Pollen from the K–Pg boundary of the La Colonia Formation, Patagonia, Argentina

Facundo De Benedetti [a,*], María C. Zamaloa [b], María A. Gandolfo [a], Néstor R. Cúneo [b]

[a]L. H. Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, New York 14853, USA

[b] Museo Paleontológico Egidio Feruglio, Consejo Nacional de Investigaciones Científicas y Técnicas, Avenida Fontana 140, 9100 Trelew, Chubut, Argentina

* Corresponding author.

E-mail addresses: fdebenedetti@mef.org.ar (F. De Benedetti), mzamaloa@gmail.com (M.C. Zamaloa), magandolfo@cornell.edu (M.A. Gandolfo), rcuneo@mef.org.ar (N.R. Cúneo).

Abstract

The La Colonia Formation, outcropping in northern Chubut Province (Patagonia, Argentina), is a Maastrichtian–Danian sequence deposited during a marine transgression of the South Atlantic Ocean. Its fine-grained sediments are associated with lagoon systems that preserved a very rich and diverse biota composed of invertebrates, vertebrates, plants, algae, and fungi. A palynological study was carried out based on 157 samples collected from four representative stratigraphic sections of this geological unit. The plant communities were dominated in terms of richness by ferns and angiosperms, but algae and gymnosperms were also well-represented. About 250 palynomorphs are recognized. The gymnosperms comprise 20 species including representatives of Araucariaceae, Cheirolepidiaceae, Ephedraceae, and Podocarpaceae while the angiosperms include 67 species within the families Araceae, Arecaceae, Aristolochiaceae, Asteraceae, Cannabaceae, Chlorantaceae, Cunoniaceae, Ericaceae, Gunneraceae, Juncaceae,

Liliaceae, Malvaceae, Nelumbonaceae, Nothofagaceae, Proteaceae, and Typhaceae and several taxa of uncertain affinities. Here, we present the systematic study of the gymnosperm and angiosperm pollen components of the flora. Two new gymnosperm species and 22 new angiosperm species are erected. Additionally, we introduce the southernmost records of Triprojectacites and Normapolles groups even though their botanical relationships and origin remain unknown. The highly diverse palynoflora of the La Colonia Formation provides critical evidence for understanding the evolution of Southern Hemisphere floras and of certain clades and families and support the hypothesis that the effect of the mass extinction event was less significant at the southernmost portion of South America than in other parts of Earth.

Keywords: Angiosperms; Gymnosperms; K–Pg boundary; Late Cretaceous; Palynology; Patagonia.

1. Introduction

There are no doubts that a mass extinction event occurred during the Cretaceous–Paleogene boundary (~ 66 Ma; Raup and Sepkoski, 1982; Bambach, 2006). The most accepted hypothesis (e.g., Alvarez et al., 1980; Schulte et al., 2010) is that this event was caused by the impact of an asteroid in the Yucatan Peninsula, while intense volcanism associated with the Deccan Traps in India would have contributed to shaping biomes during the extinction aftermath (Schoene et al., 2019; Hull et al., 2020). The biostratigraphic record of extinction dynamics and recovery from a mass extinction event provides a critical window into understanding biotic resilience globally and locally. Patterns of extinction and recovery have been studied worldwide (Schulte et al.,

2010). Nevertheless, because confirmed records of the K–Pg boundary in the Southern Hemisphere are scarce, little is known about those patterns for Southern South America.

Towards the end of the Cretaceous period and the beginning of the Paleogene, a marine transgression from the Atlantic Ocean took place in Patagonia, generating shallow epicontinental seas on indented coasts, although the Somuncurá and Deseado Massifs remained emerged (Scasso et al., 2012). This transgressive episode led to the deposition of several coastal sedimentary units, with greater or lesser terrestrial influence (Scasso et al., 2012; Cúneo et al., 2014). Among them, the La Colonia Formation represents coastal deposits dominated by tides with the development of barrier/lagoon complexes of Maastrichtian–Danian age (Cúneo et al., 2014; Clyde et al., 2021). The formation is characterized by its highly diverse and rich biota that comprises vertebrates (dinosaurs, plesiosaurs, turtles, mammals, birds, marine and freshwater fishes), invertebrates (bivalves, ostracods, and foraminifera), plants (bryophytes, pteridophytes, gymnosperms, and angiosperms), algae (dinoflagellates and green algae), and fungi. The presence of freshwater green algae (e.g., Cúneo et al., 2014), water ferns (e.g., Cúneo et al., 2013; De Benedetti et al., 2018, 2020, 2021; Hermsen et al., 2019), a species of the free-floating Araceae clade (Gallego et al., 2014) and *Nelumbo* Adamson (Gandolfo and Cúneo, 2005), reveals the occurrence of wetland communities in a diverse freshwater to brackish paleoecosystem thriving in warm to warm-temperate and humid climatic conditions (Cúneo et al., 2014; Clyde et al., 2021 and cites therein).

Here, we present the results of a palynological study carried out from samples collected at four localities from the La Colonia Fm., outcropping at the Arroyo Mirasol Chico Creek area, Chubut Province, Patagonia, Argentina (Fig. 1), that represents one of the few records of the K–Pg boundaries in southern South America. Preliminary palynological studies on these localities

were presented by Cúneo et al. (2014, 2021) and Clyde et al. (2021). The present study comprises the systematic treatment of the gymnosperm and angiosperm pollen and increases the knowledge of the K–Pg boundary palynological diversity in Patagonia that furthers our evolutionary, biogeographic, paleoecological, and stratigraphic comprehension of the Earth's biota during the last mass extinction event.

2. Materials and methods

2.1. Stratigraphy and fossil specimens sampling, preparation, and curation

The La Colonia Fm. outcrops at the central north of the Chubut Province, Patagonia, Argentina (Fig. 1). Stratigraphically, it overlies the fluvial deposits of the Campanian–Maastrichtian Puntudo Chico Formation (Ardolino and Franchi, 1996). Overlying units include brackish paludal siliciclastic facies of the Paleocene Cerro Bororó Formation, the Paleocene–Eocene El Buitre Formation basalts, and the Oligocene pyroclastic rocks of the Sarmiento Formation (Ardolino and Franchi, 1996; Sacomani et al., 2007). Biostratigraphic estimates (Ardolino and Franchi, 1996; Page et al., 1999; Náñez and Malumián, 2008; Guler et al., 2014) and recent paleomagnetic analyses (Clyde et al., 2021) support a Maastrichtian to Danian age for the La Colonia deposits.

A total of 157 samples were collected from four stratigraphic sections located at the El Buitre Hill and the Mirasol Chico Creek area: 1- Quebrada del Helecho/Cañadón del Irupé (QH/CI), 2- Cerro Bosta (CBO), 3- Cerro Buitre Norte (CBN = Plesiosaurio locality 'LCP' of De Benedetti et al., 2021), and 4- Chiva Muerta (CHM) (Fig. 1). The first two sections were described in Cúneo et al. (2014) and the two others in Clyde et al. (2021). The stratigraphic sections are provided in Appendix A. The K–Pg boundary is recognized in the CBN section based on

magnetostratigraphic and palynological data provided in Clyde et al. (2021). The other three sections (QH/CI, CBO, CHM) are interpreted as Maastrichtian in age throughout.

The samples were processed following standard palynological techniques (Traverse, 2007). Light microscope (LM) observations were made with a Nikon Eclipse 80i microscope coupled with a Nikon DS-L4 camera (Nikon Corp., Minato, Tokyo, Japan) at the Museo Paleontológico Egidio Feruglio (MEF), Trelew, Chubut Province, Argentina. Coordinates of each photographed palynomorph correspond to the mentioned microscope. Scanning electron microscope (SEM) observations were made with a desktop Phenom XL SEM (Phenom-World B. V., Eindhoven, The Netherlands) at the L.H. Bailey Hortorium, Cornell University, Ithaca, New York, U.S. Images were edited using Adobe Photoshop CS6 (Adobe, San José, California, USA). Microscope slides and SEM stubs are housed at the palynological collection of the Museo Paleontológico Egidio Feruglio under the repository acronyms MPEF-PA 125–999.

3. Results

Of the 157 processed samples, 83 were palynologically fertile. About 250 palynomorphs (including megaspores) were identified; among them, 20 belong to gymnosperms, and 67 to angiosperms (Table 1).

……INSERT TABLE 1 HERE……

New pollen species are described below, are arranged alphabetically per family (when possible), and are grouped in gymnosperms, monocots, and eudicots. Elements commonly found in Patagonian palynofloras and those that could only be assigned at the generic level (either because of their poor preservation and/or because of the few specimens recovered) are only

illustrated. Some species with different taxonomic assignments mentioned in Clyde et al. (2021) are listed in Appendix B.

Systematic palynology

GYMNOSPERMS

Family: CHEIROLEPIDIACEAE Takhtajan 1963

Genus: **Classopollis** (Pflug) Pocock and Jansonius 1961

Type species: Classopollis classoides (Pflug) Pocock and Jansonius 1961

Classopollis patagonicus De Benedetti sp. nov.

Plate I, Figs. 10–16

2014. *Classopollis* sp., in Cúneo et al. (2014), PLoS ONE, 9(8), e104749, fig. 10, F.

2021. *Classopollis* sp. 1., in Clyde et al. (2021), Cretaceous Research, 126, 104889, fig. 3, O.

Etymology: The epithet "patagonicus" refers to the Patagonian region.

Type locality: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 472 (Plate I, 10).

Paratype: MPEF-PA 472 (Plate I, 11).

Additional material: MPEF-PA 145, 147, 150, 151, 168–171, 453, 457, 470–472, 582, 608, 611, 621, 622, 652, 662, 663, 678–680, 690, 691, 693, 752, 819, 857, 864, 922, 923, 966, 978.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain oblate, equatorial outline circular. Distal pole with a subcircular cryptopore ca. 7–16 μm diameter. Proximal pole sometimes with a triradiate scar and a thin triangular area. Subequatorial circular furrow ca. 1–2 μm wide. Equatorial thickening with 5–11

striations, often anastomosed. Exine two layered; sexine with a vermiculate to pseudoreticulate structure and a microechinate sculpture; microechinae ca. 0.1–0.4 μm long.

Description: The pollen grains are oblate, with a circular equatorial outline (Plate I, 10–13). The distal pole has a subcircular cryptopore ca. 7–16 μm diameter (Plate I, 11 and 13). The proximal pole sometimes has a triradiate scar (Plate I, 10) and a triangular area of thinner exine (Plate I, 12) with a maximum width of ca. 6–9 μm but is usually absent or difficult to recognize. Proximal pole lacks exinal protuberances. Equatorial thickening ca. 6–9 μm wide and formed by striae running parallel around the equator. Striae of up to 0.5 μm wide and muri of up to 0.8 μm wide (Plate I, 14, 15). The exine is 1.5–2.0 μm thick in the equator; sexine with a columellate layer of fused verrucae, bacula and rugulae, forming a vermiculate to pseudoreticulate structure with narrow lumina, and a tectate layer with a microechinate sculpture of densely distributed microechinae or hair-like elements ca. 0.1–0.4 μm long, microechinae usually wide at the base and thinly tapered toward the tip (Plate I, 16). Small granules and papillae are intercalated among the microechinae in some specimens. The columellate layer is absent in the cryptopore and subequatorial furrow, either absent or reduced drastically in the proximal triangular area, and thicker in the equator where the columellae are larger and fuse completely or partially forming the muri of the striate equatorial band. There is some interdigitation at the boundary between the proximal columellae and the striations of the equatorial band (Plate I, 15).

Dimensions: Maximum equatorial diameter 22 (35) 54 μm (84 specimens); polar diameter 22 (28) 32 μm (4 specimens).

Occurrence: Sections QH/CI, CBO, CBN, CHM.

Comparisons: As indicated by Villar de Seoane (2014) most *Classopollis* species from Jurassic to Paleocene deposits of Argentina have been described based on LM observations. Next, we

compare *C. patagonicus* with those Argentinean species that have an echinate to microechinate sculpture and were described based on both LM and SEM. Villar de Seoane (2014) described twelve species from the Lower Cretaceous Anfiteatro de Ticó Formation, south Patagonia. Of these, *C. asper* Villar de Seoane, *C. grandis* Villar de Seoane, *C. kieseri* Reyre, *C. pujoli* Reyre, and *C. rarus* Reyre are comparable. *C. asper* is 28–41 μm in diameter, has a vermiculate structure, and microechinae of similar sizes but with rounded tips. *C. grandis* has spines of 1.5–2.5 μm long. *C. kieseri* is smaller and has smaller microechinae. *C. pujoli* is also smaller and has sculptural elements (including bacula) of up to 1 μm long. *C. rarus* is similar in the number of striae and the vermiculate structure, but the equatorial diameter is smaller and the microechinae are larger. In addition, all the Lower Cretaceous species described by Villar de Seoane (2014) have exinal protuberances in the proximal triangular area, a feature that was not observed in *C. patagonicus*. *C. martinottii* Reyre from the Lower Cretaceous of Israel (Reyre, 1970), USA (Srivastava, 1976), and Lebanon (Zavialova et al., 2010) is similar to *C. patagonicus* in the sculpture, number of striae, and dimensions of the cryptopore but it is smaller. *C. mirabilis* Reyre from the Jurassic of France is also smaller and has larger echinae (Reyre, 1970).

Family: PODOCARPACEAE Endl. 1847

Genus: **Podocarpidites** Cookson 1947

Type species: Podocarpidites ellipticus Cookson 1947

Podocarpidites rectangularis De Benedetti sp. nov.

Plate II, Figs. 6–8

2020. *Podocarpidites otagoensis* Couper, in Llorens et al. (2020), Review of Palaeobotany and Palynology, 273, 104137, plate II, 9.

182 *Etymology:* Referring to the subrectangular corpus shape in polar and equatorial view.

183 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

184 *Holotype:* MPEF-PA 817 (Plate II, 6 and 8).

185 *Paratype:* MPEF-PA 454 (Plate II, 7).

186 *Additional material:* MPEF-PA 450, 454, 458, 472, 613, 671, 817, 821, 925.

187 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian.

188 *Diagnosis:* Pollen grain bisaccate, diploxylonoid. Corpus subrectangular to elliptical in polar and
189 equatorial view, with major axis along grain length. Corpus exine up to 2 μm thick, columellate,
190 tectum psilate to perforate. Sacci about the same width and half in length than the corpus, with
191 an irregular intrareticulum. Leptoma large.

192 *Description:* The pollen grains are bisaccate and diploxylonoid (Plate II, 6 and 7). The corpus is
193 subrectangular to elliptical in polar and equatorial view, with major axis along grain length.
194 Proximally the corpus exine is up to 2 μm thick, with a psilate to perforate tectum and a dense
195 infrareticulum with muri < 1 μm width and lumina up to twice the width of muri (Plate II, 8). In
196 optical section, the exine has two layers of similar thickness separated by columellae. The sacci
197 are distally inserted surrounding a large subrectangular leptoma whose major axis extends along
198 corpus width. The sacci are about the same width and half the length of the corpus, with an
199 irregular intrareticulum. The bases of the sacci do not touch on the equatorial contour.

200 *Dimensions:* Total length 46 (65) 93 μm (12 specimens); total height ~ 30–40 μm (6 specimens);
201 corpus length 38 (47) 55 μm (12 specimens); corpus width 28–38 μm (3 specimens); corpus
202 height ~ 20–30 μm (5 specimens); sacci length 14 (26) 36 μm (8 specimens); sacci width 21–42
203 μm (3 specimens); sacci height 17–26 μm (3 specimens); lateral height of sacci 24–33 μm (3
204 specimens). Measurements based on the scheme proposed by Romero (1977).

205 *Occurrence:* Sections QH/CI, CBO, CBN.

206 *Comparisons:* The large subrectangular to elliptical corpus with a psilate to perforate tectum
207 distinguished *Podocarpidites* rectangularis from other *Podocarpidites* species. *P. elegans*
208 Romero from the Eocene of Patagonia (Romero, 1977) and *P. exiguous* Harris from the
209 Paleocene of Australia (Harris, 1965), are smaller. *P. otagoensis* Couper from the Late
210 Cretaceous of New Zealand is smaller and has a thicker exine (Couper, 1953). *P. marwickii*
211 Couper from the Early Cretaceous–Oligocene of New Zealand has a subcircular to elliptical
212 corpus in polar view and is smaller (Couper, 1953).

213 *Distribution:* Argentina, Patagonia: Aptian (Llorens et al., 2020).

214

215 ANGIOSPERMS

216 MONOCOTS

217 *Family:* ARECACEAE Bercht. and J. Presl 1820

218 Genus ***Arecipites*** Wodehouse emend. Anderson 1960

219 *Type species: Arecipites punctatus* Wodehouse 1933

220 *Arecipites botrus* De Benedetti and Zamaloa sp. nov.

221 Plate II, Figs. 21–24

222 *Etymology:* From the Latin "*botrus*" which means cluster, as this species is typically found in
223 clumps.

224 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

225 *Holotype:* MPEF-PA 470 (Plate II, 21).

226 *Paratype:* MPEF-PA 452 (Plate II, 22).

227 *Additional material:* MPEF-PA 149, 170, 452–454, 456, 460, 470–472, 580, 587, 611, 631, 925.

Stratigraphic horizon: La Colonia Formation, Maastrichtian.

Diagnosis: Pollen grain monosulcate, amb elliptical, sulcus long, reaching to margin. Exine ~ 0.5 μm thick, psilate to finely perforate.

Description: The pollen grains are monosulcate, with an elliptical amb and rounded to pointed ends (Plate II, 21 and 22). The sulcus is usually narrow and long, extended to the margins and with tapered ends, sometimes overlapping and with marginal folds. Specimens with flared or rounded ends or with one end tapered and the other flared were also observed. A weak margo is sometimes present (Plate II, 22). The exine is ~ 0.5 μm thick, columellae indistinct. The surface is psilate at LM and finely perforate at SEM, with lumina < 0.2 μm diameter (Plate II, 24). The specimens are commonly found in clumps (Plate II, 23).

Dimensions: Longer equatorial diameter 14 (17.2) 26 μm (104 specimens); shorter equatorial diameter 6.5 (10.3) 15 μm (54 specimens).

Occurrence: Sections QH/CI, CBO, CBN.

Comparisons: Arecipites has a worldwide distribution with more than 50 species ranging from Early Cretaceous to Cenozoic age (e.g., Palynodata Inc.; White, 2006). The type species *A. punctatus* from the Eocene of the USA is distinguished by having a ticker columellate exine, a coarser sculpture, and a more conspicuous margo (Wodehouse, 1933; Nichols, 2010). *A. scabratus* Simoncsics from the Miocene of Hungary is similar in size but has a thicker exine (Simoncsics, 1969). *A. asymmetricus* (Frederiksen) Frederiksen from the Eocene of USA has a similar size but has an asymmetrically oval outline and a slightly thicker exine (Frederiksen, 1983). *A. otagoensis* (Couper) Mildenhall and Pocknall from the Oligocene–Pliocene of New Zealand is larger and has a thicker exine (Couper, 1960; Mildenhall and Pocknall, 1989). *A. polaris* da Silva-Caminha et al. from the Neogene of Brazil has a similar size but it has a thicker

exine and a dense punctate sculpture (da Silva-Caminha et al., 2010). *A. rousei* Frederiksen from the Eocene of USA is similar in size but it has a slightly thicker exine which is scabrate to punctate and with distinctive columellae (Frederiksen, 1983).

Botanical affinity: A. botrus is similar to the pollen produced by modern *Phoenix dactylifera* L.

