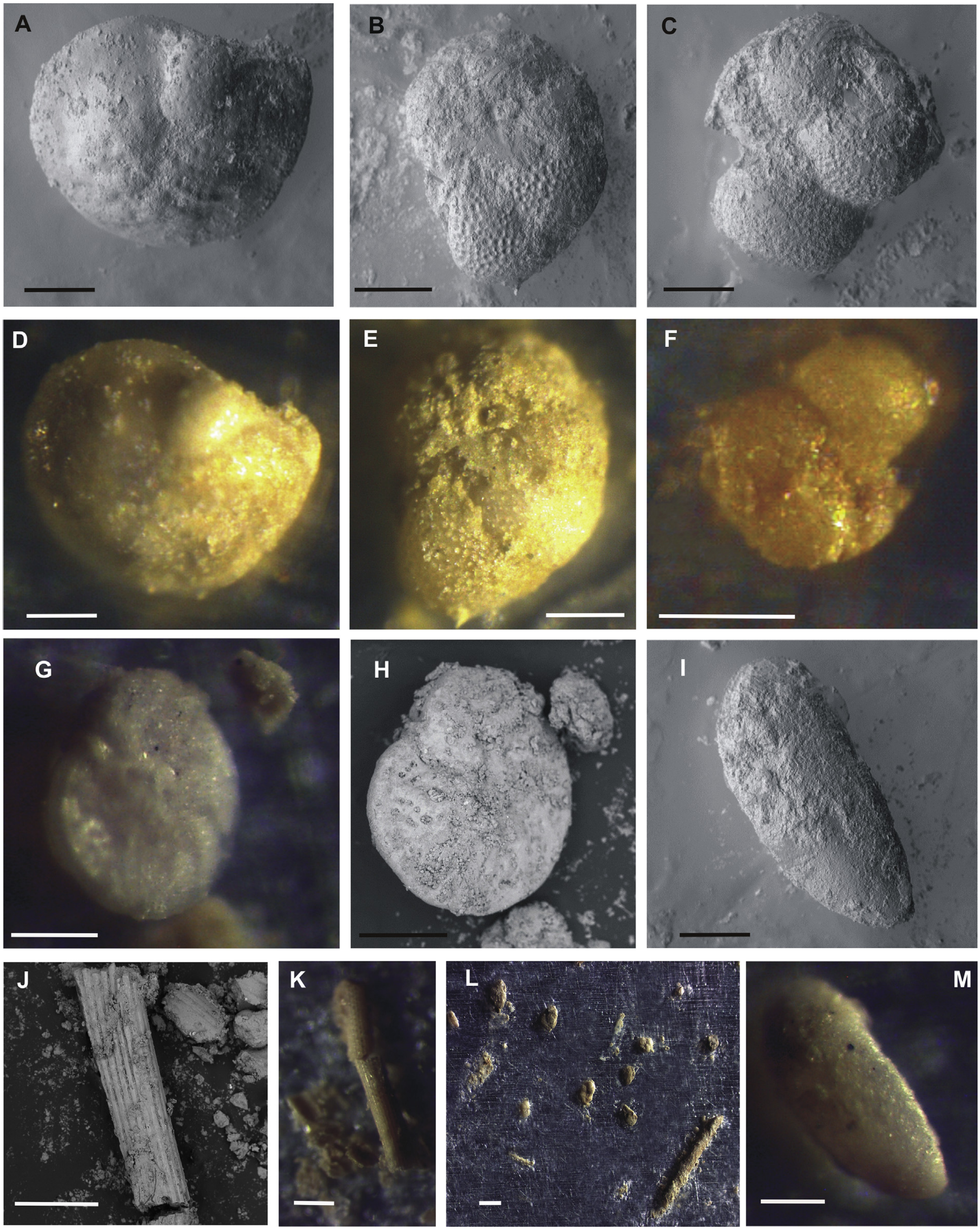


Fig. 9. Microfossils of sample CICYTTP-Pl 1364. **A**, **D.** *Planulina camachoi.* **A.** SEM picture. **D.** Stereoscope picture. **B**, **E.** Indeterminate foraminifera. **B.** SEM picture. **E.** Stereoscope picture. **C, F.** Indeterminate foraminifera. **C.** SEM picture. **F.** Stereoscope picture. **G—H.** *Anomalinoides acuta.* **G.** Stereoscope picture. **H.** SEM picture. **I, M.** *Paracypris imaguncula* **I.** SEM picture. **M.** Stereoscope picture. **J—K.** Echinoderm spines. **J.** SEM picture. **K.** Stereoscope picture. **L.** Stereoscope picture of specimens from sample CICYTTP 1364. **Scale bars** A, B, D—I, K—M 100 μm; C. 50 μm; J. 200 μm.

first thicker calcareous deposit over the alternating lime-mudstones indicates the beginning of the Roca Formation. Terrestrial palynomorphs are poorly represented in this association, whereas dinoflagellate cysts with and without operculum, mainly *Glaphyrocysta* (*G. retintexta, G. ordinata* and *G. delicata*) and other subordinate species such as *Achomosphaera heterostyla* and *Spiniferella* cf. *cornuta,* are predominant. Among the Prasinophyceae, species of the genus *Pterospermella* are well-represented. At the top