Genus: **Gemmamonocolpites** Van der Hammen and García de Mutis 1965

Type species: Gemmamonocolpites gemmatus (Van der Hammen) Van der Hammen and García de Mutis 1965

Gemmamonocolpites chubutensis De Benedetti sp. nov.

Plate II, Figs. 26–28

Etymology: The epithet "chubutensis" refers to the Chubut Province, Argentina.

Type locality: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 826 (Plate II, 26)

Paratype: MPEF-PA 828 (Plate II, 27).

Additional material: MPEF-PA 170, 679, 828, 841, 930.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain monosulcate, amb subcircular to elliptical. Exine 1.0–1.5 μm thick, columellate, tectate perforate, gemmate. Supratectal gemmae of up to 5.5 μm diameter and 4 μm high, irregularly distributed over the entire surface.

Description: The pollen grains are monosulcate, with a subcircular to elliptical amb (Plate II, 26–28). The exine is 1.0–2.0 μm thick (excluding supratectal elements), columellate. The tectum is perforate (microfoveolate to microreticulate), with lumina of < 0.5 μm diameter and muri of equal or slightly larger size, and with supratectal gemmae of 1.0–5.5 μm diameter and up to 4

μm high, irregularly distributed over the entire surface (Plate II, 28). The gemmae can be of similar or variable sizes in the same grain. Small protuberances and low rugulae are sometimes interspersed between the gemmae. The sulcus is generally obscured by the gemmae.

Dimensions: Maximum equatorial diameter 26 (33) 40 μm (5 specimens).

Occurrence: Sections CBO, CBN, CHM.

Comparisons: The most similar species to *G. chubutensis* are *G. amicus* González Guzmán, *G. barmerensis* Parmar et al., *G. dispersus* Sarmiento Perez, and *G. macrogemmatus* Muller et al. *G. amicus* from the Eocene of Colombia has similar size and columellate microreticulate exine with lumina of 0.5 μm diameter, but the gemmae are smaller (González Guzmán, 1967). *G. barmerensis* from the Paleocene–Eocene of India has smaller gemmae (Parmar et al., 2023). *G. dispersus* from the Maastrichtian–Danian of Colombia also has smaller gemmae (Sarmiento Perez, 1992). *G. macrogemmatus* Muller et al. from the Maastrichtian–Paleocene of Venezuela (e.g., Muller et al., 1987), Maastrichtian of Egypt (e.g., Schrank and Ibrahim, 1995), and Maastrichtian–Paleocene of Sudan (e.g., Cole et al., 2017), has a non-perforated exine and densely distributed gemmae of up to 3 μm diameter (Muller et al., 1987).

Genus: **Spinizonocolpites** Muller emend. Muller et al. 1987

Type species: Spinizonocolpites echinatus Muller 1968

Spinizonocolpites coloniensis De Benedetti sp. nov.

Plate III, Figs. 6–10

Etymology: The epithet "coloniensis" refers to the La Colonia Formation.

Type locality: Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 926 (Plate III, 6 and 8).

297 *Paratype:* MPEF-PA 951 (Plate III, 7).

298 *Additional material:* MPEF-PA 169, 926, 927, 942, 947, 951.

299 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.

300 *Diagnosis:* Pollen grain zonosulcate, amb subcircular to elliptical. Exine up to 1.5 μm thick,
301 hyaline, psilate. Surface with densely distributed bacula with rounded or blunt ends usually with
302 multiple papillae. Sculptural elements up to 8 μm high and 2.5 μm diameter,

303 *Description:* The pollen grains are zonosulcate, with a subcircular to elliptical amb, flattened
304 along the polar axis (Plate III, 6 and 7). The sulcus divides the grain into two almost equal parts.
305 The exine is up to 1.5 μm thick, hyaline, and psilate. The sculptural elements include bacula that
306 are ca. 2.5–8.0 μm high and 1.5–2.5 μm diameter, densely distributed over the entire surface,
307 mostly straight but occasionally curved (Plate III, 8), and with rounded or blunt ends which
308 commonly have 2 to 5 papillae (Plate III, 9 and 10).

309 *Dimensions:* Longest equatorial diameter 36 (45) 72 μm (7 specimens).

310 *Occurrence:* Section CBN.

311 *Comparisons:* The distinctive hyaline exine of *S. coloniensis* also occurs in the Late Cretaceous
312 and Paleocene Patagonian *S. hialinus* Archangelsky and Zamaloa and *S. riochiquensis* Vallati
313 and De Sosa Tomas. However, *S. hialinus* includes forms with sparsely distributed spines, coni,
314 and/or bacula (Archangelsky and Zamaloa, 1986), and *S. riochiquensis* includes forms having
315 only densely distributed rounded bacula (Vallati et al., 2020). The presence of sculptural
316 elements with multiple apical papillae is apparently unique to *S. coloniensis*.

317

318 *Spinizonocolpites variabilis* De Benedetti sp. nov.

319 Plate III, Figs. 11–14

Etymology: From the Latin "*variabilis*" which means variable, it refers to the variety of sculptural elements.

Type locality: Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 874 (Plate III, 11).

Paratype: MPEF-PA 865 (Plate III, 12).

Additional material: MPEF-PA 168, 169, 865, 870, 874, 922, 947, 977.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain zonosulcate, amb subcircular to elliptical. Exine <1 μm thick, hyaline, psilate. Sculpture includes densely distributed spines and sparse bacula, clavae, verrucae, and granules. Sculptural elements up to 1.8 μm high and 1 μm diameter. Surface with dispersed microgranules and microechinae.

Description: The pollen grains are zonosulcate, with an elliptical amb, flattened along the polar axis (Plate III, 11–13). The sulcus divides the grain into two almost equal parts. The exine is < 1 μm thick, hyaline, and psilate. The sculptural elements include densely distributed spines (up to 1.8 μm high), which can be straight or curved, cylindrical, conical, bulbous to slender, but also sparce bacula and clavae with rounded or blunt ends (up to 1.8 μm high), and scattered granules and verrucae (up to 1 μm diameter). Microgranules and microechinae of 0.2–0.5 μm diameter are distributed among the larger elements (Plate III, 14).

Dimensions: Longest equatorial diameter 26 (43) 58 μm (10 specimens).

Occurrence: Sections QH/CI, CBO, CBN, CHM.

Comparisons: The presence of clavae, verrucae, and granules distinguish *S. variabilis*. *S. coloniensis* and *S. riochiquensis* both have larger sculptural elements. *S. variabilis* is similar to *S.*

342 *hialinus* in the structure of the exine but has smaller and more densely arranged sculptural
343 elements and more variable morphologies.
344
345 *Family:* LILIACEAE Juss. 1789
346 *Genus:* **Liliacidites** Couper 1953
347 *Type species: Liliacidites kaitangataensis* Couper 1953
348 *Liliacidites buitrensis* De Benedetti sp. nov.
349 Plate III, Figs. 22–25
350 *Etymology:* The epithet "buitrensis" refers to the El Buitre Hill located near the studied outcrops.
351 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.
352 *Holotype:* MPEF-PA 819 (Plate III, 22).
353 *Paratype:* MPEF-PA 821 (Plate III, 23).
354 *Additional material:* MPEF-PA 146, 685, 819, 821, 931.
355 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.
356 *Diagnosis:* Pollen grain monosulcate, amb elliptical. Sulcus wide, extended almost the full
357 length of the grain. Exine 2.0–2.5 μm thick, two-layered, sexine thicker than nexine; nexine
358 psilate; sexine semitectate, simplicolumellate, reticulate, homobrochate. Columellae up to 1.5 μm
359 high; muri up to 0.5 μm high, flat, tectum psilate; lumina rounded polygonal, elongate to
360 irregular, 1.5–4.5 μm diameter.
361 *Description:* The pollen grains are monosulcate, with rounded elliptical amb (Plate III, 22 and
362 23). The sulcus is wide and extended almost the full length of the grain. The exine is 2.0–2.5 μm
363 thick, two-layered, the sexine is thicker than the nexine; nexine psilate; sexine semitectate,
364 simplicolumellate, reticulate, homobrochate (Plate III, 24). The columellae are conspicuous, 0.5–

365 0.8 μm in diameter, and up to 1.5 μm high. The muri are relatively flat and psilate, up to 0.5 μm
366 high and 1 μm wide. The lumina are rounded polygonal, elongate to irregular, 1.5–4.5 (usually 2
367 to 3) μm in maximum diameter. Smaller lumina of up to 0.5 μm diameter are sometimes
368 interspersed at the intersections of the muri (Plate III, 25).
369 *Dimensions:* Longest equatorial diameter 32 (43) 53 μm (5 specimens); shortest equatorial
370 diameter 31 (35) 40 μm (4 specimens).
371 *Occurrence:* Sections CBO, CBN.
372 *Comparisons: Liliacidites* comprises more than 80 species (e.g., Palynodata Inc.; White, 2006).
373 *L. variegatus* Couper originally described from the Late Cretaceous to Oligocene of New
374 Zealand has smaller lumina (Couper, 1953). *L. kaitangataensis* Couper from the Late Cretaceous
375 to Eocene of New Zealand is larger and has larger lumina that strongly decrease in size towards
376 the ends of the grain (Couper, 1953). *L. intermedius* Couper from the Late Cretaceous to
377 Miocene of New Zealand has smaller lumina (Couper, 1953). *L. waitunaensis* Couper from the
378 Oligocene of New Zealand has a thicker exine and clavate-baculate columellae (Couper, 1960).
379 *L. vermireticulatus* Archangelsky and Zamaloa first described from the Paleocene of Argentina
380 has smaller lumina and the reticulum is incomplete (Archangelsky and Zamaloa, 1986). *L.*
381 *regularis* Archangelsky from the Paleocene of Argentina has smaller lumina at the ends of the
382 grain and the columellae are smaller (Archangelsky, 1973; Archangelsky and Zamaloa, 1986).
383
384 *Liliacidites lacunosus* De Benedetti sp. nov.
385 Plate III, Figs. 26–30
386 *Etymology:* The epithet “lacunosus” refers to the wavy lumina of the reticulum.
387 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

388 *Holotype:* MPEF-PA 667 (Plate III, 26 and 27).

389 *Paratype:* MPEF-PA 701 (Plate III, 28).

390 *Additional material:* MPEF-PA 655, 666, 667, 675, 690, 700, 701, 803, 976.

391 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.

392 *Diagnosis:* Pollen grain monosulcate, amb subcircular to elliptical. Sulcus extended almost the
393 full length of the grain. Exine 1.0–1.5 μm thick, two-layered, sexine thicker than nexine; nexine
394 psilate; sexine semitectate, simplicolumellate, reticulate, heterobrochate. Columellae up to 0.5
395 μm high; muri up to 0.8 μm high, narrow, undulate, sharp-crested; lumina wavy to irregular, 1.5–
396 3.5 μm diameter, strongly diminishing toward the sulcus.

397 *Description:* The pollen grains are monosulcate, with a subcircular to elliptical amb (Plate III,
398 26–29). The sulcus is usually open, extended almost the full length of the grain. The exine is
399 1.0–1.5 μm thick, two-layered, the sexine is thicker than the nexine; nexine psilate; sexine
400 semitectate, simplicolumellate, reticulate, heterobrochate. The columellae are short and variable
401 in height, ca. 0.1–0.4 μm diameter and ca. 0.1–0.5 μm high, although they can be occasionally
402 inconspicuous. The muri are narrow, undulate or sinuous, sharp-crested and relatively high
403 compared with the columellae (ca. 0.5–0.8 μm high) (Plate III, 30). The lumina are wavy to
404 irregular, ca. 1.5–3.5 μm diameter, strongly diminishing in size toward the sulcus (reaching 0.5
405 μm diameter or less) (Plate III, 30), although this is sometimes difficult to distinguish as sulcus
406 edges are often folded.

407 *Dimensions:* Longest equatorial diameter 18 (27) 33 μm (18 specimens); shortest equatorial
408 diameter 18 (22) 26 μm (10 specimens).

409 *Occurrence:* Sections QH/CI, CBO, CBN, CHM.

410 *Comparisons: L. aviemorensis* McIntyre from the Oligocene–Miocene of New Zealand is similar
411 in having wavy lumina but has an incomplete reticulum (McIntyre, 1968). *L. waitunaensis*
412 Couper from the Oligocene of New Zealand has lumina of similar sizes but has a thicker exine
413 (Couper, 1960). *L. altimurus* Leffingwell from the Maastrichtian of USA has taller wavy and
414 sharp-crested muri and the reticulum is incomplete on the proximal face (Leffingwell, 1970). *L.*
415 *dictyotus* Singh from the Cenomanian of Canada also has sharp-crested muri with relatively
416 indistinct columellae and lumina of similar sizes but strongly reduced toward the ends of the
417 grain (Singh, 1983).
418
419 *Family:* TYPHACEAE Juss. 1789
420 *Genus:* **Sparganiaceaepollenites** Thiergart ex Potonié 1960
421 *Type species: Sparganiaceaepollenites polygonalis* Thiergart ex Potonié 1960
422 *Sparganiaceaepollenites annulatus* De Benedetti sp. nov.
423 Plate IV, Figs. 1–5
424 2014. "Typhaceous pollen grain", in Cúneo et al. (2014), PLoS ONE, 9(8), e104749, fig. 10, G.
425 2021. *Sparganiaceaepollenites* sp., in Clyde et al. (2021), Cretaceous Research, 126, 104889,
426 fig. 4, Q.
427 2021. *Sparganiaceaepollenites* sp., in Cúneo et al. (2021), XXI Congreso Geológico Argentino,
428 126, p. 266, fig. 5, j.
429 *Etymology:* Referring to the presence of a conspicuous annulus.
430 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.
431 *Holotype:* MPEF-PA 874 (Plate IV, 1).
432 *Paratypes:* MPEF-PA 580 (Plate IV, 2).

Additional material: MPEF-PA 149–151, 168, 171, 388, 396, 454, 456, 460, 580, 611, 628, 633, 685, 870,874, 922, 928–931, 976, 978.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain monoporate, amb circular to subcircular. Pore circular, ca. 1.5–4.0 µm diameter, annulate. Annulus 1.0–2.5 µm wide. Exine < 1 µm thick, two layered, nexine thinner than sexine. Sexine semitectate, simplicolumellate, columellae fused laterally and apically forming a delicate reticulum; lumina subcircular, polygonal to irregular, up to 2 µm diameter; muri membranous, up to 0.3 µm wide and 0.5 µm high, with supratectal ridges or microechinae.

Description: Pollen grains are mostly in dyads (Plate IV, 1, 3, and 4) and monads (Plate IV, 2). Grains are anisopolar, monoporate, spheroidal, with a circular to subcircular outline. The pore is circular, annulate, and ca. 1.5–4.0 µm diameter. The annulus is ca. 1.0–2.5 µm wide, formed by a thickening of the nexine. A reticulate operculum was observed in a few specimens (Plate IV, 4). The exine is ca. 0.5–0.7 µm thick, two layered, nexine thinner than sexine. The sexine is semitectate, simplicolumellate, the columellae are fused laterally and apically forming a delicate membranous reticulum. Only the bases of the columellae distinguish at SEM (Plate IV, 5). The lumina are subcircular, polygonal to irregular, ca. 0.5–1.2 (up to 2) µm in diameter, but sometimes smaller lumina ca. 0.1–0.3 µm are intercalated or surround the pore; muri of 0.2–0.3 µm wide and 0.3–0.5 µm high, with supratectal ridges or microechinae (Plate IV, 5). Pollen grains of monads can reach larger dimensions than those of dyads. This species was also found in clumps.

Dimensions: Monads 15.0 (22.0) 32.0 µm diameter (38 specimens); longest dimension of dyads 20–39 µm (15 specimens); single grain of a dyad 15.0 (18.0) 21.0 µm diameter (31 specimens).

Occurrence: Sections QH/CI, CBO, CBN, CHM.

Comparisons: S. annulatus is easily distinguished from other species of the genus because it is usually dispersed as dyads. The specimens are probably conspecific with those recorded as dyads of "*Typha* pollen" from the Late Cretaceous of the Jagüel and Roca formations, Mendoza Province, Argentina (Papú, 2006). *S. barungensis* Harris first described for the Tertiary of Australia has a thicker exine and the muri of the reticulum lack tectal ridges or microechinae (Harris, 1972). *S. delicata* Mautino and Anzótegui from the Miocene of northern Argentina has a microreticulum with smaller lumina (Mautino and Anzótegui, 2002). *S. hospahensis* Jameossanaie from the Campanian of Mexico has a larger pore (Jameossanaie, 1987). *S. microreticulatus* Kar and Jain from the Miocene of India is larger and has smaller lumina (Kar and Jain, 1978). *S. neogenicus* Krutzsch from the Miocene–Pliocene of Europe has a thicker exine and the pore lacks annulus (Krutzsch, 1970; Ziembińska-Tworzydło, 1974). *S. reticulatus* (Doktorowicz-Hrebnicka) Roche from the Tertiary of Europe is larger and lacks annulus (Roche, 1968; Krutzsch and Vanhoorne, 1977). *S. robustiporis* Martin from the Eocene–Oligocene of Australia is larger and has a coarser reticulum (Martin, 1973). *S. reticulatus* Samant et al. from the Maastrichtian of India is a later homonym of *S. reticulatus* (Doktorowicz-Hrebnicka) Roche and it is distinguished from *S. annulatus* by having larger lumina and a larger pore (Samant et al., 2022).

Botanical affinity: S. annulatus, like several species of *Sparganiaceaepollenites*, is similar to the pollen produced by *Typha* L. and *Sparganium* L., within Typhaceae Juss. (Thiergart, 1937; Harris, 1972). Affinities with other families such as Potamogetonaceae Rchb. has been also suggested (Gandolfo et al., 2009).

EUDICOTS

Family: ERICACEAE Juss. 1789

Genus: **Ericipites** Wodehouse 1933

Type species: Ericipites longisulcatus Wodehouse 1933

Ericipites verrucatus De Benedetti and Zamaloa sp. nov.

Plate IV, Figs. 12–15

Etymology: The epithet "verrucatus" refers to the verrucate sculpture of the grains.

Type locality: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 622 (Plate IV, 12).

Paratype: MPEF-PA 993 (Plate IV, 13).

Additional material: MPEF-PA 149, 150, 165, 582, 621–623, 827, 993.

Stratigraphic horizon: La Colonia Formation, Maastrichtian.

Diagnosis: Pollen grains in tetrahedral tetrads. Individual grains tricolporoidate/tricolporate, oblate, amb rounded subtriangular to subcircular. Colpi marginate, pore obscure. Exine 1.5–2.0 μm thick, nexine and sexine of similar sizes. Tectum incomplete at the mesocolpia forming granules, verrucae, and rugulae of up to 1 μm wide.

Description: The pollen grains are in obligate tetrahedral tetrads (Plate IV, 12–14). The individual grains are oblate, with a rounded subtriangular to subcircular amb, tricolporoidate/tricolporate. The colpi are marginate, extended 3/4 or more the length of the polar diameter. Pore characteristics are not clear. The exine is ca. 1.5–2.0 μm thick, two layered, the nexine and sexine are of similar sizes. The exine surface is warty on the mesocolpia (where the tectum is incomplete), and psilate on the apocolpia and next to the colpi (where the tectum is complete) (Plate). The sculptural elements include small granules and verrucae (usually less than 1 μm diameter), and rugulae of up to 1 μm wide, which are more or less fused (Plate IV, 15). The

nexine surface is psilate to scabrate and is distinguished in those specimens with loosely distributed sculptural elements. Colpi of adjacent grains meet at the junctures of the grains two by two (Fischer's law).

Dimensions: Individual grains 14 (20.5) 27 μm equatorial diameter (27 specimens); tetrads 22 (29) 41 μm maximum length (20 specimens).

Occurrence: Sections CBO, CBN, CHM.

Comparisons: A coarsely granulate-verrucate and rugulate ornamentation on the mesocolpia, which is absent on the apocolpia and colpi margins distinguishes *E. verrucatus* from other species in the genus. Most *Ericipites* species are characterized by having a relatively homogeneous sculpture from psilate to scabrate or granulate (e.g., Wodehouse, 1933; Ramanujam, 1966; González Guzmán, 1967; Archangelsky and Zamaloa, 1986). *E. taiwanensis* Huang from the Miocene of Taiwan also has a distinctive margo but is larger and the sculpture is finer (Huang, 1980). Several forms from the Paleogene and Neogene of Europe were described as modern genera of Ericaceae (e.g., Hofmann, 2018; Grímsson et al., 2020). Among them, the *Erica*-type from the Eocene of Germany is similar in having mesocolpia with a differentiated sculpture, but the tectum is faintly fossulate and perforate in the polar areas (Hofmann, 2018).

Botanical affinity: E. verrucatus is similar to the pollen produced by some species of *Gaultheria* Kalm ex L. as those illustrated by Lu et al. (2009).

Family: NELUMBONACEAE A. Rich.

Genus: **Nelumbopollenites** Skawińska 1994

Type species: Nelumbopollenites europaeus (Tarasevich) Skawińska in Ziembińska-Tworzydło et al. 1994

Nelumbopollenites patagonicus De Benedetti sp. nov.

Plate IV, Figs. 21–27

Etymology: The epithet "patagonicus" refers to the South American Patagonia region.

Type locality: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 622 (Plate IV, 21).

Paratype: MPEF-PA 622 (Plate IV, 22).

Additional material: MPEF-PA 149, 150, 165, 168, 580, 582–586, 621–625, 752, 753, 772, 788, 801, 873, 922.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain tricolpate, prolate, amb circular, oval in equatorial view. Colpi long, extended to the poles. Exine up to 3 μm thick, two-layered, sexine thicker than nexine, semitectate. Tectum thick, supported by short columellae. Sexine rugulate-foveolate/reticulate.

Description: The pollen grains are tricolpate, prolate, oval in equatorial view (Plate IV, 21, 23, and 26), circular to three-lobed when compressed from the pole (Plate IV, 22 and 24). The colpi are long and pointed and extend near the polar region. The exine is 2.0–3.0 μm thick, two layered, the sexine is thicker than the nexine, columellate, semitectate, rugulate-foveolate/reticulate. The tectum is thick, up to 2.5 μm, supported by short columellae that fuse apically forming a sinuous reticulum with muri ca. 0.6–1.8 μm wide and subcircular lumina ca. 0.3–1.6 μm (Plate IV, 27) that are sometimes fused forming long fossulae up to 2.5 μm (Plate IV, 25). A weak margo, ca. 2 μm wide, with small and narrow lumina (< 0.5 μm) was recognized in some specimens (Plate IV, 22 and 24).

Dimensions: Polar diameter 34 (58) 78 μm (27 specimens); equatorial diameter 18 (32) 53 μm (26 specimens); equatorial diameter with polar compression 32 (54) 66 μm (15 specimens).

548 *Occurrence:* Sections QH/CI, CBO, CBN, CHM.

549 *Comparisons: Nelumbopollenites* is a monotypic genus. *N. europaeus* from the Miocene–
550 Pliocene of Europe is distinguished by having a thicker exine, longer columellae, and a more
551 homogeneous rugulate-reticulate sculpture (Ziembińska-Tworzydło et al., 1994).
552 *Foveotricolpites giganteus* (Jardiné and Magloire) Jan du Chêne et al. from the Late Cretaceous
553 of northwest Africa is notably similar, it comprises large tricolpate pollen grains with long colpi,
554 a thick exine, but it has a more homogeneous foveolate surface with occasionally elongated
555 fossulae, and the lumina are smaller (Jardiné and Magloire, 1965; Jan du Chêne et al., 1978). *F.*
556 *tienabaensis* (Jardiné and Magloire) Schrank from the Late Cretaceous of northeast Africa has a
557 similar rugulate-foveolate/reticulate or vermiculate ornamentation but is smaller (Schrank,
558 1987). *Retitricolpites magloirae* Kedves from the Maastrichtian of Egypt is similar in having an
559 elliptical equatorial outline, small polar areas, and a thick exine but it has a reticulum with
560 thinner muri (Kedves, 1999). *Retitricolpites simplex* González Guzmán from the Eocene of
561 Colombia is also similar in size and exine thickness, but the sculpture is microreticulate
562 (González Guzmán, 1967; Guimarães and Nogueira, 2015).
563
564 *Family:* PROTEACEAE Juss. 1789
565 *Genus:* **Proteacidites** Cookson ex Couper 1953
566 *Type species: Proteacidites adenanthoides* Cookson ex Couper 1953
567 *Proteacidites baibianae* De Benedetti sp. nov.
568 Plate V, Figs. 6–10
569 *Etymology:* The epithet “baibianae” honors the Baibián family for allowing access to some of the
570 studied outcrops.

571 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

572 *Holotype:* MPEF-PA 853 (Plate V, 6).

573 *Paratype:* MPEF-PA 928 (Plate V, 7).

574 *Additional material:* MPEF-PA 145, 147, 168, 169, 679, 688–692, 750–753, 803, 804, 817, 820,

575 853, 871, 922, 928, 951, 965, 976.

576 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.

577 *Diagnosis:* Pollen grain triporate, angulaperturate, isopolar, amb triangular, sides straight to

578 slightly concave or convex, apices truncate. Pores subcircular, ca. 3–11 μm diameter. Exine ca.

579 1.2–3.0 μm thick, two layered, nexine equal or thicker than sexine. Nexine homogeneous. Sexine

580 columellate, tectate perforate. Columellae short, mostly indistinct, relatively thick tectum

581 composed of small, low, closely spaced rugulae and verrucae, with scattered puncta.

582 *Description:* The pollen grains are triporate, angulaperturate, isopolar, with a triangular amb and

583 straight to slightly concave or convex sides, and truncate apices (Plate V, 6–8). The equatorial

584 pores are ca. 3–11 μm diameter, subcircular, slightly concave in polar view. The exine is ca. 1.2–

585 3.0 μm thick; the nexine is homogeneous; the sexine is columellate, tectate perforate. The nexine

586 is more than twice or equal the thickness of the sexine. The columellae are short, mostly

587 indistinct, and fused apically forming a relatively thick tectum composed of small and low

588 closely spaced rugulae (ca. 1 μm x 2.5 μm) and verrucae (ca. 1 μm) (Plate V, 9).

589 *Dimensions:* Equatorial diameter 28 (41) 60 μm (40 specimens).

590 *Occurrence:* Sections QH/CI, CBO, CBN, CHM.

591 *Remarks:* The sexine is readily affected by corrosion and other taphonomic processes and

592 therefore the surface appearance varies considerably (Plate V, 10), with some grains having a

593 more pitted or reticulated appearance and others even having completely lost the sexine.

Comparisons: P. scaboratus Couper from the Late Cretaceous and Cenozoic of New Zealand has smaller pores and a psilate, scabrate, or punctate sculpture (Couper, 1960). In Patagonia, proteaceous pollen and particularly genus *Proteacidites* have been widely recorded in Cretaceous and Cenozoic deposits. However, most of these specimens were described and/or illustrated with informal names or were assigned to species previously reported in Cretaceous and Cenozoic deposits of Australia and New Zealand. Some of them are apparently conspecific with *P. baibianae*, for example those reported from Maastrichtian deposits of Chubut Province as *P. scaboratus* (Vallati et al., 2016, 2020). However, SEM studies are required to ensure the correct assignment of most of the Cretaceous and Tertiary proteaceous Patagonian species. *P. minimus* Couper from the Miocene of New Zealand is smaller (Couper, 1954). *P. rectomarginis* Cookson from the Eocene–Miocene of Australia has a coarser sculpture that sometimes forms a negative reticulum (Cookson, 1950). *P. rectus* Pocknall and Mildenhall from the Eocene–Miocene of New Zealand has small pores (Pocknall and Mildenhall, 1984). *P. stipplatus* Partridge is similar at LM, but it has a thicker exine that is densely granulate to rugulate (Stover and Partridge, 1973).

Proteacidites mirasolensis De Benedetti sp. nov.

Plate V, Figs. 11–14

Etymology: The epithet "mirasolensis" refers to the Arroyo Mirasol Chico, a creek in the vicinity of the studied outcrops.

Type locality: Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 951 (Plate V, 11).

Paratype: MPEF-PA 930 (Plate V, 12).

Additional material: MPEF-PA 169, 874, 922, 926, 928–930, 933, 946, 951, 972, 977.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain triporate, angulaperturate, isopolar, amb triangular, sides straight to slightly convex, apices truncate. Pores subcircular, ca. 3–5 μm diameter. Exine ca. 1.2–2.0 μm thick, two layered, nexine slightly thicker than sexine. Nexine homogeneous. Sexine columellate, reticulate. Columellae short, mostly indistinct, reticulum with low contorted muri up to 0.8 μm wide and irregular lumina of up to 1.7 μm. Lumina diameter reduced around the pores, where the sexine is tectate perforate.

Description: The pollen grains are triporate, angulaperturate, isopolar, with a triangular amb and straight to slightly convex sides, and truncate apices (Plate V, 11–13). The equatorial pores are ca. 3–5 μm diameter, subcircular. The exine is ca. 1.2–2.0 μm thick, two layered, thinner to the pores; the nexine is homogeneous; the sexine is columellate, reticulate. The nexine is slightly thicker than the sexine. The columellae are short, mostly indistinct, fused apically forming a reticulum composed of low highly contorted psilate muri (up to 0.8 μm wide) and irregular lumina (up to 1.7 μm) (Plate V, 14). The reticulum reduces to the pores where the exine is thinner and tectate or tectate perforate (Plate V, 13). Floor of the lumina psilate (Plate V, 14).

Dimensions: Equatorial diameter 26 (31) 37 μm (12 specimens).

Occurrence: Sections QH/CI, CBN, CHM.

Comparisons: Similar forms were described from the Late Cretaceous and Tertiary of Australia and New Zealand: *P. angulatus* Stover has smaller lumina (Stover and Partridge, 1973); *P. campbellensis* Wanntorp et al. has a reticulum with uniform and smaller lumina (Wanntorp et al. 2011); *P. hortisinus* Wanntorp et al. has a similar sculpture but the lumina are of uniform size all over the grain (Wanntorp et al. 2011); *P. kopiensis* Harris also has a similar sculpture but the

lumina are slightly larger at the central part of the grain (Harris, 1972); *P. reticuloscabratus* Harris and *P. pseudomoides* Stover differ in possessing pronounced exinal thickenings around the apertures (Stover and Partridge, 1973; Harris, 1974); *P. retiformis* Couper has larger lumina (Couper, 1960); *P.* sp. cf. *P. pseudomoides* has a similar sculpture with smaller lumina around the apertures but muri are not contorted (Mildenhall et al., 2018); and finally *P. scitus* Stover and Partridge is similar in size and exine thickness, but it has slightly larger lumina and thinner muri (Stover and Partridge, 1982).

Family: INCERTAE SEDIS

Genus: **Ailanthipites** Wodehouse 1933

Type species: Ailanthipites berryi Wodehouse 1933

Ailanthipites diminutus De Benedetti sp. nov.

Plate V, Figs. 20–23

1933. *Ailanthipites mulleri* (Kemp) Milne 1988, in Baldoni and Askin (1993), Palynology, 17(1), p. 247, plate 1, fig. 13.

Etymology: The epithet "diminutus" refers to the small overall size of the grains.

Type locality: Quebrada del Helecho/Cañadón del Irupé locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 608 (Plate V, 20)

Paratypes: MPEF-PA 388 (Plate V, 21), MPEF-PA 625 (Plate V, 22).

Additional material: MPEF-PA 388, 450, 452, 470, 471, 608, 625.

Stratigraphic horizon: La Colonia Formation, Maastrichtian.

662 *Diagnosis:* Pollen grain tricolporate, prolate spheroidal to prolate. Colpi long, extended nearly to
663 the poles, with costae endocolpi, pores lalongate. Exine 1–2 μm thick, semitectate, suprastriate-
664 inframicroreticulate. Muri ca. 0.15–0.25 μm wide, longitudinal, subparallel, dichotomous,
665 anastomosed, closely spaced. Lumina < 0.3 μm diameter.
666 *Description:* The pollen grains are tricolporate, prolate spheroidal to prolate, with a rounded
667 triangular amb, elliptical in equatorial view (Plate V, 20–22). The colpi extend nearly to the
668 poles, with costae endocolpi, pores lalongate ~ 1.5–2.0 x 3.0–4.0 μm, sometimes poorly defined.
669 The exine is 1–2 μm thick, semitectate, suprastriate-inframicroreticulate (Plate V, 23). The muri
670 are 0.15–0.25 μm wide, longitudinally aligned, subparallel, dichotomous, anastomosed, and
671 more closely spaced at the poles and colpi margins (Plate V, 23). The inframicroreticulum has
672 lumina < 0.3 μm diameter.
673 *Dimensions:* Polar diameter 12 (17) 21 μm (8 specimens); equatorial diameter 10 (15) 20 μm (15
674 specimens).
675 *Occurrence:* Sections QH/CI, CBO.
676 *Comparisons: A. diminutus* is easily distinguished from most species of the genus by its small
677 size and small ornamentation. *A. berryi* from the Eocene of USA has a very similar sculpture but
678 it is larger (Wodehouse, 1933). *A. pseudostriatus* (McIntyre) Mildenhall from the Cenozoic of
679 New Zealand is slightly larger and has larger lumina (Mildenhall et al., 2018). *A. nonprolatus*
680 from the Eocene of USA is also slightly larger and has larger lumina and larger pores
681 (Frederiksen, 1983). *A. mulleri* from the Oligocene of the Indian Ocean has coarser muri and the
682 inframicroreticulum is less evident (Kemp and Harris, 1977; Milne, 1988). *Striatricolporites*
683 *poloreticulatus* da Silva-Caminha et al. from the Neogene of Brazil is larger and has wider muri
684 and larger lumina (da Silva-Caminha et al., 2010).

685

686 *Ailanthipites feruglioi* De Benedetti sp. nov.

687 Plate V, Figs. 24–27

688 2008. *Striatricolporites* sp., in Narváez and Sabino (2008), Ameghiniana, 45(2), fig. 5, 2.

689 *Etymology:* The epithet "feruglioi" honors the distinguished Italian geologist Egidio Feruglio,

690 who spent most of his career in Argentina.

691 *Type locality:* Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

692 *Holotype:* MPEF-PA 803 (Plate V, 24).

693 *Paratype:* MPEF-PA 933 (Plate V, 25).

694 *Additional material:* MPEF-PA 168, 803, 933.

695 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian.

696 *Diagnosis:* Pollen grain tricolporate, oblate to oblate spheroidal. Colpi long, extended nearly to

697 the poles, with margo, pores diffuse. Exine ca. 1–2 μm thick, semitectate, suprastriate-

698 inframicroreticulate. Muri ca. 0.2–0.3 μm wide, longitudinal, subparallel, dichotomous,

699 anastomosed, closely spaced, rounded in cross section, psilate. Lumina < 0.5 μm diameter.

700 *Description:* The pollen grains are tricolporate, oblate to oblate spheroidal, with a subcircular

701 amb (Plate V, 24–26). The colpi are extended nearly to the poles, with margo. Pores are diffuse.

702 The exine is 1–2 μm thick, semitectate, suprastriate-inframicroreticulate. The longitudinal muri

703 are ca. 0.2–0.3 μm wide, rounded in cross section, subparallel, dichotomous, anastomosed,

704 leaving spaces of up to 0.5 μm between them in the mesocolpia at the equator, and have a psilate

705 surface (Plate V, 27). The lumina of the inframicroreticulum are < 0.5 μm diameter. The muri are

706 more closely spaced at the colpi margins (forming the margo) and sometimes at the poles where

707 lumina and/or spaces between muri are absent (Plate V, 26).

Dimensions: Equatorial diameter 23 (25) 26 µm (3 specimens).

Occurrence: Section CBN.

Comparisons: The material described here is conspecific with the specimen described by Narváez and Sabino (2008) as "*Striatricolporites* sp." for the Campanian–Maastrichtian of northern Argentina. *A. berryi* is prolate (Wodehouse, 1933). *A. gamerroi* (Archangelsky) Mautino and Anzotegui, which is widely distributed from the Maastrichtian to the Pliocene of Argentina (e.g., Mautino and Anzotegui, 2014), has a similar sculpture but is subprolate to prolate. *A. mulleri* was reported in Maastrichtian deposits of Patagonia (Baldoni and Askin, 1993) but it is subprolate to prolate spheroidal and has coarser muri. *A. paenestriatus* (Stover) Milne from the Eocene of Australia has larger pores and slightly larger size (Milne, 1988). *A. pseudostriatus* has larger lumina (Mildenhall et al., 2018). *Striatricolporites conspicuus* Muller and *S. minor* Muller from the Eocene of Malaysia both are larger (Muller, 1968). *S. archangelskyi* Herngreen from the Senonian of Brazil is larger and has a thicker exine (Herngreen, 1975).

Ailanthipites hexagonalis De Benedetti sp. nov.

Plate V, Figs. 28–30

Etymology: The epithet "hexagonalis" refers to the hexagonal outline of the grains in equatorial view.

Type locality: Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 799 (Plate V, 28).

Paratypes: MPEF-PA 700 (Plate V, 29), MPEF-PA 830 (Plate V, 30).

Additional material: MPEF-PA 685, 841, 972.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain tricolporate, prolate, outline hexagonal in equatorial view. Colpi long, pores lalongate. Exine ca. 1.0–1.5 μm thick, semitectate, suprastriate-inframicroreticulate. Muri radially disposed of up to 0.4 μm wide and 0.5 μm height, subparallel, dichotomous, anastomosed, closely spaced.

Description: The pollen grains are tricolporate, prolate, with a conspicuous hexagonal outline in equatorial view (Plate V, 28–30). The "equatorial zone" is occasionally narrower than the non-equatorial zones owing to the varying thickness of the exine (Plate V, 29 and 30). The "polar zones" are blunt. The colpi are long, extended to the poles, with small apocolpia. The pores are lalongate, ca. 4–6 μm x 2.5–3.0 μm (Plate V, 28). The exine is ca. 1.0–1.5 μm thick at the poles, two layered, the sexine is thicker than the nexine. The sexine is semitectate, suprastriate-inframicroreticulate. The muri are radially disposed, ca.0.2–0.4 μm wide and up to 0.5 μm high, subparallel, dichotomous, anastomosed, and closely spaced.

Dimensions: Polar diameter 30 (34) 38 μm; equatorial diameter 19 (20) 23 (6 specimens).

Occurrence: Sections CBO, CBN.

Comparisons: The distinctive hexagonal outline characterizes *A. hexagonalis*. No comparable forms have been found in the Mesozoic and Cenozoic palynofloras worldwide.

Genus: **Krutzschipollis** Góczán emend. Polette and Batten 2017

Type species: Krutzschipollis spatiosus Góczán in Góczán et al. 1967

Krutzschipollis argentinum De Benedetti and Zamaloa sp. nov.

Plate VI, Figs. 4–7

Etymology: The epithet "argentinum" refers to the country Argentina.

754 *Type locality:* Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

755 *Holotype:* MPEF-PA 804 (Plate VI, 4 and 5).

756 *Paratype:* MPEF-PA 861 (Plate VI, 6).