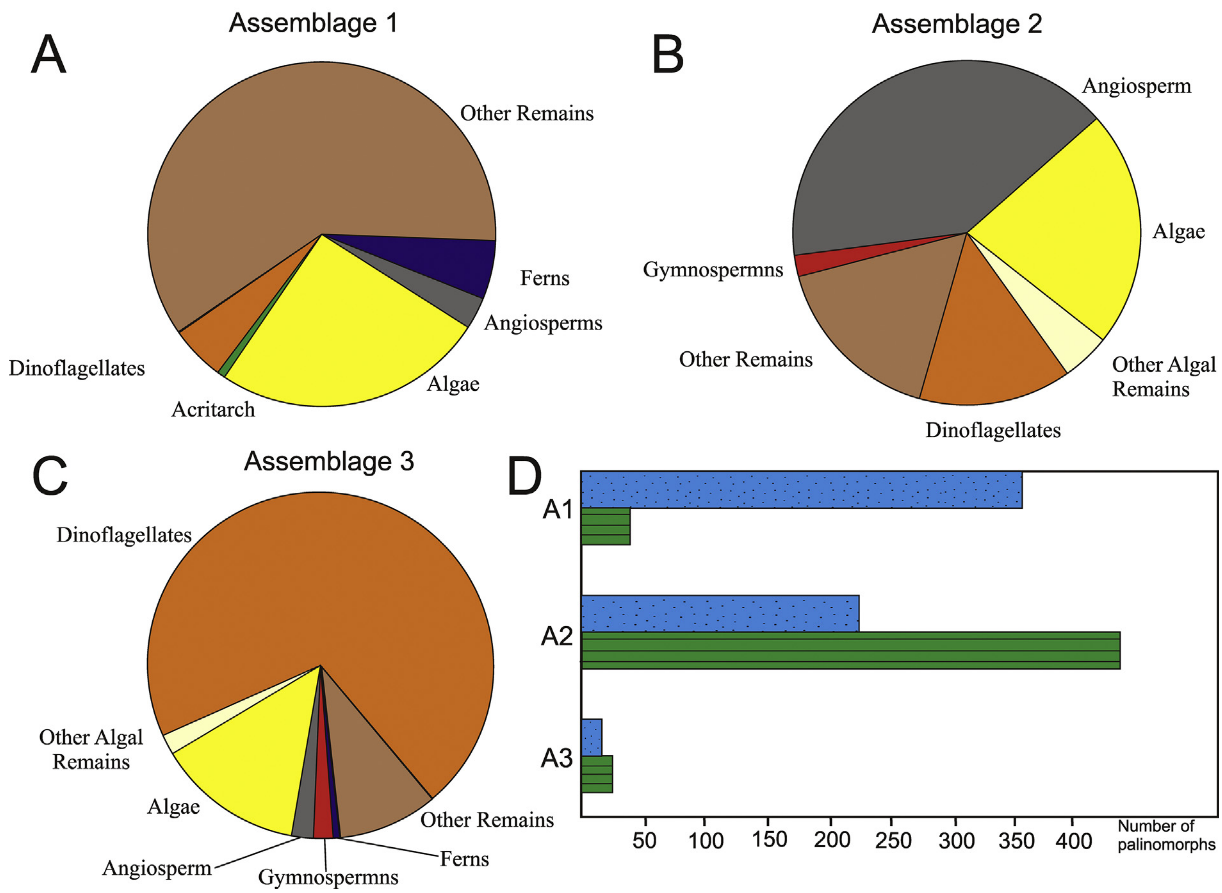


Fig. 10. **A**—**C**. Statistical percentage composition of the palynological groups documented in the associations of the Jagüel Formation. **D**. Marine (dot) versus terrestrial (bars) components in each set based on the number of specimens.

of the section, taxonomic groups found at underlying levels, such as pollen grains and spores, disappear and indeterminable algal remains are scarce and poorly preserved. Marine invertebrates, such as *Cubitostrea ameghinoi* (Ihering), are recognized *in situ*, which indicates a shallow subtidal environment of deposition (Casadío, 1998; Brezina et al., 2017). This is supported by the presence of the ichnofossil *Thalassinoides* (ichnogenus of the "cross-facies trace fossils" type), made by infaunal crustaceans and other types of arthropods, in those shallow facies (Frey et al., 1978; Cónsole Gonella and Aceñolaza, 2009; El-Sabbagh et al., 2017). Altogether, these features indicate that deposition occurred in low energy, shallow, inland marine environment with oxic-suboxic bottoms and terrigenous input probably preserved in relatively sub-anoxic microenvironments. This would have also favored the preservation of complete dinoflagellate cysts (with operculum).

5.2. Age of the assemblages

5.2.1. Association 1

Dinoflagellates mainly recorded from the Campanian—Danian such as *Trithyrodinium evittii*, *Fromea fragilis* (Ravn, 2017), *Senoniasphaera inornata* (De Coninck and Smit, 1982; Yepes, 2001) and the Chlorophyta *Palambages* forms A Manum and Coockson (*e.g.*, Stover et al., 1996; Roncaglia et al., 1999), along with the stratigraphic position of the assemblage (Figs. 2 and 11), support its Maastrichtian age. *Baltisphaeridium angulosum*, identified by Heisecke (1970) in the Danian of Patagonia, extends its range into Maastrichtian (Table 5). This age is confirmed by the presence of the foraminifer *Guembelitria cretacea* (Bertels 1973; Riccardi, 1988 and references therein), and it agrees with the nannofossil CC26 Zone and other microfossils documented in the same outcrop studied herein (Musso et al., 2012; Ceolín et al., 2015).

5.2.2. Association 2

Although an age not older than the Danian is supported by the angiosperms *Longapertites andreisii, Ulmoideipites patagonicus and Retitrescolpites baculatus,* and dinoflagellates *Batiacasphaera cassicula* and *Glaphyrocysta ordinata* (Fig. 11 and Table 5) (Archangelsky, 1973; Wilson, 1988; Powell et al., 1996; Stover et al., 1996; Antolinez and Oboh-Ikuenobe, 2006; Scafati et al., 2009; Barreda et al., 2012), some species documented in the sample CICYTTP-Pl 1365 have a wider range. Such is the case of *Trithyrodinium suspectum* from the Campanian—Danian (Manum and Cookson, 1964; Davey, 1969).

The NP1-2 and 3 nannofossil zones attributed to the Danian, c. 20 m from the base of the profile by Musso et al. (2012), also agrees with the record of numerous Danian ostracod species documented by Ceolín et al. (2015). *Paracypris bertelsae* Ceolín et al., *Palmoconcha similis* (Bertels), *Hysterocythereis inconnexa* (Bertels) Ceolín et al., *Petalocythereis schilleri* (Bertels) Ceolín et al., *Buntonia rocanortensis* Bertels (not found by Ceolín et al., 2015), *Huantraiconella prima* Bertels, together with the foraminifera *Cibicides succedens* Brotzen (Bertels) were recognized in the sample CICYTTP-Pl 1365 (Table 3). This age is confirmed by other (marine) fossils, such as *Pycnodonte* (*Phygraea*) *burckhardti* and *Gryphaeostrea callophylla* collected in Cerro Azul and documented by various authors in this

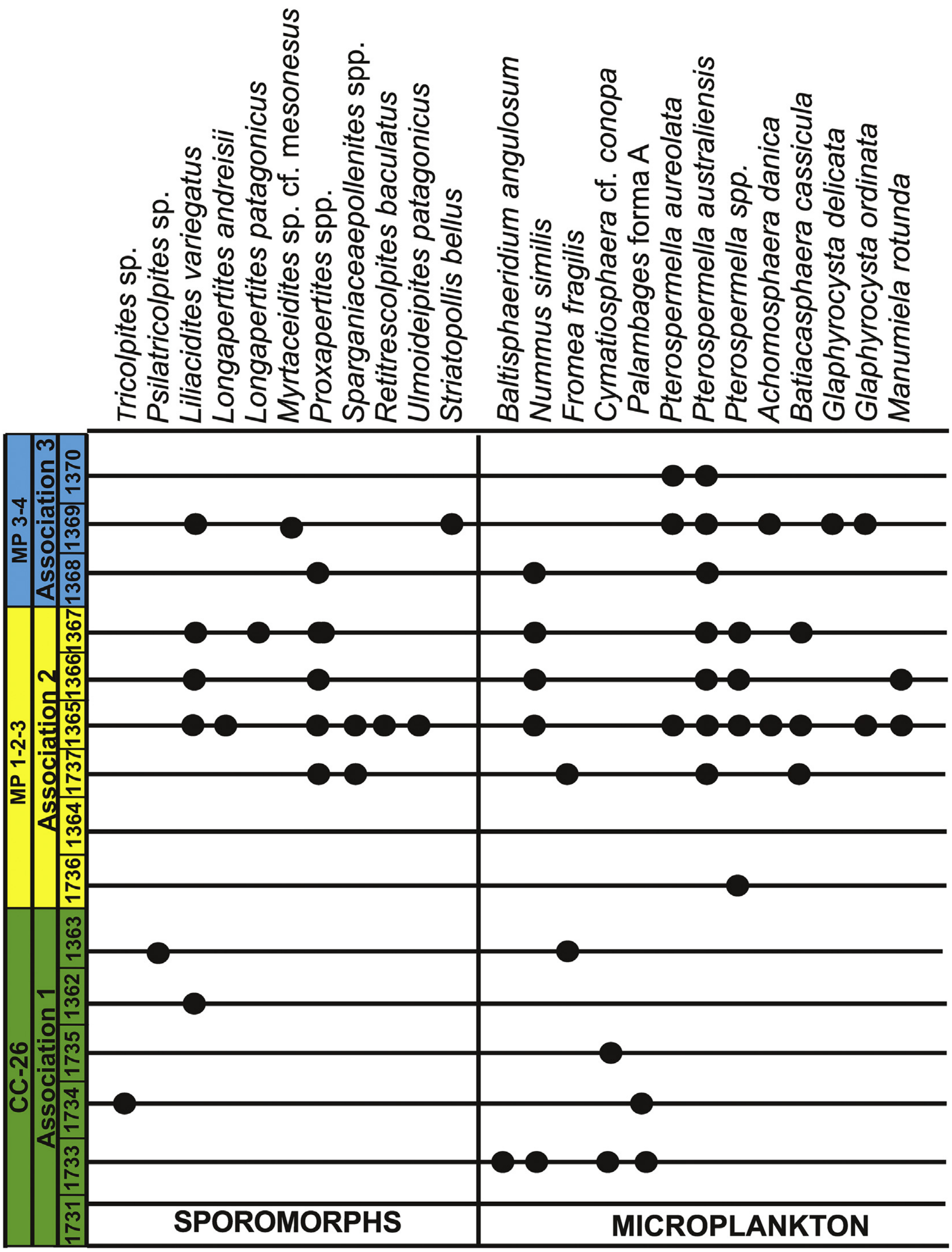


Fig. 11. Stratigraphic distribution of selected palynomorph species present in the A1-A3 associations of the Jagüel Formation.

region (Casadío, 1998; Del Río et al., 2011; Brezina et al., 2017). They correspond to the NP1 and NP2 nannofossil zones (Table 4) assigned to the lower Danian in the localities of General Roca (Río Negro) and Cerros Bayos (La Pampa).

5.2.3. Association 3

The sample CICYTTP-P1 1369 presents species with ranges mainly in the Paleogene. This, together with its stratigraphic position, supports a Paleocene age for the A3. *Striatopollis bellus,* known from the Cenozoic of Africa and South America; *Myrtaceidites* sp. cf. *mesonesus* (cosmopolitan) from Argentina (e.g., Ruiz and Quattrocchio, 1997; Palynodata, 2006; Raine et al., 2011); and *Glaphyrocysta ordinata* (dominant), *G. delicata* and *G. retiintexta* from the Paleocene–Eocene are recognized in this assemblage (Quattrocchio and Sarjeant, 2003; Heilmann and Van Simaeys, 2005; Slimani et al., 2010).

Marine invertebrates such as *Cubistostrea ameghinoi*, "*Dosinia*" *burckhardti*, "*Rostellaria*" *rothi* included in the NP3 and NP4 nannofossil zones assigned to the upper Danian (Table 4) were identified in the section studied according to records in the General Roca region and in the outcrop Bajada de Jagüel (Neuquén; Del Río et al., 2011; Brezina et al., 2017) Tables 1–5.

Table 1
Distribution of palynomorph species present in the palynological associations of the Jagüel Formation. Nanofossil biozonation taken from Muso et al. (2012). Asterisks (*) indicate first mention of species. Botanical affinities taken from Raine et al. (2011) among other references mentioned in the text.