757 *Additional material:* MPEF-PA 145, 677, 679, 688, 691, 804, 861, 874, 947.

758 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.

759 *Diagnosis:* Pollen grain tricolporate, oblate, amb rounded triangular. Colpi short, with ektannuli,
760 ca. 2.5 μm wide in the equator, tapering to the poles. Pores indistinct. Exine 3.5–5.0 μm thick,
761 two layered, sexine thicker than nexine, columellae indistinct. Sculpture of poorly defined
762 rugulae, longitudinally oriented in the equator, delimiting central polar areas of smaller granulate
763 to verrucate sculpture.

764 *Description:* The pollen grains are tricolporate, oblate, with a triangular rounded amb (Plate VI,
765 Figs. 4–7). The colpi are short, beak-shaped in polar view, extended ca. 5–9 μm from the equator
766 to the poles, with a distinctive psilate ektannulus ca. 2.5 μm wide in the equator, with protruding
767 margins, tapering to the poles (Plate VI, Figs. 4, 5, and 7). The pores are mostly indistinct. The
768 exine is 3.5–5.0 μm thick in the interradial regions, two layered, the sexine is thicker than the
769 nexine. The nexine is ca. 1 μm thick, homogeneous. The sexine is 2.5–4.0 μm thick, columellae
770 indistinct. The sculpture consists of more or less defined rugulae of up to 1.5 μm wide that are
771 longitudinally oriented in the equator, grading to granulate and verrucate sculpture in polar areas
772 (Plate VI, Fig. 7). In some specimens, the sexine is strongly folded and apparently separated
773 from the nexine delimiting a distinctive central body (Plate VI, Fig. 6).

774 *Dimensions:* Equatorial diameter 23 (29) 34 μm (10 specimens).

775 *Occurrence:* Sections CBO, CBN, CHM.

Comparisons: Most *Krutzschipollis* species are distinguished from *K. argentinum* by having a thicker nexine with conspicuous endopores that are usually associated with a wide atrium (Polette and Batten, 2017). The most similar species is *K. crassis* (Góczán) Góczán emend. Polette and Batten from the Campanian of Hungary, but it is larger and has a thicker nexine and conspicuous endopores associated with shallow to moderately deep atria (e.g., Góczán et al., 1967; Polette and Batten, 2017).

Genus: **Nyssapollenites** Thiergart 1937

Type species: Nyssapollenites pseudocruciatus (Potonié) Thiergart 1937

Nyssapollenites scabratus De Benedetti and Zamaloa sp. nov.

Plate VI, Figs. 8–12

Etymology: The epithet "scabratus" refers to the scabrate surface of the grains.

Type locality: Quebrada del Helecho/Cañadón del Irupé locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 470 (Plate VI, 8).

Paratype: MPEF-PA 471 (Plate VI, 9).

Additional material: MPEF-PA 149, 210, 450–454, 457, 458, 470–472, 980.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain tricolporate, oblate spheroidal to subprolate, amb subcircular to rounded subtriangular, outline subcircular to elliptical in equatorial view. Colpi extended nearly to the poles, with costae endocolpi, pores lalongate. Exine < 1 μm thick, two-layered, scabrate, and sparsely punctate.

798 *Description:* The pollen grains are isopolar, oblate spheroidal to subprolate, with a subcircular to
799 subtriangular rounded amb, and a subcircular to elliptical outline in equatorial view, tricolporate
800 (Plate VI, 8–10). The colpi are costate, extended nearly to the poles. The pores are lalongate. The
801 exine is < 1 μm thick and two-layered. The exine surface is scabrate at LM (Plate VI, 8) and
802 bullate (irregular protrusions) at SEM with numerous evenly distributed microgranules (~ 0.1–
803 0.2 μm diameter and height) and less numerous puncta (~ 0.1 μm diameter) (Plate VI, 11 and
804 12). The grains are commonly found in clumps (Plate VI, 10).
805 *Dimensions:* Polar diameter 7.0 (10.2) 15.0 μm (43 specimens); equatorial diameter 5.5 (10.4)
806 15.0 μm (68 specimens).
807 *Occurrence:* Sections QH/CI, CBO, CHM, CBN.
808 *Comparisons: N. scabratus* distinguishes for its small dimensions. Somewhat similar forms have
809 been described from a fossil inflorescence of Euphorbiaceae affinity carrying in situ pollen of *N.*
810 *endobalteus* (McIntyre) Kemp and Harris emend. Mildenhall and Pocknall from the Miocene of
811 New Zealand (Lee et al., 2010; Kaulfuss et al., 2023). *N. endobalteus* shares with *N. scabratus* a
812 scabrate exine composed of irregular protrusions with microgranules and puncta. However, *N.*
813 *endobalteus* is slightly larger and has shorter colpi and a thickened nexine around the
814 endoapertures (Lee et al., 2010).
815
816 *Genus:* **Parviprojectus** Mtchedlishvili emend. Wu and Li 2022
817 *Type species: Parviprojectus reticulatus* Mtchedlishvili 1961
818 *Parviprojectus archangelskyi* De Benedetti and Zamaloa sp. nov.
819 Plate VI, Figs. 13–18

820 1986. *Callistopollenites* sp., in Archangelsky and Zamaloa (1986), Ameghiniana, 23 (1–2), p. 39
821 and 40, lám. 2, figs. 24–27.
822 *Etymology:* The epithet "archangelskyi" honors the distinguished Argentinean paleobotanist and
823 palynologist Dr. Sergio Archangelsky.
824 *Type locality:* Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.
825 *Holotype:* MPEF-PA 967 (Plate VI, 13 and 14).
826 *Paratype:* MPEF-PA 701 (Plate VI, 15).
827 *Additional material:* MPEF-PA 170, 396, 972.
828 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.
829 *Diagnosis:* Pollen grain isopolar, tricolpate, prolate ellipsoidal, equatorial projections lingulate.
830 Exine ca. 1.0–1.5 μm thick, two layered, sexine thicker than nexine. Sexine semitectate
831 striate/striate-reticulate. Muri spindle shaped, aligned latitudinally along colpi edges,
832 meridionally along the central part of mesocolpia, and concentrically around the equatorial
833 projections.
834 *Description:* The pollen grains are isopolar, tricolpate, with an ellipsoidal body and three short
835 and rounded to slightly conical equatorial projections (Plate VI, 13–16). The colpi are long and
836 narrow, extended across projections onto the body and nearly to the poles. The exine is about
837 1.0–1.5 μm thick (measured in the poles), two layered, the sexine is thicker than the nexine. The
838 three equatorial projections have endexinous thickenings (usually difficult to distinguish) from
839 their base to near the tip, where the exine is thinnest. The sexine is semitectate striate (Plate VI,
840 17 and 18). The striae are aligned latitudinally along the colpi borders, meridionally along the
841 central part of the mesocolpia, and concentrically around the equatorial projections. The muri are
842 spindle shaped or fusiform, ca. 0.2–1.5 μm wide and up to 1 μm high, occasionally bifurcated,

larger in the central part of the mesocolpia and smaller towards the polar areas and colpi. In the polar areas and next to the colpi the exine is striate-microreticulate with lumina ca. 0.1–0.4 μm (Plate VI, 18).

Dimensions: Body: length 26 (32) 36 μm, width 17 (20) 24 μm, length/width ratio 1.5–1.75. Projection: length 5.8–7.7 μm, base width 8.5–12 μm, terminal width 4.8–5.6 μm, length/width ratio 0.5–0.7. (4 specimens). Terminology follows Wu and Li (2022).

Occurrence: Sections QH/CI, CBO, CBN.

Comparisons: Archangelsky and Zamaloa (1986) described from the Paleocene of Patagonia similar specimens to *Parviprojectus archangelskyi* and assigned them to the genus *Callistopollenites* Srivastava. *Callistopollenites* comprises seven species, all of them reported from Campanian–Maastrichtian deposits of the Northern Hemisphere (e.g., Srivastava, 1969, 1972; Takahashi, 1984; Prasad and Pundeer, 2002; Li et al., 2011). However, *Callistopollenites* is characterized by being almost spheroidal and by having aspidate pores while *P. archangelskyi* is subprolate to prolate and tricolpate with equatorial projections, so the new species has characteristics of *Parviprojectus*, which has a stratigraphic and geographic distribution restricted to the Campanian–Danian of the Northern Hemisphere (Wu and Li, 2022). The type species *P. reticulatus*, originally described from the Maastrichtian–Danian of Russia, has larger lanceolate equatorial projections and the ornamentation is striate-reticulate with a conspicuous and larger reticulum (Mtchedlishvili, 1961; Wu et al., 2022). Other species of *Parviprojectus* are distinguished from *P. archangelskyi* by having larger equatorial projections and a reticulate or a thinner striate-reticulate sculpture (e.g., Braman, 2013, 2018; Wu et al., 2022).

Distribution: Danian of Chubut Province, Argentina (Archangelsky and Zamaloa, 1986). This constitutes the first record of the genus for the Southern Hemisphere.

Genus: **Periporopollenites** Pflug and Thomson 1953

Type species: Periporopollenites stigmosus (Potonié) Pflug and Thomson 1953

Periporopollenites delicatus De Benedetti sp. nov.

Plate VI, Figs. 19–22

Etymology: The epithet "delicatus" refers to the delicate muri of the reticulum.

Type locality: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 460 (Plate VI, 19 and 20).

Paratype: MPEF-PA 471 (Plate VI, 21).

Additional material: MPEF-PA 151, 457, 461, 470, 575, 577, 582, 688, 946.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain pantoporate, outline circular to subcircular. Pores circular, annulate, 6 to 9 or more, ca. 1–4 μm diameter, occasionally operculate. Exine < 1 μm thick, two layered, nexine thinner than sexine. Sexine semitectate, simplicolumellate, reticulate; lumina subcircular, polygonal to irregular, ca. 0.5–1.5 μm diameter, muri ca. 0.2–0.3 μm wide and 0.3–0.5 μm high, with supratectal ridges or microechinae.

Description: The pollen grains are pantoporate, with a circular to subcircular outline (Plate VI, 19–21). The pores are circular, annulate, variable in number from 6 to 9 or maybe more, sometimes indistinct but probably fewer than 12, variable in size in the same grain, ca. 1–4 μm diameter (usually 1.5 to 2.5 μm), occasionally operculate. The distance between pores is greater than the pore diameter. The annulus is ca. 1.0–2.0 um wide, formed by a thickening of the nexine (Plate VI, 20). The exine is < 1 μm thick, two layered, nexine thinner than sexine. The sexine is semitectate, simplicolumellate, the columellae are short and fused laterally to form a

membranous reticulum. The lumina are subcircular, polygonal to irregular, ca. 0.5–1.5 μm diameter; muri ca. 0.2–0.3 μm wide and 0.3–0.5 μm high, with supratectal ridges or microechinae. Occasionally, the lumina are smaller (ca. 0.1–0.3 μm) over the opercula and around the pores (Plate VI, 22). Sometimes operculate pores are difficult to distinguish in both LM and SEM and therefore the minimum number of pores may be undercounted. This species is commonly found in clumps.

Dimensions: Maximum equatorial diameter 15 (26) 34 μm (26 specimens).

Occurrence: Sections QH/CI, CBO, CBN.

Comparisons: Periporopollenites comprises about 40 species (e.g., Palynodata Inc.; White, 2006). The type species *P. stigmosus* originally described from the Oligocene–Miocene of Germany is larger, has a finer reticulum, and larger pores without opercula (Thomson and Pflug, 1953). *P. asiaticus* Takahashi from the Eocene–Miocene of Japan has a delicate reticulate sculpture but it has larger pores and thicker exine (Takahashi, 1961). *P. reticulatus* Jan du Chêne from the Eocene of Nigeria has larger pores and thicker exine (Jan du Chêne et al., 1978). *Multiporopollenites intermedius* D'Apolito et al. from the Miocene of Brazil has a similar sculpture but with slightly coarser muri and up to 16 pores (D'Apolito et al., 2021).

Genus: **Retitricolporites** (Van der Hammen) Van der Hammen and Wymstra 1964

Type species: Retitricolporites guianensis Van der Hammen and Wymstra 1964

Retitricolporites ganganensis De Benedetti sp. nov.

Plate VI, Figs. 26–30

Etymology: The epithet "*ganganensis"* refers to Gan Gan, a small town near the La Colonia Fm. outcrops.

Type locality: Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 620 (Plate VI, 26).

Paratype: MPEF-PA 942 (Plate VI, 27).

Additional material: MPEF-PA 145, 168, 169, 381, 383, 584, 620, 625, 932, 942, 947.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain tricolporate, subspheroidal to prolate. Colpi extended nearly to the poles. Pores lalongate, usually indistinct. Exine 1.0–1.5 μm thick, two layered, sexine thicker than nexine. Sexine simplicolumellate, semitectate, reticulate. Lumina polygonal, rounded to irregular, up to 1.8 μm diameter in the mesocolpia, smaller lumina in the apocolpia and colpi margins. Muri up to 0.6 μm wide.

Description: The pollen grains are tricolporate, subspheroidal to prolate (Plate VI, 26–29). The colpi extend nearly to the poles. The pores are lalongate, ca. 4–8μm in long, but usually indistinct (Plate VI, 27). The exine is 1.0–1.5 μm thick, two-layered. The nexine is ca. 0.5 μm. The sexine is ca. 1 μm, columellate, semitectate. The columellae are fused apically forming a reticulum. The lumina are polygonal, rounded to irregular, ca. 0.8–1.8 μm diameter in the mesocolpia, decreasing gradually or strongly towards the apocolpia and colpi margins up to ~ 0.5 μm or less (Plate VI, 28 and 29). The muri are ca. 0.3–0.6 μm wide, occasionally with small perforations (ca. 0.1–0.2 μm) in the conjunction of several lumina (Plate VI, 30).

Dimensions: Polar diameter 24 (30) 35 μm (13 specimens); equatorial diameter 14 (20) 28 μm (14 specimens).

Occurrence: Sections CBO, CBN.

Comparisons: The type species *R. guianensis* from the Eocene–Oligocene of Guiana is similar in size but has larger lumina (Van der Hammen and Wymstra, 1964). *R. chubutensis* Archangelsky

935 from the Paleocene of Patagonia has larger lumina and thicker exine (Archangelsky, 1973). *R.*
936 *lachkarii* Kedves from the Maastrichtian of Egypt has homogeneous lumina (Kedves, 1999). *R.*
937 *saskiae* González Guzmán from the Eocene of Colombia is larger, has shorter colpi, and a
938 thicker exine (González Guzmán, 1967). *R. maculatus* Kedves from the Eocene of Hungary is
939 larger and it has mostly polygonal lumina (Kedves, 1978).
940
941 *Retitricolporites irupensis* De Benedetti sp. nov.
942 Plate VII, Figs. 1–5
943 *Etymology:* The epithet "irupensis" refers to the Cañadón del Irupé locality.
944 *Type locality:* Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.
945 *Holotype:* MPEF-PA 820 (Plate VII, 1 and 2).
946 *Paratype:* MPEF-PA 663 (Plate VII, 3).
947 *Additional material:* MPEF-PA 171, 663, 820, 822, 830, 926, 949.
948 *Stratigraphic horizon:* La Colonia Formation, Maastrichtian to early Danian.
949 *Diagnosis:* Pollen grain tricolporate, suboblate to subprolate, amb subcircular to semilobate.
950 Colpi extended nearly to the poles. Pores usually indistinct. Exine 3.0–4.5 μm thick, two layered,
951 reduced towards the colpi margins. Nexine up to 2 μm thick. Sexine up to 3 μm thick,
952 columellate, semitectate, reticulate. Lumina polygonal, rounded to irregular, up to 4.5 μm
953 diameter in the mesocolpia, slightly smaller at the apocolpia, and strongly reduced in the colpi
954 margins. Muri up to 1 μm wide.
955 *Description:* The pollen grains are tricolporate, isopolar, suboblate, to subprolate (Plate VII, 1–
956 4). The colpi are slightly sunken, producing an elliptic outline in equatorial view and subcircular
957 to semilobate in polar view. The colpi are long, costate, extended nearly to the poles, and

delimiting a small polar area. The pores are apparently lalongate but generally indistinct. The exine is ca. 3.0–5.0 μm thick in the equatorial area of the mesocolpia (nexine 1–2 μm, sexine 2–3 μm including a tectum of less than 1 μm thick) and thinner towards the colpi margins, reticulate. The reticulum is simplicolumellate, with columellae ca. 0.6–1.0 μm diameter (Plate VII, 1). The lumina are polygonal to irregular, ca. 2.0–4.5 μm diameter in the mesocolpia, slightly smaller in the apocolpia (ca. 1.5–2.5 μm), and strongly reduced in the colpi margins (up to ca. 0.5 μm diameter) (Plate VII, 2–4). The muri are ca. 0.4–1.0 μm wide (Plate VII, 5). The foot layer is smooth and lacks free columellae.

Dimensions: Polar diameter 23(47) 55 μm (7 specimens); equatorial diameter 28 (39) 60 μm (6 specimens).

Occurrence: Sections CBO, CBN.

Comparisons: Larger dimensions, a thicker exine with long columellae, and larger lumina distinguished *R. irupensis* from *R. ganganensis* and *R. chubutensis*. The type species *R. guianensis* is smaller and has a thinner exine (Van der Hammen and Wymstra, 1964). *R. marianis* González Guzmán from the Eocene of Colombia is smaller and has smaller lumina (González Guzmán, 1967).

Genus: **Rousea** Srivastava 1969

Type species: Rousea subtilis Srivastava 1969

Rousea robusta De Benedetti sp. nov.

Plate VII, Figs. 11–13

Etymology: The epithet “robusta” refers to the robustness of the muri of the reticulum.

Type locality: Cerro Buitre Norte locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 819 (Plate VII, 11).

Paratype: MPEF-PA 822 (Plate VII, 12).

Additional material: MPEF-PA 819, 820, 822.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain oblate, tricolpate, amb subtriangular, sides straight to slightly convex. Colpi long, with a finely punctate margo. Exine up to 2 μm thick, semitectate, reticulate. Lumina up to 3.6 μm diameter in the mesocolpia, elongated, rounded, to irregular in outline, slightly smaller to strongly reduced in the apocolpia. Muri up to 2 μm wide.

Description: The pollen grains are tricolpate, oblate, with a subtriangular amb and with straight to slightly convex sides (Plate VII, 11–13). The colpi are long, extended nearly to the poles, wedge shaped, and with a finely punctate margo ca. 2 μm wide. The exine is 1.3–2.0 μm thick, two layered, the sexine is thicker than the nexine. The nexine is mostly indistinct. The sexine is semitectate, reticulate. The reticulum has robust columella and a thick tectum. The lumina are 1.0–3.6 μm diameter at the center of the mesocolpia, elongated, rounded, to irregular in outline, and slightly smaller to strongly reduced in the apocolpia, which can be punctate in some specimens (lumina ca. 0.1 μm) (Plate VII, 13). Muri ca. 0.6–2.0 μm wide.

Dimensions: Equatorial diameter 30 (35) 44 μm (4 specimens).

Occurrence: Section CBN.