First mention	Nanofossil Biozones	CC-26						MP 1-2-3						MP 3-4		
* Río Negro Province	Palynological Assemblage	Assemblage 1						Assemblage 2						Assemblage 3		
** Basin	Unit	Jagüel														
***Argentina	Stages	upper Maastrichtian						lower Danian						Upper Danian		
BIOLOGICAL AFFINITY	Taxa/sample	1731	1733	1734	1735	1362	1363	1736	1364	1737	1365	1366	1367	1368	1369	1370
Ferns (3)																
(Lygodium-type) Schizaeaceae	*Biretisporites potoniaei* (Delcourt and Sprumont, 1955)*						1								2	
	Biretisporites spp.*						2									
Cyatheaceae/Dicksoniaceae/ Matoniaceae	*Deltoidospora* spp*						3									
Gymnosperms(3)																
Araucariaceae	*Araucariacites australis* (Cookson, 1947)**							6		6		2			1	
Cycadales	*Cycadopites* sp.*													1	1	
Ephedraceae	*Ephedripites* sp.1, sp. 2*														4	
Angiosperms (14)																
Liliaceae/Monimiaceae	*Liliacidites variegatus* (Couper, 1953)*					1					3	6	2		3	
	Liliacidites spp.*										2	3	2		1	
Arecaceae	*Longapertites* spp.*										15	2	3			
	Longapertites andreisii Archangelsky 1973*										5					
	Longapertites patagonicus Archangelsky 1973*												1			
Myrtaceae	*Myrtaceidites* sp. *cf. mesonesus* (Cookson and Pike, 1954)**														1	
Araceae	*Proxapertites* spp.**									1	270	22	10	4		
	Psilatricolpites sp.**						1									
–	*Retitrescolpites baculatus* Jaramillo and Dilcher, 2001***										3					
Buxaceae?	*Striatopollis bellus* (Sah, 1967)***														1	
Sparganiaceae/Typhaceae	*Sparganiaceapollenites*spp.**									1	5					
Haloragaceae	*Tricolpites* sp.*			1												
Ulmaceae	*Ulmodeipites patagonicus* Archangelsky 1973**										1	1	1			
	Indeterminate form									1	1	1				
Algae(20)																
Chlorophyta	*Lancettopsis lanceolata*? (Mädler, 1963)**										2					
	Palambages form A (Manum and Cookson, 1964)**		3	3												
	Paralecaniela indentata (Deflander and Cookson) Cookson and Eisenack emend Elsik*										4					
	Paralecaniela sp.*										10		2	3		
Oedogoniaceae	*Oedogonium cretaceum* Zippi, 1998**						2									
Prasinoficeae	*Cymatiosphaera cf. conopa* en (Norvick and Burger, 1975)**		2		2											
	Cymatiosphaera sp. (*cf. C. garecai* Heisecke)*										1	11		1		
	Cymatiosphaera spp.*										10			1	1	1
	Pterospermella aureolata (Deflander and Cookson) (Eisenack and Cramer, 1973)**										17				3	2
	Pterospermella australiensis (Deflandre and Cookson) (Eisenack and Cramer, 1973)**									3	36	1	1	2	9	5
	Pterospermella aff. *harti* (Sarjeant) (Eisenack and Cramer, 1973)**										6	2		1	7	1
	Pterospermella spp.*						5				5	1	3			
	Zygospora spp.				2				2	2	28	8	1		11	1
	Zygospora type *Debarya**							3		2						
Zygnemataceae	*Gelasinicysta vangeelii* type in Scafati et al., 2009*									3						
	Lecaniella spp.*	4					2				7	3	2		5	3
	Ovoidites grandis Zippi, 1998**														2	
	Ovoidites sp.**										4			1		2
Polyphyletic (Prasinoficeae-Zygnemataceae-copepod eggs)	*Leiosphaeridia* spp.*						3				9	3	2			
–	Other algal remains							1		4	33				9	

5.3. First record of species

Only few contributions of palynological results of the Roca Formation, near the city of General Roca (Archangelsky and Romero, 1974), the Upper Cretaceous at El Caín locality (Baldoni, 1991), and Los Alamitos Formation (Papú and Sepúlveda, 1995) in Río Negro have been published. However, no palynological data are known from the Maastrichtian–Danian Jagüel Formation and thus, this is the first palynological study ever made. In Tables 1 and 2, taxa with their first mention in the

Table 2
Distribution of dinoflagellates species and other components present in the palynological associations of the Jagüel Formation. Nanofossil biozonation taken from Muso et al. (2012). Asterisks (*) indicate first mention of species.