Comparisons: R. microreticulata Archangelsky and Zamaloa, *R. minuscula* Archangelsky and Zamaloa, and *R. patagonica* Archangelsky from the Danian of Patagonia are all distinguished by having thinner muri (Archangelsky, 1973; Archangelsky and Zamaloa, 1986). The type species *R. subtilis* from the Maastrichtian of Canada has larger lumina and a thicker exine (Srivastava, 1969). *R. georgensis* (Brenner) Dettmann from Albian to Cenomanian of North America,

1004 Europe, and Australia is prolate and has smaller lumina and thinner muri (e.g., Ward, 1986; and
1005 cites therein). *R. crassimurina* Pocknall and Nichols from the Paleocene of USA is
1006 duplicolumellate (Pocknall and Nichols, 1996). *R. wilsonii* (Kimyai) Singh from the Cenomanian
1007 of USA is subprolate to prolate and has thinner muri (Singh, 1983).
1008
1009 *Genus:* **Stellatopollis** Doyle et al. 1975
1010 *Type species: Stellatopollis barghoornii* Doyle et al. 1975
1011 *Stellatopollis crassibaculata* (Freile) Ward 1986 emend. De Benedetti
1012 Plate VII, Figs. 14–17
1013 1972. *Liliacidites crassibaculatus* Freile, in Freile (1972), Revista del Museo de La Plata (n. s.),
1014 Paleontología 6 (38), p. 49 and 50, lam II, figs. 11 and 12.
1015 1986. *Stellatopollis crassibaculata* (Freile) Ward, in Ward (1986), Palaeontographica Abteilung
1016 B, 202 (1–6), p. 36.
1017 *Original diagnosis (translated from Spanish):* "Pollen grain monocolpate. Outline elliptical to
1018 subspherical in polar view. Colpus extended the entire longitudinal axis in its polar view.
1019 Proximal exine thick, 1.5–2 μm thick, more delicate distally; composed of two layers: endexine
1020 thinner than ektexine. The exine has a reticulated ornamentation, with small lumina (1 μm or
1021 less) and simplibaculate muri with thick columellae of irregular bases. Lumina somewhat smaller
1022 at the ends of the grain."
1023 *Emended diagnosis:* Pollen grain monosulcate, amb elliptical to subcircular. Sulcus long, poorly
1024 defined. Exine 1.0–1.5 μm thick, two layered, columellae indistinct. Nexine smooth, thinner than
1025 sexine. Sexine semitectate, reticulate. Reticulum composed of low muri and polygonal to
1026 subcircular lumina ca. 0.5–2.8 μm diameter. Muri with short club-like supratectal projections up

to 1.2 μm height and 1.6 μm width, 5 to 9 clubs per lumina, forming a crotonoid or stellate pattern. Heads of the projections mostly polygonal, but also elliptical, subcircular, to irregular in surface view. Projections in contact or separated up to 0.8 μm apart.

Description: The pollen grains are monosulcate, with an elliptical to subcircular amb (Plate VII, 14–16). The sulcus extends 3/4 to the entire length of the grain, with the margins poorly defined. The exine is ca. 1.0–1.5 μm thick, two layered, columellae indistinct. The nexine is smooth and thinner than the sexine. The sexine is semitectate, with a reticulum composed of low muri (< 0.3 μm high and 0.3–0.5 μm wide) and polygonal to subcircular lumina (ca. 0.5–2.8 μm). The muri bear short (0.5–1.2 μm high) and relatively large (0.3–1.6 μm wide) club-like supratectal projections, about 5 to 9 per lumina, forming a crotonoid or stellate pattern (Plate VII, 17). The heads of the projections are mostly polygonal, but also triangular, elliptical, subcircular, to irregular in surface view. Heads in contact or separated by as much as 0.8 μm. There is a wide range in sculpture size and density. Sometimes smaller supratectal projections are densely disposed along the sulcus.

Dimensions: Longest equatorial diameter 28 (33) 44 μm (28 specimens); shortest equatorial diameter 16 (24) 35 μm (25 specimens).

Studied material: MPEF-PA 168, 171, 388, 611, 628, 666, 685, 689–691, 701, 800, 801, 830, 872, 927, 930, 946, 947, 957, 962, 972.

Occurrence: Sections QH/CI, CBO, CBN.

Comparisons: The relatively thin exine and small supratectal projections distinguished *S. crassibaculata* from other species in the genus. *S. barghoornii* from the Lower Cretaceous of USA is larger, has a thicker exine and larger sculpture (Doyle et al., 1975). TEM studies of *S. barghoornii* demonstrated that the projections are supratectal sculptural elements on top of a

perforate tectum supported by short columellae (Doyle et al., 1975). *S. araripensis* (De Lima) Ward, *S. densiornata* (De Lima) Ward, and *S. dubia* (De Lima) Ward, from the Lower Cretaceous of Brazil are distinguished by being larger and/or by having mostly triangular projections in groups of six (De Lima, 1989; Ward, 1986). *S. bituberensis* Penny from the Barremian of Egypt has larger lumina and thicker exine (Penny, 1986). *S. dejaxii* Ibrahim from the Barremian of Egypt has larger lumina, wider muri, and dense larger supratectal projections with mostly globular heads (Ibrahim, 2002). *S. doylei* Ibrahim from the Barremian–Aptian of Egypt has mostly triangular supratectal projections (Ibrahim, 2002). *S. grandis* (Rao and Ramanujam) Ward from the Neogene of India has a thicker exine (Rao and Ramanujam, 1976). *S. hughesii* Penny from the Barremian–Aptian of Egypt has about 14 supratectal projections around each lumina (Penny, 1986). *S. largissimus* Singh from the Cenomanian of Canada has larger size and thicker exine (Singh, 1983). *S. limai* Ibrahim from the Aptian of Egypt has larger lumina and the projections differ in morphology (Ibrahim, 2002).

Distribution: Argentina, Patagonia: Maastrichtian–Paleocene (Freile, 1972).

Genus: **Symplocoipollenites** Potonié ex Potonié emend. Słodkowska 1994

Type species: Symplocoipollenites vestibulum (Potonié) Potonié ex Potonié1960

Symplocoipollenites microechinatus De Benedetti sp. nov.

Plate VII, Figs. 21–24

Etymology: The epithet “microechinatus” refers to the microechinate surface of the grains.

Type locality: Cerro Bosta locality, La Colonia Fm., Chubut Province, Argentina.

Holotype: MPEF-PA 454 (Plate VII, 21).

Paratype: MPEF-PA 453 (Plate VII, 22).

Additional material: MPEF-PA 453–458, 460, 461, 580, 582, 628.

Stratigraphic horizon: La Colonia Formation, Maastrichtian to early Danian.

Diagnosis: Pollen grain tricolporate, oblate, amb rounded triangular, sides straight or slightly concave or convex. Colpi short, pores circular to elliptic, vestibulate. Exine < 1 μm thick, two layered, microechinate.

Description: The pollen grains are tricolporate, oblate, with a rounded triangular amb and with straight or slightly concave or convex sides (Plate VII, 21 and 22). The colpi are short, occasionally slit-like. The pores are circular to elliptic, with vestibulum. The exine is < 1 μm thick, two layered, tectate-columellate, with the columellae mostly indistinct (Plate VII, 23), scabrate at LM (Plate VII, 21–23) and microechinate at SEM (Plate VII, 24). The microechinae are irregularly distributed, and ca. 0.1–0.3 μm in height and diameter (Plate VII, 24). These grains are commonly found in clumps.

Dimensions: Equatorial diameter 9 (12) 17 μm (32 specimens).

Occurrence: Sections QH/CI, CBO, CBN.

Comparisons: S. microechinatus is the only species of *Symplocoipollenites* known to have a microechinate sculpture. Most species included in the genus are larger and differ in sculpture. *S. austellus* Partridge from the Maastrichtian and Cenozoic of Patagonia is larger, and it has thicker exine (Baldoni and Askin, 1993; Barreda, 1997). *Symplocoipollenites* sp. cf. *S. kutchensis* Venkatachala and Kar from the Cenomanian of Patagonia has similar size but it has annulate pores and thicker exine (Santamarina et al., 2020).

4. Discussion

4.1. Palynological diversity, living analogs, and paleoenvironment

Approximately 250 palynomorphs were identified in the studied assemblages of the La Colonia Fm. Pollen grains comprise 35 % of the diversity (8 % gymnosperms and 27 % angiosperms), spores of bryophytes, lycophytes, and ferns represent another 35 %, and the remaining 30 % includes algal and fungal remains. Among the species described above, some are of particular interest for evolutionary, biostratigraphic, and paleoenvironmental interpretations.

Gymnosperms include members of the extinct family Cheirolepidiaceae and of the families Araucariaceae, Ephedraceae, and Podocarpaceae, and *Cycadopites* sp. of uncertain taxonomic placement (Table 1). All gymnosperm taxa found in the La Colonia samples, except for the two new species and *Classopollis* sp. 1, are known from contemporaneous deposits of Patagonia.

The angiosperm component comprises more than 16 families (Table 1); the most diverse are the monocot Arecaceae and eudicot Proteaceae with 11 and 10 species respectively.

Among the monocots, the Araceae *Pandaniidites* pollen has been previously reported for the La Colonia Fm. in co-occurrence with macrofossil remains of *Aquaephyllum auriculatum* Gallego et al., evidencing the presence of lemnaceous representatives in the freshwater aquatic paleocommunity of this unit (Gallego et al., 2014). The specimens described in Gallego et al. (2014) and the one illustrated in Cúneo et al. (2021) as *Pandaniidites* sp. are conspecific to *P. radicus* Leffingwell. This species has been reported from the Campanian–Eocene of North America (e.g., Leffingwell, 1970; Nichols et al., 1986). This is the first record of *P. radicus* for the Maastrichtian–Danian of the Southern Hemisphere.

Arecaceae (palm) pollen is represented by several genera including *Arecipites*, *Confertisulcites*, *Gemmamonocolpites*, *Longapertites*, *Proxapertites*, and *Spinizonocolpites*. In addition to *Spinizonocolpites hialinus* and *S. riochiquensis*, the new species *S. coloniensis* and *S. variabilis*, were discovered in the La Colonia Fm. The oldest records of *Spinizonocolpites* are

from the Early Cretaceous (Barremian–Albian) of Patagonia (Martínez et al., 2016). In the Late Cretaceous (Campanian–Maastrichtian), it is known from Central and South America, Africa, and Asia (e.g., Muller, 1968; Schrank, 1987; Gee, 2001; Vallati et al., 2020) and has been mostly related to the tropical mangrove *Nypa fruticans* Wurmb (e.g., Frederiksen, 1994). *Nypa* is one of the oldest and more widely distributed palm found in the fossil record with representatives of leaves, seeds, fruits, and pollen (Lenz et al., 2020). Currently, *Nypa* is restricted to tropical to subtropical coasts of southeast Asia, growing in tidal mudflats in quiet estuaries along waters of lower salinity or shallow lagoons having freshwater rather than hypersaline influence (Collinson, 1993; Lenz et al., 2020). Cretaceous *Spinizonocolpites* parent plants were probably not restricted to tropical intertidal environments as they also lived in lacustrine environments (e.g., Singh, 1999; Lenz et al., 2020). The new species *Arecipites botrus* is notably like the pollen produced by the modern palm *Phoenix dactylifera*, which is native to tropical to subtropical regions of North Africa, the Arabian Peninsula, and India (Chao and Krueger, 2007). *Gemmamonocolpites chubutensis* resembles the modern pollen of *Borassus* L. and *Hyphaene* Gaertn. of the subfamily Coryphoideae Burnett, which are native to tropical regions of Africa, Asia, and Papua New Guinea (e.g., Parmar et al., 2023). The high diversity of palm pollen reported from the Maastrichtian–Danian of Patagonia provides important evidence for the paleogeographic history of Arecaceae in high southern latitudes.

Another interesting discovery is the first record of *Inaperturotetradites scabratus* in the Southern Hemisphere. This species has been widely recorded in Cenomanian to Paleocene deposits of North America (e.g., Tschudy, 1973; Braman, 2001; Bercovici et al., 2009). *I. scabratus* exhibits minutely granulate sculpture, probably inaperturate or with obscure apertures,

and it is dispersed as tetrahedral tetrads, a set of characters found in the pollen of extant Juncaceae as illustrated in Halbritter and Berger (2018) and Passarini Lopes et al. (2021).

Pollen monoporate reticulate of *Sparganiaceaepollenites* type has been related to Typhaceae (Thiergart, 1937; Harris, 1972). Modern pollen of *Typha angustifolia* L. is dispersed as monads while pollen of *Typha latifolia* L. is dispersed in tetrads (Shih and Finkelstein, 2008). Interestingly, the hybrids between these species produce mixtures of monads, dyads, triads, and tetrads (Finkelstein, 2003) similar to the dispersion units found in *Sparganiaceaepollenites annulatus*.

The botanical affinity of the new species *Nelumbopollenites patagonicus* within Nelumbonaceae is supported by its morphology but also by the presence of fossil leaves and fruits of *Nelumbo puertae* Gandolfo and Cúneo recovered from the La Colonia Fm. outcrops at the Cañadón del Irupé locality (Gandolfo and Cúneo, 2005). Today, the family is restricted to tropical and subtropical areas of North and Central America, Asia, and Australia (Williamson and Schneider, 1993). Nevertheless, the macrofossil record of the Nelumbonaceae is quite extensive, ranging from the Albian to Miocene of both hemispheres and indicates that the family had a nearly cosmopolitan distribution during the Late Cretaceous (e.g., Gandolfo and Cúneo, 2005; Li et al., 2014). However, pollen grains related to *Nelumbo* have not been previously registered from Late Cretaceous deposits (e.g., Kuprianova and Tarasevich, 1983). Nevertheless, similar forms to *N. patagonicus* have been reported as species of *Foveotricolpites* from the Late Cretaceous of Africa, and as *Retitricolpites simplex* from Paleogene and Neogene of northern South America (see references above). The new species is the first confirmed record of pollen of the family for the SH contributing to further understanding of its biogeographical past distribution and the changes over time.

1164 The fossil record of Ericaceae extends back to the Late Cretaceous and consists mostly of leaf
1165 impressions, seeds, and pollen (Nixon and Crepet, 1993; Kubitzki, 2004). The new species
1166 *Ericipites verrucatus* increases the pollen diversity knowledge of the family in the Late
1167 Cretaceous. The family Ericaceae is represented mainly by evergreen shrubs and shrublets
1168 (Thiele-Pfeiffer, 1980), sometimes deciduous, rarely lianas, small trees, or herbs (Stevens et al.,
1169 2004). *E. verrucatus* is particularly similar to the pollen produced by some species of *Gaultheria*,
1170 which includes shrubs widespread in temperate regions and tropical montane habits and it has
1171 extant representatives in Patagonia (Luteyn, 2002).
1172 Based on the modern analogs of the pollen recovered from the La Colonia samples, we
1173 suggest that the environment in which the paleocommunity grew is consistent with a warm
1174 tropical to subtropical freshwater to brackish low energy lagoon, supporting the
1175 paleoenvironment previously proposed by Gandolfo et al. (2014) and Cúneo et al. (2014) for the
1176 La Colonia Fm. The assemblage is composed of elements that are autochthonous herbs (e.g.,
1177 Araceae, Juncaceae, Typhaceae, and Nelumbonaceae), while others are parautochthonous or
1178 allochthonous herbs, shrubs, and trees (e.g., Araucariaceae, Cheirolepidiaceae, Podocarpaceae,
1179 Arecaceae, Cunoniaceae, Ericaceae, Gunneraceae, Liliaceae, Malvaceae, and Proteaceae).
1180
1181 *4.2. Iconic Northern Hemisphere Triprojectacites and Normapolles pollen groups recorded in*
1182 *Patagonia*
1183 **Triprojectacites:** The extinct Triprojectacites pollen complex is largely known since the mid-
1184 20th century when Rouse (1957) described the genus *Aquilapollenites*. This pollen group, also
1185 known as Aquilapolles or Triprojectates (Farabee, 1991), is characterized by a distinctive
1186 morphology consisting of three (occasionally four or five) equatorial projections which exhibit

colpate apertures and endexinous thickenings (Wu and Li, 2022). With more than 300 species in about 39 genera (Wu and Li, 2022), members of the Triprojectacites complex are highly heterogeneous morphologically (e.g., sculpture and body types). Recently Wu and Li (2022) proposed a new generic classification system for Triprojectacites and reduced the number of genera to eight. Triprojectacites is not a natural group but a cluster of morphologically similar pollen grains whose botanical origin remains enigmatic. A wide range of botanical affinities with angiosperms families has been proposed, at least for part of the species, including Santalaceae, Loranthaceae, Olacaceae, Proteaceae, Caprifoliaceae, Apiaceae, Elaeagnaceae, and Surianaceae (Farabee, 1991).

Triprojectacites were recorded from the Turonian in Asia and persisted until the Oligocene in Arctic areas reaching the highest diversity and abundance in the Northern Hemisphere during the Campanian–Maastrichtian. They dominated the palynological assemblages to the extent that this circumboreal region is commonly referred to as the *Aquilapollenites* Palynofloral Province (Farabee, 1993; Herngreen and Chlonova, 1981; Vajda and Bercovici, 2014).

While Triprojectacites were widely distributed in the Late Cretaceous–Paleogene of the Northern Hemisphere (Herngreen et al., 1996; Polette and Batten, 2017; Wu et al., 2022), the records in the Southern Hemisphere, and especially in South America are extremely scarce, including: *Aquilapollenites magnus* Regali et al. from the Maastrichtian of Brazil (e.g., Regali et al., 1974), Bolivia (e.g., Vajda-Santivanez, 1999), and northern Argentina (e.g., Llorens et al., 2022); and *Mtchedlishvilia saltenia* Moroni from the Danian of North and Central Argentina (e.g., Moroni, 1984; Quattrocchio and Volkheimer, 2000; Quattrocchio, 2006; Llorens et al., 2022). *Parviprojectus archangelskyi* sp. nov. from the La Colonia Fm. has the morphological

characters of Triprojectacites members, and it is the southernmost representative of the complex recorded so far.

Interestingly, some authors proposed hypotheses on the paleoecology of some members of the Triprojectacites group. Among them, Srivastava (1973) suggested their preference for marshy or paludal environments while Tekleva et al. (2020) proposed an aquatic or semiaquatic environment for some species. The La Colonia Fm. sediments containing water ferns (e.g., De Benedetti et al., 2021; Hermsen et al., 2019), were probably deposited in a similar scenario of wetland environments.

Normapolles: The Normapolles complex, defined by its characteristic oblate triporate or brevitricolp(or)ate pollen often with elaborate apertural wall structure (Pflug, 1953), was an important and diverse component of many Late Cretaceous and Early Paleocene palynofloras of the Northern Hemisphere mid-latitudes where they constituted the Normapolles Phytogeographic Province. This region extended from eastern and southern North America and Europe to western Siberia and China (e.g., Herngreen et al., 1996; Vajda and Bercovici, 2014). They comprise a heterogeneous polyphyletic group not directly comparable with pollen of any living angiosperms. These plants probably occupied diverse environments and although there are no conclusive botanical affinities for most taxa, some of them are proposed to exhibit morphological similarities with members of the Fagales, Betulaceae, Myricaceae, and Juglandaceae (e.g., Friis et al., 2006; Daly and Jolley, 2015). The Normapolles group first appeared during the Cenomanian, diversified rapidly reaching the acme during the Santonian-Maastrichtian, with new forms appearing during the Paleogene, and becoming extinct by the late Eocene to Oligocene (Friis et al., 2006). The high diversity and frequently constrained stratigraphic ranges of many Normapolles pollen make them good index fossils. The final extinction of the

Normapolles took place later and more gradually than that of the *Aquilapollenites* plants and associates (Batten, 1981).

The Normapolles were abundant and diverse and represented a major proportion of angiosperms in northern mid-latitudes during the Late Cretaceous and early Danian. They are not recorded so far in South America; so, the presence in Patagonia of *Krutzschipollis argentineana* sp. nov., a species morphologically related to the group, represents the first record of the complex in high southern latitudes.