First mention	Nanofossil Biozones	CC-26						MP 1-2-3						MP 3-4		
* Río Negro Province	Palynological Assemblage	Assemblage 1						Assemblage 2						Assemblage 3		
** Basin	Unit	Jagüel														
***Argentina	Stages	upper Maastrichtian						lower Danian						Upper Danian		
Taxa/sample		1731	1733	1734	1735	1362	1363	1736	1364	1737	1365	1366	1367	1368	1369	1370
Acritarch (1)																
Baltisphaeridium angulosum Heisecke 1970*			1													
Dinoflagellates (26)																
Achomosphaera danica (Lejeune-Carpentier) (Lejeune-Carpentier and Sarjeant, 1981)*											2				4	
Achomosphaera heterostyla (Heisecke) (Stover and Evitt, 1978)**															8	
Batiacasphaera cassicula Wilson 1988**										1	3		1			
Cerebrocysta cf.waipawaensis Wilson, 1988**											3					
Fromea fragilis (Cookson and Eisenack) (Stover and Evitt, 1978)**							2			1						
Glaphyrocysta delicata Wilson, 1988**															51	
Glaphyrocysta cf. *delicata***															29	
Glaphyrocysta ordinata (Williams and Downie) (Stover and Evitt, 1978)**										6					41	
*Glaphyrocysta cf. ordinata***													1			
Glaphyrocysta retiintexta (Cookson) (Stover and Evitt, 1978)**												1			113	
Impagidinium crassimuratum Wilson, 1988**										1	2					
Kallosphaeridium parvum (Jan Du Chêne, 1988)**											3				2	
Manumilela rotunda Wilson, 1988**											14	1				
*cf. Muratodinium fimbriatum***														1		
Nummus similis (Cookson and Eisenack) (Burger, 1980)**			1								7	6	3	2		
Paleocystodinium australinum (Cookson) (Lentin and Williams, 1976)*												1				
Senoniasphaera inornata (Drugg) (Stover and Evitt, 1978)**							1				4	1		4	1	
Spiniferella cornuta (Gerlach) (Stover and Hardenbol, 1994)*														1		
Spiniferella cornuta (Davey and Williams) (Below, 1982)**											1					
Thalassiphora patula (Williams and Downie) (Stover and Evitt, 1978)**								1			1					
Trithyrodinium evittii Davey 1969**							2	1			5					
Trithyrodinium suspectum (Manum and Cookson 1964) Davey 1969**											1					
Opercules															22	
Indeterminate chorate Cf. G. spp												1			20	
Indeterminate chorate dinoflagellates											5	10	12	5	5	
Indeterminate proximal dinoflagellates											5	1				
Indeterminate dinoflagellate											17	4		5	7	
Other																
Arthropod eggs							6				7					
Indeterminate spheroidal structures							66				145	1	3	5	26	
Indeterminate 1															3	
Indeterminate 2															6	
Indeterminate 3															2	
Cuticles																
Clear cuticles											3				1	
Dark cuticles and others							1		1		6				1	
Palynomorphs filled with organic matter						15										

province of Río Negro (*), province and basin (**) or in Argentina (***) are distinguished.

Out of the 19 spores and polen species found, this is the first record of *Biretisporites potoniei* reported in Rio Negro. It has previously been documented for the Triassic and Lower Cretaceous of Argentina (Zavattieri and Prámparo, 2006). The same happens with *Ulmoideipites patagonicus,* which has previously been recognized for the Paleocene of Chubut (Archangelsky, 1973) and it is now also documented for the first time in Rio Negro. Species with the first record in Argentina are *Retitrescolpites baculatus* from the Paleocene–Eocene of Colombia, and *Striatopollis bellus,* more frequent in the Paleogene–Neogene (see Palynodata).

Aquatic palynomorphs, *Baltisphaeridium angulosum*, recorded in the Maastrichtian, and 18 species of dinoflagellates, are first recorded for the Neuquén basin in this study. Among them, *Glaphyrocysta* and *Batiacasphaera cassicula* were initially documented in the Paleocene–Eocene of Australia by Wilson (1988). A first record of *Achomosphaera danica* for the province was identified by Papú et al. (2000) and cited as *Areoligera senonensis* in the Jagüel Formation in Neuquén. *Manumiella rotunda* is the first record for

Table 3
Distribution of microfossil and miscellaneous species found in samples from Cerro Azul, and their range according to the nannofossils zonation (Casadío, 1998; Del Río et al., 2011; Musso et al., 2012; Ceolín et al., 2015; Brezina et al., 2017).

Nanofossil Biozones	CC-26						MP 1-2-3						MP 3-4		
Palynological Assemblage	Assemblage 1						Assemblage 2						Assemblage 3		
Unit	Jagüel														
Stages	upper Maastrichtian						lower Danian						Upper Danian		
Microfossils Taxa/sample	1731	1733	1734	1735	1362	1363	1736	1364	1737	1365	1366	1367	1368	1369	1370
Foraminifera															
Amonolinoides acuta (Plummer, 1926)										2					
cf. Archaeoglobigerina cretaceae (d'Orbigny, 1840)								3							
Cibicides succedens (Brotzen, 1948)								1		3					
Discorbinella castellaroae (Bertels, 1964)								3							
Globorotalia sp.								1							
Guadripina boltoskoyi (Bertels)					1										
Guembelitria cretacea (Cushman, 1933)					11			1							
Type *Lenticulina rivadaviensis* (Camacho, 1954)								2							
Microforaminifer						2									
Migros hanseni (Bertels)								1							
Planulina camachoi (Bertels, 1964)								2							
Polymorphina sp.					1										
Pseudonodosaria conica = *Glandulina conica* (Neugeboren, 1850)								3							
Cf. Pullenia cretacea (Cushman, 1936)								2							
Rugotruncana subpennyi (Bertels, 1970)								1							
Ostracods															
Bairdoppilata sp.								2							
Cytherella saraballentae Ceolín and Whatley 2015								3							
Paracypris imaguncula Ceolín and Whatley 2015								3							
Echinoderms															
Spicules								3							

Danian of Argentina. Vellekoop et al. (2017) recorded the genera *Glaphyrocysta* under the list "Group *Glaphyrocysta* and *Areoligera*" and "*Spiniferites* Complex", grouping forms of *Spiniferites* and *Achomosphaera*, without clarifying most of the species comprised in those categories. The ones clarified, however, are not the ones identified in this study. Therefore, due to the lack of description of species in these groups, the species found in this study included in *Glaphyrocysta* together with *Achomosphaera heterostyla* and *Spiniferites multibrevis* are the first records for the basin.