In summary, although the iconic Cretaceous–Paleogene Triprojectacites and Normapolles groups were widely distributed in the Northern Hemisphere they were also found in the Southern Hemisphere. Clearly, their origin and evolution are still unknown but it is possible that the SH members of these groups could have arrived from southern North America to northern South America during the Late Cretaceous and then spread and reached Patagonia where they have sporadic presence or, alternatively, the plants that produced the SH Triprojectacites and Normapolles pollen could have had a completely different origin and evolution patterns from those of the NH.

4.3. K–Pg transition

Patterns of extinction and recovery from the K/Pg mass extinction event have been studied worldwide; however, records of the K–Pg boundary in the SH are scarce (Schulte et al., 2010), resulting in a poor understanding of its effects. U–Pb geochronologic, biostratigraphic, and magnetostratigraphic data indicate that the La Colonia Formation is Maastrichtian to early Danian in age and preserves Chron C29r which is the ~700,000 year-long interval of reversed polarity containing the K–Pg boundary (Clyde et al., 2021). The Cerro Buitre Norte locality

preserves Maastrichtian and Danian deposits providing valuable information on the taxa that crossed the boundary and those that did not.

Remarkably, no significant changes in the diversity and/or abundance of gymnosperm and angiosperm pollen have been recorded between the La Colonia Maastrichtian and Danian palynofloras (Clyde et al., 2021). Most gymnosperm pollen has a wide geographic distribution and has been found in other Mesozoic and Cenozoic deposits in Patagonia. Exceptions are *Classopollis* sp. 1, *Podocarpidites rectangularis*, and *Microcachryidites cesariae*. *Classopollis* sp. 1 and *P. rectangularis* were only recorded in La Colonia Maastrichtian samples. *M. cesariae* has been previously reported from the Early Cretaceous of Argentina (Llorens, 2012; Olivo et al., 2019) and its stratigraphic range is here extended to the Maastrichtian.

Out of the 67 angiosperm pollen taxa 17 of them are restricted to Maastrichtian samples while only one species to Danian samples (i.e., *Dryadopollis* sp. 3, which is a singleton; Table 1). Four of the 17 Maastrichtian taxa (*B. brevis*, *Confertisulcites* sp., *S. exiguus*, and *V. labyrinthus*) have been also recorded in other Paleogene deposits of Patagonia and/or South America, and several others are based on singletons or doubletons (i.e., *Proteacidites* sp. 2, *P.* sp. 3, *Ailanthipites* sp. 1, *Rhoipites* sp., and *Tricolporites* sp.). If all these species are excluded from the analysis the percentage of angiosperms that did not cross the K–Pg boundary locally is approximately 12 %.

Thus, there is no evidence of a mass extinction across the K–Pg boundary in the studied sections, which is consistent with other Patagonian palynological records (e.g., Barreda et al., 2012).

5. Conclusions

In summary, the highly diverse palynoflora of the La Colonia Fm. provides critical evidence for understanding the evolution of Southern Hemisphere floras while the newly described species enhance our knowledge of gymnosperms and angiosperm fossil taxa in Patagonia and worldwide. Within the La Colonia paleopalynoflora, the conifer family Podocarpaceae was the most diverse among the gymnosperms and the monocot family Arecaceae and the eudicot family Proteaceae were the most diverse among the angiosperms. The presence of several ecological markers, such as Araceae, Juncaceae, Typhaceae, and Nelumbonaceae, supports the previous interpretation of a freshwater/brackish environment for the analyzed sequence.

Additionally, evidence presented here indicates the presence of Triprojectacites and Normapolles groups in southernmost latitudes during the Maastrichtian–Danian even though their botanical relationships and origin remain unknown. The comparison between the Maastrichtian and Danian palynofloras of the studied sections of the La Colonia Fm. supports the hypothesis that the effect of the mass extinction event marking the K/Pg boundary was less significant in the southernmost portion of South America than in other parts of Earth.

Data availability

Supplementary photographs for the fossil species described herein are available in a Figshare collection at http.

Acknowledgments

We thank P. Puerta, A. Iglesias, and L. Hermsen for help with field work during the 2010 season when the bulk of the samples were collected, and E. Ruigomez for curatorial work at the MEF. This work is part of FDB's Ph.D. Thesis work completed at Facultad de Ciencias Exactas y

Naturales, Universidad de Buenos Aires, Argentina and it was supported by the National Science Foundation grants DEB-0919071, DEB-0918932, DEB-1556666, DEB-1556136, EAR-1925755, and EAR-1925481 to MAG and Peter Wilf, and an International Association for Plant Taxonomy (IAPT) grant to FDB.

References

Alvarez, L.W., Alvarez W., Asaro, F., Michel, H.V., 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. Science, 208: 1095–108.

Archangelsky, S., 1973. Palinología del Paleoceno de Chubut. I. Descripciones sistemáticas. Ameghiniana, 10: 339–399.

Archangelsky, A., Zamaloa, M., 1986. Nuevas descripciones palinológicas de las formaciones Salamanca y Bororó, Paleoceno de Chubut (República Argentina). Ameghiniana, 23: 35–46.

Ardolino, A., Franchi, M., 1996. Descripción Geológica de la Hoja 4366-I Telsen. Provincia del Chubut. Dirección Nacional del Servicio Geológico. Boletín 215. Buenos Aires.

Baldoni, A.M., Askin, R.A., 1993. Palynology of the lower Lefipán Formation (Upper Cretaceous) of Barranca de Los Perros, Chubut Province, Argentina part II. Angiosperm pollen and discussion. Palynology, 17: 241–264.

Bambach, R.K., 2006. Phanerozoic biodiversity mass extinctions. Annual Review of Earth and Planetary Sciences, 34: 127–155.

Barreda, V.D., 1997. Palynomorph assemblage of the Chenque Formation, Late Oligocene?-Miocene from Golfo San Jorge basin, Patagonia, Argentina. Part 3. Polycolpate and tricolporate pollen. Ameghiniana, 34: 131–144.

Barreda, V.D., Cúneo, N.R., Wilf, P., Currano, E.D., Scasso, R.A., Brinkhuis, H., 2012. Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low extinction, and a *Classopollis* spike. PLoS One, 7(12): e52455.

Batten, D.J., 1981. Stratigraphic, palaeogeographic and evolutionary significance of late Cretaceous and early Tertiary Normapolles pollen. Review of Palaeobotany and Palynology, 35: 125–137.

Bercovici, A., Pearson, D., Nichols, D., Wood, J., 2009. Biostratigraphy of selected K/T boundary sections in southwestern North Dakota, USA: toward a refinement of palynological identification criteria. Cretaceous Research, 30: 632–658.

Braman, D.R., 2001. Terrestrial palynomorphs of the upper Santonian–? lowest Campanian Milk River Formation, southern Alberta, Canada. Palynology, 25: 57–107.

Braman, D.R., 2013. Triprojectate pollen occurrence in the western Canada sedimentary basin and the group's global relationships. Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta.

Braman, D.R., 2018. Terrestrial palynostratigraphy of the Upper Cretaceous (Santonian) to lowermost Paleocene of southern Alberta, Canada. Palynology, 42: 102–147.

Chao, C.T., Krueger, R.R., 2007. The date palm (*Phoenix dactylifera* L.): overview of biology, uses, and cultivation. HortScience, 42: 1077–1082.

Clyde, W.C., Krause, J.M., De Benedetti, F., Ramezani, J., Cúneo, N.R., Gandolfo, M.A., Smith, T., 2021. New South American record of the Cretaceous–Paleogene boundary interval (La Colonia Formation, Patagonia, Argentina). Cretaceous Research, 126: 104889.

Cole, J.M., Abdelrahim, O.B., Hunter, A.W., Schrank, E., Ismail, M.S.B., 2017. Late Cretaceous spore-pollen zonation of the Central African Rift System (CARS), Kaikang Trough, Muglad

1345 Basin, South Sudan: angiosperm spread and links to the Elaterates Province. Palynology, 41:
1346 547–578.
1347 Collinson, M.E., 1993. Taphonomy and fruiting biology of recent and fossil *Nypa*. Studies in
1348 Palaeobotany and Palynology in Honour of Professor W.G. Chaloner, F.R.S. The
1349 Palaeontological Association. Special Papers in Palaeontology, 49: 165–180.
1350 Cookson, I., 1950. Fossil pollen grains of proteaceous type from Tertiary deposits in Australia.
1351 Australian Journal of Biological Sciences, 3: 166–177.
1352 Couper, R.A., 1953. Upper Mesozoic and Cainozoic spores and pollen grains from New Zealand.
1353 New Zealand Geological Survey, Paleontological Bulletin, 22: 77 p.
1354 Couper, R.A., 1954. Plant microfossils from New Zealand No. 1. Transactions of the Royal
1355 Society of New Zealand, 81: 479–483.
1356 Couper, R.A., 1960. New Zealand Mesozoic and Cainozoic plant microfossils. New Zealand
1357 Geological Survey, Paleontological Bulletin, 32: 87 p.
1358 Cúneo, N.R., Hermsen, E.J., Gandolfo, M.A., 2013. *Regnellidium* (Salviniales, Marsileaceae)
1359 macrofossils and associated spores from the Late Cretaceous of South America. International
1360 Journal of Plant Sciences, 174: 340–349.
1361 Cúneo, N.R., Gandolfo, M.A., Zamaloa, M.C., Hermsen, E.J., 2014. Late Cretaceous Aquatic
1362 Plant World in Patagonia, Argentina. PLoS ONE, 9(8): e104749.
1363 Cúneo, N.R., Andruchow-Colombo, A., De Benedetti, F., Gandolfo, M.A., 2021. D.13.
1364 Megafloras de las Formaciones La Colonia y Lefipán, Cretácico Superior de Chubut. In:
1365 Giacosa, R.E. (Ed.), XXI Congreso Geológico Argentino. Geología y recursos naturales de la
1366 provincia del Chubut. Puerto Madryn, pp. 261–272.

1367 Daly, R.J., Jolley, D.W., 2015. What was the nature and role of Normapolles angiosperms? A
1368 case study from the earliest Cenozoic of Eastern Europe. Palaeogeography, Palaeoclimatology,
1369 Palaeoecology, 418: 141–149.
1370 D'Apolito, C., Jaramillo, C., Harrington, G., 2021. Miocene palynology of the Solimões
1371 Formation (well 1-AS-105-AM), western Brazilian Amazonia. Smithsonian Contributions to
1372 Paleobiology, 105: 1–134.
1373 da Silva-Caminha, S.A., Jaramillo, C.A., Absy, M.L., 2010. Neogene palynology of the
1374 Solimões basin, Brazilian Amazonia. Palaeontographica Abteilung B, 284: 13–79.
1375 De Benedetti, F., Zamaloa, M.C., Gandolfo, M.A., Cúneo, N.R., 2018. Heterosporous ferns from
1376 Patagonia: the case of *Azolla*. In: Krings, M., Harper, C.J., Cúneo, N.R., Rothwell, G.W. (Eds.),
1377 Transformative Paleobotany. Academic Press, London, pp. 361–373.
1378 De Benedetti, F., Zamaloa, M.C., Gandolfo, M.A., Cúneo, N.R., 2020. Reinterpretation of
1379 *Paleoazolla*: a heterosporous water fern from the Late Cretaceous of Patagonia, Argentina.
1380 American Journal of Botany, 107: 1054–1071.
1381 De Benedetti, F., Zamaloa, M.C., Gandolfo, M.A., Cúneo, N.R., 2021. Water fern spores
1382 (Salviniales) from the Late Cretaceous of Patagonia, Argentina. Review of Palaeobotany and
1383 Palynology, 290: 104428.
1384 De Lima, M.R., 1989. Palinología da Formação Santana (Cretáceo do nordeste do Brasil). IV-
1385 descrição sistemática dos polens das turmas plicates e poroses, esporos, incertae sedis e
1386 microplancton marinho. Ameghiniana, 26: 63–81.
1387 Doyle, J.A., Van Campo, M., Lugardon, B., 1975. Observations on exine structure of
1388 *Eucommiidites* and Lower Cretaceous angiosperm pollen. Pollen et Spores, 17: 429–486.

1389 Farabee, M.J., 1991. Botanical affinities of some Triprojectacites fossil pollen. American Journal
1390 of Botany, 78: 1172–1181.
1391 Farabee, M.J., 1993. Morphology of triprojectate fossil pollen: form and distribution in space and
1392 time. The Botanical Review, 59: 211–249.
1393 Finkelstein, S.A., 2003. Identifying pollen grains of *Typha latifolia*, *Typha angustifolia*, and
1394 *Typha* x *glauca*. Canadian Journal of Botany, 81: 985–90.
1395 Frederiksen, N.O., 1983. Middle Eocene palynomorphs from San Diego, California. American
1396 Association of Stratigraphic Palynologists Foundation, Contribution Series 12: 155 p.
1397 Frederiksen, N.O., 1994. Middle and late Paleocene angiosperm pollen from Pakistan.
1398 Palynology, 18: 91–137.
1399 Freile, C., 1972. Estudio palinológico de la Formación Cerro Dorotea (Maestrichtiano-
1400 Paleoceno) de la Provincia de Santa Cruz. I. Revista del Museo de la Plata, 6: 39–63.
1401 Friis, E.M., Pedersen, K.R., Schönenberger, J., 2006. Normapolles plants: a prominent
1402 component of the Cretaceous rosid diversification. Plant Systematics and Evolution, 260: 107–
1403 140.
1404 Gallego, J., Gandolfo, M.A., Cúneo, N.R., Zamaloa, M.C., 2014. Fossil Araceae from the Late
1405 Cretaceous of Patagonia, Argentina, with implications on the origin of free-floating aquatic
1406 aroids. Review of Palaeobotany and Palynology, 211: 78–86.
1407 Gandolfo, M.A., Cúneo, N.R., 2005. Fossil Nelumbonaceae from the La Colonia Formation
1408 (Campanian-Maastrichtian, Upper Cretaceous), Chubut, Patagonia, Argentina. Review of
1409 Palaeobotany and Palynology, 133: 169–178.

1410 Gandolfo, M.A., Zamaloa, M.C., Cúneo, N.R., Archangelsky, A., 2009. Potamogetonaceae fossil
1411 fruits from the Tertiary of Patagonia, Argentina. International Journal of Plant Sciences, 170:
1412 419–428.
1413 Gandolfo, M.A., Cúneo, N.R., Hermsen, E.J., 2014. Reporte preliminar sobre la paleoflora de la
1414 Formación La Colonia (Campaniano-Maastrichtiano, Cretácico tardío), Chubut, Patagonia,
1415 Argentina. Boletín de la Sociedad Geológica Mexicana, 66: 11–23.
1416 Gee, C.T., 2001. The mangrove palm *Nypa* in the geologic past of the New World. Wetlands
1417 Ecology and Management, 9: 181–194.
1418 Góczán, F., Groot, J.J., Krutzsch,W., Pacltová, B., 1967. Die Gattungen des "Stemma
1419 Normapolles Pflug 1953b" (Angiospermae) – Neubeschreibungen und Revision europäischer
1420 Formen (Oberkreide bis Eozän). Paläontologische Abhandlungen, Abt. B., 2: 427–633.
1421 González Guzmán, A., 1967. A palynological study on the upper Los Cuervos and Mirador
1422 formations. (Lower and Middle Eocene; Tibú area, Colombia). Leiden E.J. Brill, 129 p.
1423 Grímsson, F., Bouchal, J. M., Xafis, A., Zetter, R., 2020. Combined LM and SEM study of the
1424 middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: part V.
1425 Magnoliophyta 3–Myrtales to Ericales. Grana, 59: 127–193.
1426 Guimarães, J.T.F., Nogueira, A.C.R., 2015. Palynology of the Middle Miocene—Pliocene Novo
1427 Remanso Formation, Central Amazonia, Brazil. Ameghiniana, 52: 107–134.
1428 Guler, M.V., Borel, C.M., Brinkhuis, H., Navarro, E., Astini, R., 2014. Brackish to freshwater
1429 dinoflagellate cyst assemblages from the La Colonia Formation (Paleocene), Northeastern
1430 Patagonia, Argentina. Ameghiniana 51: 141–153.
1431 Halbritter, H., Berger, A., 2018. *Juncus triglumis*. In: PalDat - A palynological database.
1432 https://www.paldat.org/pub/Juncus_triglumis/303335; accessed 2023-05-31

1433 Harris, W.K., 1965. Basal Tertiary microfloras from the Princetown area, Victoria, Australia.
1434 Palaeontographica Abteilung B., 115: 75–106.
1435 Harris, W.K., 1972. New form species of pollen from southern Australian early Tertiary
1436 sediments. Royal Society of South Australia Transactions, pp. 53–65.
1437 Hermsen, E.J., Jud, N.A., De Benedetti, F., Gandolfo, M.A., 2019. *Azolla* Sporophytes and
1438 Spores from the Late Cretaceous and Paleocene of Patagonia, Argentina. International Journal of
1439 Plant Sciences, 180: 737–754.
1440 Herngreen, G.F.W., 1975. Upper Senonian pollen assemblage of borehole 3-Pia-10-Al state of
1441 Alagoas, Brazil. Pollen et Spores, 17: 93–140.
1442 Herngreen, G.F.W., Chlonova, A.F., 1981. Cretaceous microfloral provinces. Pollen et Spores,
1443 23: 441–555.
1444 Herngreen, G.F.W., Kedves, M., Rovnina, L.V., Smirnova, S.B., 1996. Chapter 29C –
1445 Cretaceous palynofloral provinces: a review. In: Jansonius, J., McGregor, D.C.
1446 (Eds.), Palynology: principles and applications. American Association of Stratigraphic
1447 Palynologists Foundation, Vol 3, pp. 1157–1188.
1448 Hofmann, C.C., 2018. Light and scanning electron microscopic investigations of pollen of
1449 Ericales (Ericaceae, Sapotaceae, Ebenaceae, Styracaceae and Theaceae) from five lower and
1450 mid-Eocene localities. Botanical Journal of the Linnean Society, 187: 550–578.
1451 Huang, T.C., 1980. Miocene Palynomorphs of Taiwam (V)-Angiosperm Grains. Taiwania, 25:
1452 57–103.
1453 Hull, P.M., Bornemann, A., Penman, D.E., Henehan, M.J., Norris, R.D., Wilson, P.A., et al.,
1454 2020. On impact and volcanism across the Cretaceous-Paleogene boundary. Science, 367: 266–
1455 272.

1456 Ibrahim, M.I., 2002. New angiosperm pollen from the upper Barremian–Aptian of the Western
1457 Desert, Egypt. Palynology, 26: 107–133.
1458 Jameossanaie, A., 1987. Palynology and age of South Hospah coal-bearing deposits, McKinley
1459 County, New Mexico. New Mexico Bureau of Mines & Mineral Resources, Bulletin 112: 66 p.
1460 Jan du Chêne, R.E., Klasz, I., Archibong, E.E., 1978. Biostratigraphic study of the borehole
1461 OJO-1, SW Nigeria, with special emphasis on the Cretaceous microflora. Revue de
1462 Micropaleontologie, 21: 123–139.
1463 Jardiné, S., Magloire, L., 1965. Palynologie et stratigraphie du Crétacé des bassins du Sénégal et
1464 de Côte d'Ivoire. Mémoires du Bureau de Recherches Géologiques et Miniéres, 32: 187–245.
1465 Kaulfuss, U., Bannister, J.M., Conran, J.G., Kennedy, E.M., Mildenhall, D.C., Lee, D.E., 2023.
1466 Review of flowers and inflorescences with in situ pollen from the Miocene Foulden and Hindon
1467 Konservat-Lagerstätten, southern New Zealand. Review of Palaeobotany and Palynology, 311:
1468 104830.
1469 Kar, R., Jain, K., 1978. Palynology of Neogene sediments around Quilon and Varkala, Kerala
1470 Coast, South India - 2. Spores and pollen grains. Journal of Palaeosciences, 27: 113–131.
1471 Kedves, M., 1978. Paleogene fossil sporomorphs of the Bakony Mountains. Part III. Studia
1472 Biologica Academiae Scientiarum Hungaricae 15. Akadémiai Kiadó, Budapest, 134 pp.
1473 Kedves, M., 1999. Upper Cretaceous pollen grains from Egypt III. Plant Cell Biology and
1474 Development, 10, 14–29.
1475 Kemp, E.M., Harris, W.K., 1977. The palynology of early Tertiary sediments, Ninetyeast Ridge,
1476 Indian Ocean. The Palaeontological Association, London. Special Papers in Palaeontology, 19:
1477 70 p.