5.4. Paleobiogeography

The Cretaceous-Paleogene (K–P) boundary has been intensively studied for several decades as it encompasses one of the greatest extinction events and global environmental crisis most likely triggered by an asteroid impact in the Yucatán Peninsula (Mexico) at about 65.5 Ma, beyond other possible related causes. Although the precise causes of this worldwide catastrophe are still a matter of debate, notorious changes in the biota during the early Paleogene are mainly associated with vertebrates, invertebrates, and the zooplancton (*e.g.*, Keller, 2008; Schulte et al., 2010; de Palma et al., 2019). The response of the vegetation and phytoplankton is relatively less marked but it shows a gradual change (*e.g.*, McElwain and Punyasena 2007; Vajda and Bercovici, 2012). McElwain and Punyasena (2007) referred to the pollen and spore data as the only sources of continuous terrestrial information despite limitations in taxonomic resolution and taphonomic filters; and its record of species-level change at the boundary in different depositional environments account only for 15% of the observed in other groups. Changes on the vegetation of paleophytoprovinces are also response of the impact in Mexico and sea level changes at different latitudes. Hence, local and regional studies are still necessary to understand those changes from near to far-field areas of that site. The Southern Hemisphere includes the tropical to sub-tropical *Palmae* Province, the high-latitude *Nothofagidites*/*Proteacidites* Province, and a transitional zone of mixed floristic composition (Fig. 12). Vajda and Bercovici (2012) documented that Maastrichtian extinct key-species at the KPB within the *Palmae* Province include *Aquilapollenites magnus, Buttinia andreevi, Crassitricolporites brasiliensis, Proteacidites dehaani, Gabonisporis vigourouxii*, and *Proxapertites*. In the *Nothofagidites/Proteacidites* Province (southern Argentina and Chile, New Zealand and Antarctica), taxa such as *Tricolporites lilliei, Triporopollenites sectilis, Quadraplanus brossus, Nothofagidites kaitangata*, and *Grapnelispora evansii* are

Table 4
Distribution of invertebrate species found in samples from Cerro Azul, and their range according to the nannofossils zonation (Casadío, 1998; Del Río et al., 2011; Musso et al., 2012; Ceolín et al., 2015; Brezina et al., 2017).

SAMPLES	NANNOFOSSIL ZONES/TAXA	Lower Danian		Upper Danian		
		NP1	NP2	NP3	NP4	NP5
1369	*"Rostellaria" rothi*				■	
1368	*"Rostellaria" rothi*				■	
	Cubistostrea ameghinoi			■	■	
	"Dosinia" burckhardti			■	■	
1364	*Pycnodonte (Phygraea) burckhardti*	■	■	■	■	
	Gryphaeostrea callophylla	■	■	■	■	
	Cubistostrea ameghinoi			■	■	
	Turritella burckhardti			■		■
	Venericardia iherinii var. *Burckhardti*	■	■	■	■	

Grey shade signifies presence of the taxon.

characterized by having their last occurrences at this boundary. Except for *Proxapertites* and *Araucariacites* that range throughout this boundary, none of these taxa are recorded in the assemblages of the Jagüel Formation (Fig. 11 and Table 5). Species of *Nothofagidites* and most of the gymnospermic pollen grains of *Podocarpidites, Microcachryidites antarcticus* and *Phyllocladidites mawsonii*, which are especially typical of the N/P Province, are not documented at Cerro Azul. Therefore, characteristic species of *Proxapertites, Longapertites* and *Spinozonocolpites* of the Paleotropical Palmae Province, which are documented in our Danian A2-3 and Maastrichtian—Paleocene palynofloras of northern Patagonia (Volkheimer et al., 2007; Scafati et al., 2009; Vallati, 2010; Povilauskas, 2013; Vallati et al., 2016), confirm that they belong to the Mixed Paleofloral Province (Fig. 12). This is in agreement with Romero (1986), Vajda-Santivanez (1999), Vajda and Bercovici (2012) and Vallati (2013). On the other hand, Quattrocchio et al. (2011) proposed the Danian Ulmaceae Province extended from northernmost Argentina up to the San Jorge Basin (Chubut province). The appearance of *Ulmodeipites patagonicus* in our A2 and its presence in the upper Maastrichtian/Danian Flora and Eslabón formations (Vajda-Santivanez, 1999) support this phytogeographic scheme.

In the marine realm, the upper Maastrichtian A1 of the Jagüel Formation at Cerro Azul documents few dinoflagellate species (Table 2 and Fig. 11) that are still present in the following assemblages (*Senoniasphaera inornata, Fromea fragilis, Thalassiphora patula, Trithyrodinium evittii*), in which other species appear (e.g., *Achomosphaera danica, A. heterostila, Batiacasphaera cassicula, Glaphyrocysta ordinata* and *delicata, Manumiella rotunda, Paleocystodinium australinum, Trithyrodinium suspectum*).

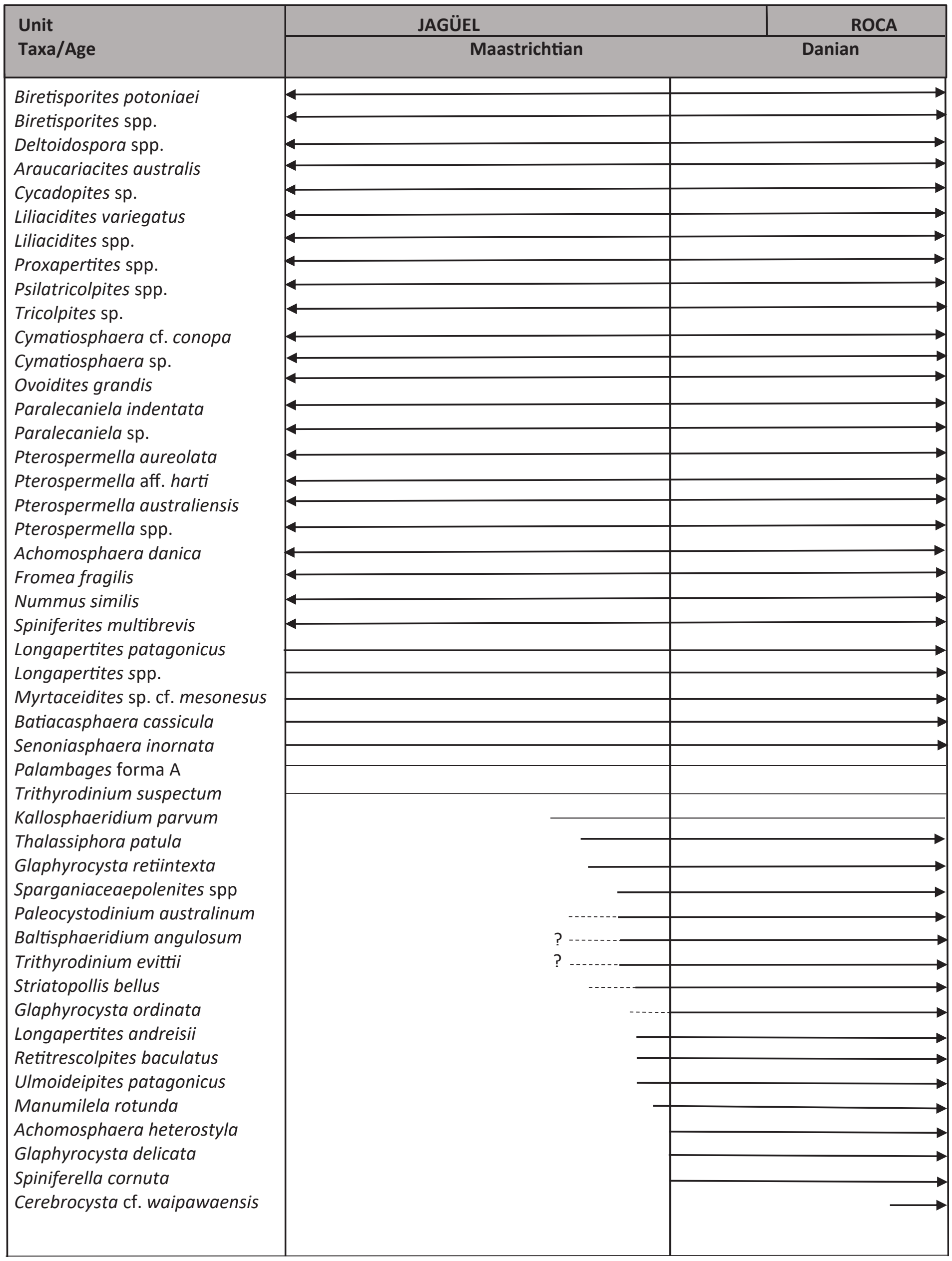
Beyond the first record of species in eastern Neuquén Basin mentioned above (Table 2), *Senoniasphaera inornata* and *Paleocystodinium australinum* reveal a wide distribution from southern (e.g., Quattrocchio and Sarjeant, 2003; di Pasquo and Martin, 2013) to mid-paleolatitudes in Neuquén and Colorado basins, where *Trithyrodinium evittii* appears (see Quattrocchio and Sarjeant 1996; Vellekoop et al., 2017). Instead, *Glaphyrocysta ordinata, Achomosphaera danica, Thalassiphora patula* are mostly present in Neuquén basin and *Batiacasphaera cassicula* in Chile and Antarctica (see Pérez Pincheira, 2020).

The Atlantic transgression with shallow sea deposits covering wide areas of Patagonia started in the upper Campanian. A maximum increase of sea level occurred in the upper Maastrichtian when, due to the lack of topographic barriers during a stable tectonic period, it extended up to the northwestern part of Neuquén Basin (Wichmann, 1927; Uliana and Dellapé, 1981; Uliana and Biddle, 1988; Aguirre-Urreta et al., 2011; Guler et al., 2019). Remains of marine reptiles and Weddellian fauna of invertebrates, and typical calcareous nannofossils from high latitudes included in Zone CC26 are recognized associated with microfossils, which would have been deposited in marine distal platform environments (Gasparini et al., 2002, 2003; Concheyro et al., 2002; Aguirre-Urreta et al., 2011; Guler et al., 2019). This arm of the sea (Fig. 12) remained in the region for several million years involving the Maastrichtian—Danian boundary. During the Danian, the Weddellian invertebrate fauna in northern Patagonia was replaced by warm-water taxa sharing affinity with faunas from northern Brazil, Caribbean and northern Africa (Casadío, 1998; Casadío et al., 2005; Bogan and Agnolin, 2010; Bogan and Gallina, 2011; Aguirre-Urreta et al., 2011; Prámparo et al., 2014). Associated with the dinoflagellates present at Cerro Azul, numerous marine fossils deposited in subtidal to shallow marine platform (bivalves, gastropods, decapods, serpulids, coral and various microfossils, see Musso et al., 2012; Ceolín et al., 2015, and more references in sections 1 and 2 herein), also recorded in northern Patagonia, confirm this change of affinity with tropical faunas. This would have been the result of an oceanic anticlockwise circulation pattern established in the Atlantic (Casadío, 1998). Tidal currents were subject to the Corion effect and wind stress in the Southern Hemisphere created a northeast swell. Therefore, according to Barrio (1990b), tidal currents affected by the Corion force associated with westerly winds generated a transport clockwise that governed the movement of sediment in the Neuquén basin (Fig. 12). A change to shallow brackish marine and terrestrial environments due to a gradual regression process was generated towards the end of the Danian (Legarreta et al., 1989; Nañez and Malumián, 2008; Scafati et al., 2009; Ballent et al., 2011; Malumián and Nañez, 2011; Guler et al., 2019). In the lower part of the Roca Formation, in the studied locality, fossils are less frequent, giving testimony of this paleoenvironmental and climatic change, culminating with the evaporites in their upper part due to a large evaporation process during the last stages of the regression, especially in its inter- and supramareal sector.

6. Conclusions

A palynological study of the Jagüel Formation at Cerro Azul in northwestern Río Negro yielded 64 sporomorphs, freshwater and

Table 5
Table of biostratigraphic ranges of species recorded in the associations of the Jagüel Formation at Cerro Azul. Taxa ordered according to their appearance in the associations.



marine microplankton, and miscellaneous taxa. Three palynological associations are defined based on the vertical distribution of species. A1 is characterized by having few spores, chlorophytes and dinoflagellates and other remains, and is attributed to the upper Maastrichtian. A2 and A3 of Danian age are composed of more diverse angiosperm pollen grains, chlorophytes, and dinoflagellates. In addition, other fossil materials collected (invertebrates, microfossils, vertebrates, others) were also analyzed, which contributed to environmental interpretations, correlation, and age of the palynological associations.