1478 Kuprianova, L.A., Tarasevich, V.F., 1983. Pollen morphology of recent and fossil species of the
1479 genus *Nelumbo* (Nelumbonaceae). Botanicheskii Zhurnal, 68: 137–146.
1480 Krutzsch, W., 1970. Atlas der mittel- und jungtertiären dispersen Sporen- und Pollen- sowie der
1481 Mikroplanktonformen des nördlichen Mitteleuropas: Monoporate, monocolpate, longicolpate,
1482 dicolpate und ephedroide (polyplicate) Pollenformen. Vol VII. VEB Gustav Fischer Verlag Jena,
1483 Berlin.
1484 Krutzsch, W., Vanhoorne, R., 1977. Die pollenflora von Epinois und Loksbergen in Belgien.
1485 Palaeontographica Abteilung B., 163: 1–110.
1486 Lee, D.E., Bannister, J.M., Raine, J.I., Conran, J.G., 2010. Euphorbiaceae: Acalyphoideae fossils
1487 from early Miocene New Zealand: Mallotus–Macaranga leaves, fruits, and inflorescence with in
1488 situ *Nyssapollenites endobalteus* pollen. Review of Palaeobotany and Palynology, 163: 127–138.
1489 Leffingwell, H.A., 1970. Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene)
1490 Formations of the type Lance area, Wyoming. In: Kosanke, R.M., Cross, A.T. (Eds.),
1491 Symposium on Palynology of the Late Cretaceous and Early Tertiary. The Geological Society of
1492 America, Special Papers, 127: 64 p.
1493 Lenz, O., Diekmeier, S., Wilde, V., 2020. *Nypa* pollen diversity in middle Eocene mangroves at
1494 the edge of the southern Proto-North Sea (Helmstedt, northern Germany) – a statistical approach.
1495 Grana, 60: 97–118.
1496 Li, J., Batten, D.J., Zhang, Y., 2011. Palynological record from a composite core through Late
1497 Cretaceous–early Paleocene deposits in the Songliao Basin, Northeast China and its
1498 biostratigraphic implications. Cretaceous Research, 32: 1–12.

1499 Li, Y., Svetlana, P., Yao, J., Li, C., 2014. A review on the taxonomic, evolutionary and
1500 phytogeographic studies of the lotus plant (Nelumbonaceae: *Nelumbo*). Acta Geologica Sinica
1501 (English Edition), 88: 1252–1261.
1502 Llorens, M., Pérez Loinaze, V.S., Narváez, P.L., Zelaya, A.M., Pincheira, E.P., Gorustovich, S.,
1503 2022. A mid-latitude Maastrichtian palynological record from the Yacoraite Formation (Salta
1504 Group), northwestern Argentina. Cretaceous Research, 140: 105332.
1505 Lu, L., Fritsch, P.W., Wang, H., Li, H.T., Li, D.Z., Chen, J.Q., 2009. Pollen morphology of
1506 *Gaultheria* L. and related genera of subfamily Vaccinioideae: Taxonomic and evolutionary
1507 significance. Review of Palaeobotany and Palynology, 154: 106–123.
1508 Luteyn, J.L., 2002. Diversity, adaptation, and endemism in neotropical Ericaceae:
1509 biogeographical patterns in the Vaccinieae. The Botanical Review, 68: 55–87.
1510 Martin, H.A., 1973. The palynology of some Tertiary and Pleistocene deposits, Lachlan River
1511 Valley, New South Wales. Australian Journal of Botany Supplementary Series, 3: 1–57.
1512 Martínez, L.C., Archangelsky, S., Prámparo, M.B., Archangelsky, A., 2016. Early Cretaceous
1513 palm pollen tetrads from Patagonia, Argentina. Cretaceous Research, 59: 129–139.
1514 Mautino, L.R., Anzótegui, L.M., 2002. Palinología de la Formación Chiquimil (Mioceno
1515 Superior), en Río Vallecito, provincia de Catamarca, Argentina. Parte 2. Polen. Ameghiniana,
1516 39: 271–284.
1517 Mautino, L.R., Anzótegui, L.M., 2014. Novedades palinológicas de las formaciones San José y
1518 Chiquimil (Mioceno medio y tardío), noroeste de Argentina. Revista del Museo Argentino de
1519 Ciencias Naturales, 16: 143–164.
1520 McIntyre, D.J., 1968. Further new pollen species from New Zealand Tertiary and uppermost
1521 Cretaceous deposits. New Zealand Journal of Botany, 6: 177–204.

1522 Mildenhall, D.C., Pocknall, D.T., 1989. Miocene-Pleistocene spores and pollen from Central
1523 Otago, South Island, New Zealand. New Zealand Geological Survey Paleontological, Bulletin,
1524 59: 128 p.
1525 Mildenhall, D., Conran, J., Kennedy, E., Lee, D., Bannister, J., Lindqvist, J., Ferguson, D., 2018.
1526 Palynology of the late Oligocene-early Miocene Newvale Mine, Gore Lignite Measures,
1527 Southland, New Zealand. Palaeontographica Abteilung B., 298: 23–91.
1528 Milne, L.A., 1988. Palynology of a late Eocene lignitic sequence from the western margin of the
1529 Eucla Basin, Western Australia. Association of the Australasian Palaeontologists Memoir, 5:
1530 285–310.
1531 Moroni, A.M., 1984. *Mchedlishvilia saltenia* n. sp. en sedimentitas del Grupo Salta, Provincia de
1532 Salta. III Congreso Argentino de Paleontología y Bioestratigrafía, Corrientes, 1982, pp. 129–140.
1533 Mtchedlishvili, N., 1961. Triprojectacites. In: Samoilovitch, S., Mtchedlishvili, N. (Eds.), Spores
1534 and Pollen of West Siberia, the JurassicePaleogene. Trudy Vsesojuzn. Neft. Issl. Geological
1535 Rass. Institute, Leningrad, pp. 203–230.
1536 Muller, J., 1968. Palynology of the Pedawan and plateau sandstone formations (Cretaceous-
1537 Eocene) in Sarawak, Malaysia. Micropaleontology, 14: 1–37.
1538 Muller, J., de Di Giacomo, E., Van Erve, A.W., 1987. A palynological zonation for the
1539 Cretaceous, Tertiary and Quaternary of northern South America. American Association of
1540 Stratigraphic Palynologists, Contribution Series, 19: 7–76.
1541 Náñez, C., Malumián, N., 2008. Paleobiogeografía y paleogeografía del Maastrichtiense marino
1542 de la Patagonia, Tierra del Fuego y la Plataforma Continental Argentina, según sus foraminíferos
1543 bentónicos. Revista Española de Paleontología, 23: 273–300.

1544 Narváez, P.L., Sabino, I.F., 2008. Palinología de la Formación Las Curtiembres (Cretácico
1545 Tardío, Cuenca del Grupo Salta), área de la quebrada Las Conchas, noroeste argentino.
1546 Ameghiniana, 45: 473–482.
1547 Nichols, D.J., 2010. Reevaluation of the holotypes of the Wodehouse pollen species from the
1548 Green River Formation (Eocene, Colorado and Utah). American Association of Stratigraphic
1549 Palynologists Foundation, Contribution Series 44: 97 p.
1550 Nichols, D.J., Jarzen, D.M., Orth, C.J., Oliver, P.Q., 1986. Palynological and iridium anomalies
1551 at Cretaceous-Tertiary boundary, south-central Saskatchewan. Science, 231: 714–717.
1552 Nixon, K.C., Crepet, W.L., 1993. Late Cretaceous fossil flowers of ericalean affinity. American
1553 Journal of Botany, 80: 616–623.
1554 Page, R., Ardolino, A., de Barrio, R.E., Franchi, M., Lizuain, A., Page, S., Silva Nieto, D., 1999.
1555 Estratigrafía del Jurásico y Cretácico del Macizo de Somún Curá, provincias de Río Negro y
1556 Chubut. In: Caminos R. (Ed.), Geología Regional Argentina, Servicio Geológico Minero
1557 Argentino. Instituto de Geología y Recursos Minerales, Buenos Aires. Anales 29, pp. 460–488.
1558 Palynodata Inc., White, J.M., 2006. Palynodata Datafile: 2006 version, with Introduction by J.M.
1559 White. Geological Survey of Canada Open File 5793, 1 CD-ROM.
1560 Papú, O.H., 2006. Estudio Paleopalinológico de Sedimentitas Campanianas-Maastrichtianas
1561 (Formación Loncoche, equivalentes laterales de la Formación Jagüel y Formación Roca,
1562 Cretácico superior) en el Sur de Mendoza, Argentina. Bioestratigrafía, Paleoambientes,
1563 Paleoclimas y Paleobiogeografía. Ph.D. Thesis. Universidad Nacional de Cuyo, Mendoza,
1564 Argentina. Unpublished.

1565 Parmar, S., Morley, R.J., Bansal, M., Singh, B.P., Morley, H., Prasad, V., 2023. Evolution of
1566 family Arecaceae on the Indian Plate modulated by the Early Palaeogene climate and tectonics.
1567 Review of Palaeobotany and Palynology, 313: 104890.
1568 Passarini Lopes, F., Oriani, A., Coan, A.I., 2021. Development of the permanent tetrad wall in
1569 *Juncus* L. (Juncaceae, Poales). Protoplasma, 258: 495–506.
1570 Penny, J.H.J., 1986. An Early Cretaceous angiosperm pollen assemblage from Egypt. Special
1571 Papers in Palaeontology, 35: 121–134.
1572 Pflug, H.D., 1953. Zur Entstehung und Entwicklung des angiospermiden Pollen in der
1573 Erdgeschichte. Palaeontographica Abteilung B., 95: 60–171.
1574 Pocknall, D.T., Mildenhall, D.C., 1984. Late Oligocene-early Miocene spores and pollen from
1575 Southland, New Zealand. New Zealand Geological Survey Paleontological Bulletin, 51: 1–66.
1576 Pocknall, D.T., Nichols, D.J., 1996. Palynology of coal zones of the Tongue River Member
1577 (upper Paleocene) of the Fort Union Formation, Powder River Basin, Montana and Wyoming.
1578 American Association of Stratigraphic Palynologists Foundation, Contribution Series, 32: 1–57.
1579 Polette, F., Batten, D.J., 2017. Fundamental reassessment of the taxonomy of five Normapolles
1580 pollen genera. Review of Palaeobotany and Palynology,243: 47–91.
1581 Prasad, B., Pundeer, B.S., 2002. Palynological events and zones in Cretaceous-Tertiary
1582 Boundary sediments of Krishna-Godavari and Cauvery basins, India. Palaeontographica
1583 Abteilung B., 262: 39–70.
1584 Quattrocchio, M.E., 2006. Palynology and palaeocommunities of the Paleogene of Argentina.
1585 Revista Brasileira de Paleontologia, 9: 101–108.
1586 Quattrocchio, M.E., Volkheimer, W., 2000. Danian microfloral provinces in Argentina. Spanish
1587 Journal of Palaeontology, 15: 3–11.

1588 Ramanujam, C.G.K., 1966. Palynology of the Miocene lignite from south Arcot district, Madras,
1589 India. Pollen Spores, 8: 149–203.
1590 Rao, K., Ramanujam, C., 1976. Palynology of the Neogene Quilon beds of Kerala state in South
1591 India I - Spores of pteridophytes and pollen of monocotyledons. Journal of Palaeosciences, 25:
1592 397–427.
1593 Raup, D.M., Sepkoski Jr, J.J., 1982. Mass extinctions in the marine fossil record. Science, 215:
1594 1501–1503.
1595 Regali, M.S.P., Uesugui, N., Santos, A.S., 1974. Palinologia dos sedimentos Meso-Cenozoicos
1596 do Brasil (II). Boletim Técnico da Petrobrás, 17: 263–301.
1597 Reyre, Y., 1970. Stereoscan observations on the pollen genus *Classopollis* Pflug 1953.
1598 Palaeontology, 13: 303–322.
1599 Roche, É., 1968. Espèces nouvelles de spores et pollens du Landénien supérieur de Belgique
1600 (Sondage de Kallo). Bulletin de la Société Belge de Géologie, de Paléontologie et d'Hydrologie,
1601 76: 145–165.
1602 Romero, E.J., 1977. Polen de gimnospermas y fagáceas de la formación Río Turbio (Eoceno),
1603 Santa Cruz, Argentina. Ph.D. Thesis, Universidad Nacional de La Plata.
1604 Rouse, G.E., 1957. The application of a new nomenclatural approach to Upper Cretaceous plant
1605 microfossils from western Canada. Canadian Journal of Botany, 35: 349–375.
1606 Sacomani, L.E., Panza, J.L.A., Parisi, C., Pezzuchi, H.D., Ardolino, A.A., 2007. Hoja Geológica
1607 4366-III. Las Plumas. Servicio Geológico Minero Argentino. Instituto de Geología y Recursos
1608 Minerales. Buenos Aires. Boletín 291: 74 p.

1609 Samant, B., Puranik, S., Kapgate, D.K., Mohabey, D.M., Dhobale, A., 2022. Palynoflora from an
1610 Upper Cretaceous freshwater paleolake in central India: paleoecological implications. Cretaceous
1611 Research, 139: 105302.
1612 Santamarina, P.E., Barreda, V.D., Iglesias, A., Varela, A.N., 2020. Palynology from the
1613 Cenomanian Mata Amarilla Formation, southern Patagonia, Argentina. Cretaceous Research,
1614 109: 104354.
1615 Sarmiento Perez, G., 1992. Palinología de la Formación Guaduas. Estratigráfica y Sistemática.
1616 Boletín Geológico, 32: 45–126.
1617 Scasso, R.A., Aberhan, M., Ruiz, L., Weidemeyer, S., Medina, F.A., Kiessling, W., 2012.
1618 Integrated bio-and lithofacies analysis of coarse-grained, tide-dominated deltaic environments
1619 across the Cretaceous/Paleogene boundary in Patagonia, Argentina. Cretaceous Research, 36:
1620 37–57.
1621 Schrank, E., 1987. Biostratigraphic importance of microfloras from the Late Cretaceous clastic
1622 series of northwestern Sudan. Cretaceous Research, 8: 29–42.
1623 Schrank, E., Ibrahim, M.I.A., 1995. Cretaceous (Aptian-Maastrichtian) palynology of
1624 foraminifera-dated wells (KRM-1, AG-18) in northwestern Egypt. Berliner Geowissenschafliche
1625 Abhandlungen (A), 177: 44 p.
1626 Schoene, B., Eddy, M.P., Samperton, K.M., Keller, C.B., Keller, G., Adatte, T., Khadri, S.F.,
1627 2019. U-Pb constraints on pulsed eruption of the Deccan Traps across the end-Cretaceous mass
1628 extinction. Science, 363: 862–866.
1629 Schulte, P., Alegret, L., Arenillas, I., Arz, J.A., Barton, P.J., Bown, P.R., et al., 2010. The
1630 Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary. Science,
1631 327: 1214–1218.

1632 Simoncsics, P., 1969. Sporen-, Pollen-und Moortypen aus dem Miozänen Braunkohlengebiet
1633 von Nógrád I. Acta Biologica Szeged, 15: 37–49.
1634 Shih, J.G., Finkelstein, S.A., 2008. Range dynamics and invasive tendencies in *Typha latifolia*
1635 and *Typha angustifolia* in eastern North America derived from herbarium and pollen records.
1636 Wetlands, 28: 1–16.
1637 Singh, C., 1983. Cenomanian microfloras of the Peace River area, northwestern Alberta. Alberta
1638 Research Council, Bulletin 44: 332 p.
1639 Singh, R.S., 1999. Diversity of *Nypa* in the Indian subcontinent: Late Cretaceous to recent.
1640 Journal of Palaeosciences, 48: 147–154.
1641 Srivastava, S.K., 1969. Some angiosperm pollen from the Edmonton Formation (Maestrichtian),
1642 Alberta, Canada. In: Santapau H., et al. (Eds.), J. Sen Memorial Volume, J. Sen Memorial
1643 Committee and Botanical Society of Bengal, Calcutta, p. 47–67.
1644 Srivastava, S.K., 1972. Taxonomic notes on pollen genera *Callistopollenites*, *Tricolporites*, and
1645 *Carpinipites*. Canadian Journal of Botany, 50: 9–12.
1646 Srivastava, S.K., 1973. Paleoecology of pollen genera *Aquilapollenites* and *Mancicorpus* in
1647 Maestrichtian deposits of North America. 24th International Geological Congress, Section 7,
1648 Paleontology, Montreal, p. 111–120.
1649 Srivastava, S.K., 1976. The fossil pollen genus *Classopollis*. Lethaia, 9: 437–457.
1650 Stover, L.E., Partridge, A.D., 1973. Tertiary and Late Cretaceous spores and pollen from the
1651 Gippsland Basin, southeastern Australia. Proceedings of the Royal Society of Victoria, 85: 237–
1652 286.
1653 Stover, L.E., Partridge, A.D., 1982. Eocene spore- pollen from the Werillup Formation, Western
1654 Australia. Palynology, 6: 69–96.

1655 Stevens, P.F., Luteyn, J., Oliver, E.G.H., Bell, T.L., Brown, E.A., Crowden, R.K., et al., 2004.
1656 Ericaceae. In: Kubitzki, K. (Ed.). The Families and Genera of Vascular Plants, Springer-Verlag,
1657 Berlin, Vol. 6: 145–194.
1658 Takahashi, K., 1961. Pollen und Sporen des westjapanischen Alttertiärs und Miozäns: Ⅱ. Teil.
1659 Memoirs of the Faculty of Science, Kyushu University, Series D., Geology, 11: 279–345.
1660 Takahashi, K., 1984. Stratigraphic significance of three important pollen groups in the late Upper
1661 Cretaceous and Early Paleogene. Japanese Journal of Palynology, 30: 15–24.
1662 Tekleva, M., Polevova, S., Bugdaeva, E., Markevich, V., Sun, G., 2020. Three *Aquilapollenites*
1663 species from the late Maastrichtian of China: New data and comparisons. Review of
1664 Palaeobotany and Palynology, 282: 104288.
1665 Thiele-Pfeiffer, H., 1980. Die Miozäne mikroflora aus dem Braunkohlentagebau oder bei
1666 Wackersdorf/Oberpfalz. Paläeontographica Abteilung B., 174: 95–224.
1667 Thiergart, F., 1937. Die Pollenflora der Niederlausitzer Braunkohle, besonders im Profil der
1668 Grube Marga bei Senftenberg. Jahrbuch Preuss. Geologischen Landesanstalt, 58: 282–356.
1669 Thomson, P.W., Pflug, H., 1953. Pollen und Sporen des mitteleuropaischen Tertiars.
1670 Palaeonographica Abteilung B., 94: 1–138.
1671 Traverse, A., 2007. Paleopalynology. 2nd ed. Springer Science & Business Media, Pennsylvania,
1672 813 pp.
1673 Tschudy, B.D., 1973. Palynology of the Upper Campanian (Cretaceous) Judith River Formation,
1674 North-Central Montana. United States Government Printing Office, Washington, Geological
1675 Survey Professional Paper, 770.
1676 Vajda-Santivanez, V., 1999. Miospores from Upper Cretaceous-Paleocene strata in northwestern
1677 Bolivia. Palynology, 23, 181–196.