The integration of the botanical and biological affinity of the identified species and palynofacial features, together with micro- and invertebrate fossils found in this locality, confirms that the deposition of the associations occurred preferably in shallow and mixed marine environments with connections to freshwater bodies (swamps, river flood plains) under warm and humid climate. Pollen of araucariaceae and other few gymnosperms came from relatively close areas. The absence of *Nothofagidites* species is highlighted. A1, deposited in mixed to low energy shallow marine environments, is associated with freshwater bodies by terrestrial input. A2 is characterized by coastal lagoons near shallow marine depocenter. A3 reflects the deposition in shallow inland marine environment with favorable nutrient conditions for increasing the frequency of dinoflagellates and chlorophytes. Anoxic to sub-anoxic bottom waters and low energy would have favored the preservation of complete dinoflagellate cysts, including some with operculum. It is, to date, the locality with the largest number of *Proxapertites* type pollen grains registered in the country. The first record of

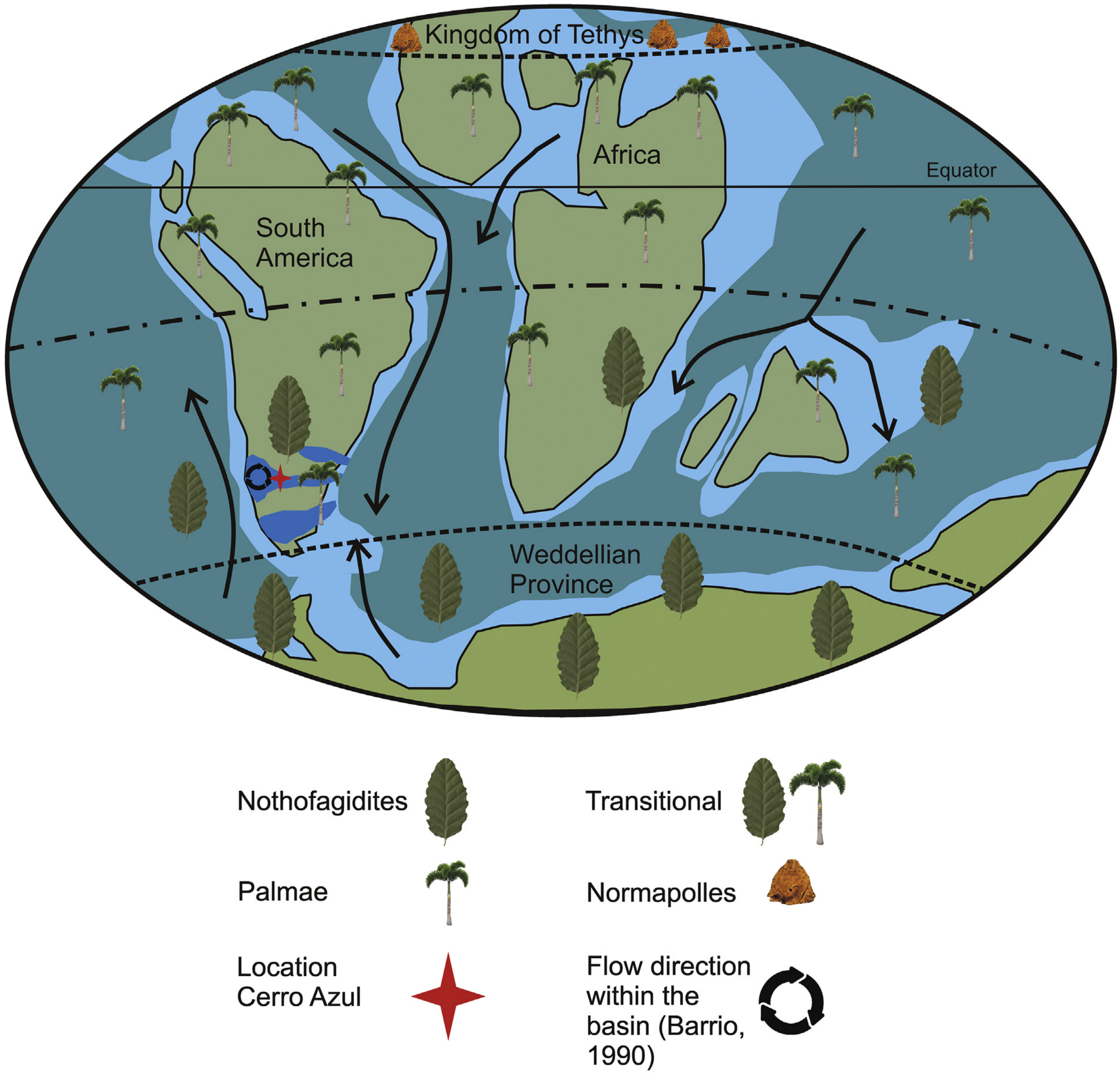


Fig. 12. Study area (red star) within the Neuquén Basin in the context of the Palaeofloristic Provinces and directions of marine currents (arrows) (modified from Barrio, 1990b; Casadío, 1998; Vajda and Bercovici, 2012) and Patagonian basins (modified from Aguirre-Urreta et al., 2011) for the Late Cretaceous/Danian. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

angiosperm pollen grains *Retitrescolpites baculatus* and *Striatopollis*, among other taxa, recognized in Argentina was also found in this locality. There are also first records of several pollen, dinoflagellates and chlorophyte taxa for the Neuquén basin and Río Negro province. Numerous species, shared mainly with palynofloras of the upper Maastrichtian Palmae in tropical latitude in central and northern South America (*Longapertites, Proxapertites, Spinozonocolpites*) and *Nothofagidites* Realms of southern Patagonia and Antarctica (*e.g., Proteacidites, Aracauriacites australis*), confirm that the palynofloras of Neuquén and Colorado basins are part of the Mixed Floristic Realm in the Upper Cretaceous and Danian.

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