Vajda, V., Bercovici, A., 2014. The global vegetation pattern across the Cretaceous–Paleogene mass extinction interval: A template for other extinction events. Global and Planetary Change, 122: 29–49.

Vallati, P., Casal, G., Foix, N., Allard, J., Tomas, A.D.S., Calo, M., 2016. First report of a Maastrichtian palynoflora from the Golfo San Jorge Basin, central Patagonia, Argentina. Ameghiniana, 53: 495–505.

Vallati, P., Tomas, A.D.S., Casal, G., 2020. A Maastrichtian terrestrial palaeoenvironment close to the K/Pg boundary in the Golfo San Jorge basin, Patagonia, Argentina. Journal of South American Earth Sciences, 97: 102401.

Van der Hammen, T., Wymstra, T.A., 1964. A palynological study on the Tertiary and Upper Cretaceous of British Guiana. Leidse Geologische Mededelingen, 30: 183–241.

Villar de Seoane, L.M., 2014. Estudio morfológico del género *Classopollis* (Pflug) Pocock & Jansonius (Cretácico, Argentina). Revista Brasileira de Paleontología, 17: 91–104.

Wanntorp, L., Vajda, V., Raine, J.I., 2011. Past diversity of Proteaceae on subantarctic Campbell Island, a remote outpost of Gondwana. Cretaceous Research, 32: 357–367.

Ward, J.V., 1986. Early Cretaceous angiosperm pollen from the Cheyenne and Kiowa formations (Albian) of Kansas, USA. Palaeontographica Abteilung B., 202: 1–81.

Williamson, P.S., Schneider, E.L., 1993. Nelumbonaceae. In: Kubitzki, K. (Ed.). The Families and Genera of Vascular Plants. Springer-Verlag, Berlin, Vol. 2: 470–473.

Wodehouse, R.P., 1933. Tertiary pollen-II The oil shales of the Eocene Green River formation. Bulletin of the Torrey Botanical Club, 60: 479–524.

Wu, Y., Li, J., 2022. Genus classification of Triprojectacites Mtchedlishvili, 1961 emend. Stanley 1970. Grana, 61: 161–181.

Wu, Y., Li, J., Lin, M., Koppelhus, E., 2022. Triprojectacites in the Songliao Basin, Northeast China: Systematics, biostratigraphy and evolution. Cretaceous Research, 135: 105193.

Zamaloa, M.C., Andreis, R.R., 1995. Asociación palinológica del Paleoceno temprano (Formación Salamanca) en Ea. Laguna Manantiales, Santa Cruz, Argentina. 4° Congreso Argentino Paleontología y Bioestratigrafía. Trelew, Chubut, Argentina, 6: 301–305.

Zavialova, N., Buratti, N., Roghi, G., 2010. The ultrastructure of some Rhaetian Circumpolles from southern England. Grana, 49: 281–299.

Ziembinska-Tworzydlo, M., 1974. Palynological characteristics of the Neogene of Western Poland. Acta Palaeontologica Polonica, 19: 309–432.

Ziembińska-Tworzydło, M., Grabowska, I., Kohlman-Adamska, A., Skawińska, K., Słodkowska, B., Stuchlik, L., Sadowska, A., Ważyńska, H., 1994. Taxonomical revision of selected pollen and spores taxa from Neogene deposits. Acta Palaeobotanica, Supplementum, 1: 5–30.

Figure 1. Geologic map showing the studied area where the La Colonia Formation outcrops, in the vicinity of the El Buitre Hill and Mirasol Chico Creek, Chubut Province, Patagonia, Argentina (modified from Clyde et al., 2021).

Table 1. Gymnosperm and angiosperm pollen recovered from the La Colonia Formation.

Plate I. 1–3. *Araucariacites australis* Cookson 1947. 1. MPEF-PA 652 (113.2/45.9). 2, 3. MPEF-PA 147. 3. Detail of sculpture. 4, 5. *Callialasporites trilobatus* (Balme) Dev 1961. 4. MPEF-PA 803 (106.4/33). 5. MPEF-PA 147. 6–8. *Dilwynites granulatus* Harris 1965. 6. MPEF-PA 828 (99.5/23). 7, 8. MPEF-PA 165. 8. Detail of sculpture. 9. *Dilwynites tuberculatus* Harris

1724 1965. MPEF-PA 472 (106.5/34.4). 10–16. *Classopollis patagonicus* sp. nov. 10. Holotype.
1725 MPEF-PA 472 (92.8/36.4). 11. MPEF-PA 472 (100.3/33.3). 12. MPEF-PA 170. 13. MPEF-PA
1726 151. 14, 15. MPEF-PA 171. 16. MPEF-PA 168. 14 and 15. Longitudinal section. Note the
1727 interdigitation at the boundary between the proximal columellae and the striations of the
1728 equatorial band (black arrowhead), and the subequatorial furrow (white arrowhead). 16. Detail of
1729 sculpture. 17–19. *Classopollis* sp. 1. 17. MPEF-PA 820 (100.7/37.7). 18, 19. MPEF-PA 168. 19.
1730 Detail of sculpture. 20. *Ephedripites jansonii* (Pocock) Muller 1968. MPEF-PA 471 (98.8/20.2).
1731 21. *Ephedripites multicostatus* Brenner 1963. MPEF-PA 929 (95.5/36.8). 22. *Gamerroites*
1732 *psilasaccus* (Archangelsky and Romero) Archangelsky 1988. MPEF-PA 608 (105.5/24.8). 23,
1733 24. *Lygistepollenites florinii* (Cookson and Pike) Stover and Evans 1973. 23. MPEF-PA 454
1734 (103.8/23.2). 24. MPEF-PA 147. 25, 26. *Microcachryidites antarcticus* Cookson 1947. 25.
1735 MPEF-PA 460 (104/30.4). 26. MPEF-PA 147. 27, 28. *Microcachryidites cesariae* Llorens 2012.
1736 27. MPEF-PA 457 (95.8/21.4). 28. MPEF-PA 145. 29, 30. *Phyllocladidites mawsonii* Cookson
1737 1947 ex Couper 1953. 29. MPEF-PA 452 (114.4/41.2). 30. MPEF-PA 147.
1738 Scale bars: 1, 2, 4–7, 9–14, 17, 18, 20–30 = 10 μm; 3, 8, 15, 16, 19 = 1 μm.
1739
1740 **Plate II.** 1. *Podocarpidites ellipticus* Cookson 1947. MPEF-PA 458 (106.3/25). 2.
1741 *Podocarpidites marwickii* Couper 1953. MPEF-PA 827 (102.7/32.5). 3, 4. *Podocarpidites*
1742 *rugulosus* Romero 1977. 3. MPEF-PA 609 (113.3/34.8). 4. MPEF-PA 151. 5. *Podocarpidites*
1743 *verrucosus* Volkheimer 1972. MPEF-PA 820 (95.2/33). 6–8. *Podocarpidites rectangularis* sp.
1744 nov. 6, 8. Holotype. MPEF-PA 817 (107.2/34.8). 7. MPEF-PA 454 (93.3/32.3). 8. Detail of
1745 sculpture. 9, 10. *Trichotomosulcites microsaccatus* (Couper) Schrank 2010. 9. MPEF-PA 454
1746 (95.6/32.7). 10. MPEF-PA 150. 11. *Cycadopites* sp. MPEF-PA 451 (99.6/27.2). 12. *Rosannia*

manika Srivastava emend. Srivastava and Braman 2010. MPEF-PA 171. 13–15. *Clavatipollenites* sp. 13. MPEF-PA 453 (102/40.7). 14, 15. MPEF-PA 170. 15. Detail of sculpture. 16, 17. *Pandaniidites radicus* Leffingwell 1970. 16. MPEF-PA 452 (108.5/37.3). 17. MPEF-PA 150. 18–20. *Arecipites minutiscabratus* (McIntyre) Milne 1988. 18. MPEF-PA 608 (95.5/41.7). 19, 20. MPEF-PA 170. 20. Detail of sculpture. 21–24. *Arecipites botrus* sp. nov. 21. Holotype. MPEF-PA 470 (108.1/31.2). 22. MPEF-PA 452 (96.4/47). 23, 24. MPEF-PA 149. 23. Clump. 24. Detail of sculpture. 25. *Confertisulcites* sp. MPEF-PA 453 (100/39.4). 26–28. *Gemmamonocolpites chubutensis* sp. nov. 26. Holotype. MPEF-PA 826 (102.2/44.2). 27. MPEF-PA 828 (99.6/25.9). 28. MPEF-PA 170. 29, 30. *Longapertites andreisii* Archangelsky 1973. 29. MPEF-PA 388 (103/29). 30. MPEF-PA 170.

Scale bars: 1–7, 9–14, 16, 18, 19, 23, 25–30 = 10 μm; 8, 15, 20, 24 = 1 μm; 17, 21, 22 = 5 μm.

Plate III. 1. *Proxapertites operculatus* Van der Hammen 1956. MPEF-PA 667 (112.7/27.6). 2, 3. *Spinizonocolpites hialinus* Archangelsky and Zamaloa 1986. 2. MPEF-PA 611 (106.9/29.1). 3. MPEF-PA 169. 4, 5. *Spinizonocolpites riochiquensis* Vallati and De Sosa Tomas 2020. 4, 5. MPEF-PA 578 (98.6/35.6). 5. Detail of sculpture. 6–10. *Spinizonocolpites coloniensis* sp. nov. 6, 8. Holotype. MPEF-PA 926 (100.7/34.7). 7. MPEF-PA 951 (102.5/24.6). 9, 10. MPEF-PA 169. 8, 10. Detail of sculpture. 11–14. *Spinizonocolpites variabilis* sp. nov. 11. Holotype. MPEF-PA 874 (92.5/27.3). 12. MPEF-PA 865 (115.2/24.2). 13, 14. MPEF-PA 169. 14. Detail of sculpture. 15–17. *Inaperturotetradites scabratus* Tschudy 1973. 15. MPEF-PA 460 (94.8/34). 16, 17. MPEF-PA 149. 17. Detail of sculpture. 18, 19. *Liliacidites regularis* Archangelsky 1973. 18. MPEF-PA 472 (103.4/41.5). 19. MPEF-PA 168. 20, 21. *Liliacidites variegatus* Couper 1953. 20. MPEF-PA 453 (99/32). 21. MPEF-PA 145. 22–25. *Liliacidites buitrensis* sp. nov. 22. Holotype.

1770 MPEF-PA 819 (111.6/44.5). 23. MPEF-PA 821 (95.8/28.6). 24, 25. MPEF-PA 146. 25. Detail of
1771 sculpture. 26–30. *Liliacidites lacunosus* sp. nov. 26, 27. Holotype. MPEF-PA 667 (112.4/32.1).
1772 28. MPEF-PA 701 (96.2/23.2). 29, 30. MPEF-PA 168. 30. Detail of sculpture.
1773 Scale bars: 1–3, 5, 7–9, 11–13, 15, 16, 18–24, 26–29 = 10 μm; 4, 6 = 20 μm; 8, 25 = 5 μm; 10,
1774 14, 30 = 2 μm; 17 = 1 μm.
1775
1776 **Plate IV.** 1–5. *Sparganiaceaepollenites annulatus* sp. nov. 1. Holotype. MPEF-PA 874
1777 (94.7/27). 2. MPEF-PA 580 (94/34). 3–5. MPEF-PA 168. 4. Note the operculum (arrowhead). 5.
1778 Detail of sculpture. 6, 7. *Cricotriporites minutiporus* (Muller) Jaramillo and Dilcher 2001. 6.
1779 MPEF-PA 454 (94.1/32). 7. MPEF-PA 170. 8. *Dryadopollis* sp. 1. MPEF-PA 171. 9.
1780 *Dryadopollis* sp. 2. MPEF-PA 151. 10. *Dryadopollis* sp. 3. MPEF-PA 173. 11. *Ericipites*
1781 *scabratus* Harris 1965. MPEF-PA 801 (97.8/23). 12–15. *Ericipites verrucatus* sp. nov. 12.
1782 Holotype. MPEF-PA 622 (103.9/45.9). 13. MPEF-PA 993 (102.8/41.7). 14, 15. MPEF-PA 150.
1783 15. Detail of sculpture. 16, 17. *Tricolpites reticulatus* Cookson ex Couper emend. Jarzen and
1784 Dettmann 1989. 16. MPEF-PA 622 (103.7/30.8). 17. MPEF-PA 168. 18, 19. *Bombacacidites*
1785 *brevis* (Dueñas) Muller et al. 1987. 18. MPEF-PA 452 (110.2/45.3). 19. MPEF-PA 150. 20.
1786 *Intratriporopollenites* sp. MPEF-PA 803 (109.1/43.1). 21–27. *Nelumbopollenites patagonicus*
1787 sp. nov. 21. Holotype. MPEF-PA 622 (94.2/27.1). 22. MPEF-PA 622 (93.9/34.5). 23. MPEF-PA
1788 149. 24, 25. MPEF-PA 165. 26, 27. MPEF-PA 150. 25, 27. Detail of sculpture. 28.
1789 *Nothofagidites saraensis* Menéndez and Caccavari 1975. MPEF-PA 614 (99.7/34.5). 29.
1790 *Peninsulapollis gillii* (Cookson) Dettmann y Jarzen 1988. MPEF-PA 455 (97.1/43.5). 30.
1791 *Peninsulapollis* sp. 1. MPEF-PA 628 (109.5/20.1).

1792 Scale bars: 6, 11–14, 16–24, 26, 28–30 = 10 μm; 1–4, 7 = 5 μm; 8–10, 15 = 2 μm; 5, 25, 27 = 1
1793 μm.
1794
1795 **Plate V.** 1, 2. *Propylipollis lateflexus* (Archangelsky) Baldoni and Askin 1993. 1. MPEF-PA 752
1796 (111/40.8). 2. MPEF-PA 170. 3–5. *Proteacidites scaboratus* Couper 1960. 3. MPEF-PA 874
1797 (92.9/36.1). 4, 5. MPEF-PA 169. 5. Detail of sculpture. 6–10. *Proteacidites baibianae* sp. nov. 6.
1798 Holotype. MPEF-PA 853 (93.5/29.1). 7. MPEF-PA 928 (99.6/32.8). 8, 9. MPEF-PA 145. 10.
1799 MPEF-PA 168. 9. Detail of sculpture. 11–14. *Proteacidites mirasolensis* sp. nov. 11. Holotype.
1800 MPEF-PA 951 (101.2-22.8). 12. MPEF-PA 930 (102.9/31.6). 13, 14. MPEF-PA 169. 14. Detail
1801 of sculpture. 15. *Proteacidites* sp. 1. MPEF-PA 654 (110.5/41.2). 16. *Proteacidites* sp. 2. MPEF-
1802 PA 700 (102.6/25). 17. *Proteacidites* sp. 3. MPEF-PA 690 (100.6/38.2). 18, 19.
1803 *Triporopollenites ambiguus* (Stover) Stover and Partridge 1973. 18. MPEF-PA 653 (115/33). 19.
1804 MPEF-PA 168. 20–23. *Ailanthipites diminutus* sp. nov. 20. Holotype. MPEF-PA 608
1805 (98.6/33.2). 21. MPEF-PA 388 (102.4/17.5). 22. MPEF-PA 625 (97.2/35.7). 23. MPEF-PA 150.
1806 24–27. *Ailanthipites feruglioi* sp. nov. 24. Holotype. MPEF-PA 803 (109.5/48). 25. MPEF-PA
1807 933 (108.5/30.9). 26, 27. MPEF-PA 168. 27. Detail of sculpture. 28–30. *Ailanthipites*
1808 *hexagonalis* sp. nov. 28. Holotype. MPEF-PA 799 (109.4/28.5). 29. MPEF-PA 700 (103.9/16.4).
1809 30. MPEF-PA 830 (102.8/34.9).
1810 Scale bars: 1–4, 6–8, 10–13, 15–19, = 10 μm; 5, 27 = 1 μm; 9, 14 = 2 μm; 20–26, 28–30 = 5 μm.
1811
1812 **Plate VI.** 1–3. *Ailanthipites* sp. 1. 1. MPEF-PA 874 (112.9/22.8). 2, 3. MPEF-PA 169. 3. Detail
1813 of sculpture. 4–7. *Krutzschipollis argentinum* sp. nov. 4, 5. Holotype. MPEF-PA 804 (96.1/38.3).
1814 6. MPEF-PA 861 (104.2/37.3). 7. MPEF-PA 145. 8–12. *Nyssapollenites scabratus* sp. nov. 8.

1815 Holotype. MPEF-PA 470 (95.5/42.2). 9. MPEF-PA 471 (107.6/33.3). 10. MPEF-PA 470
1816 (102.8/33.9). 11, 12. MPEF-PA 149. 10. Clump. 12. Detail of sculpture. 13–18. *Parviprojectus*
1817 *archangelskyi* sp. nov. 13, 14. Holotype. MPEF-PA 967 (113/27.2). 15. MPEF-PA 701
1818 (92.6/18.5). 16. MPEF-PA 145. 17, 18. MPEF-PA 170. 18. Detail of sculpture. 19–22.
1819 *Periporopollenites delicatus* sp. nov. 19, 20. Holotype. MPEF-PA 460 (94.6/31.2). 21. MPEF-
1820 PA 471 (97.3/27.7). 22. MPEF-PA 151. Note the operculate pores (arrowheads). 23, 24.
1821 *Psilatricolpites psilascabratus* (Norton) Archangelsky 1973. 23. MPEF-PA 929 (98.2/27.7). 24.
1822 MPEF-PA 169. 25. *Retitricolporites chubutensis* Archangelsky 1973. MPEF-PA 700
1823 (102.7/34.8). 26–30. *Retitricolporites ganganensis* sp. nov. 26. Holotype. MPEF-PA 620
1824 (110/22.5). 27. MPEF-PA 942 (99.7/42.8). 28. MPEF-PA 168. 29, 30. MPEF-PA 169. 30. Detail
1825 of sculpture.
1826 Scale bars: 1, 2, 17 = 5 μm; 3, 12, 30 = 1 μm; 4–10, 13–16, 19–29 = 10 μm; 11, 18 = 2 μm.
1827
1828 **Plate VII.** 1–5. *Retitricolporites irupensis* sp. nov. 1, 2. Holotype. MPEF-PA 820 (114.1/25.8).
1829 3. MPEF-PA 663 (105.2/27.1). 4, 5. MPEF-PA 171. 5. Detail of sculpture. 6, 7. *Rhoipites*
1830 *baculatus* Archangelsky 1973. 6. MPEF-PA 381 (110.5/15.2). 7. MPEF-PA 145. 8. *Rhoipites* sp.
1831 1. MPEF-PA 582 (94.3/40.8). 9. *Rousea minuscula* Archangelsky and Zamaloa 1986. MPEF-PA
1832 460 (92.2/44.5). 10. *Rousea patagonica* Archangelsky 1973. MPEF-PA 750 (111.7/31.5). 11–13.
1833 *Rousea robusta* sp. nov. 11. Holotype. MPEF-PA 819 (97.5/33.5). 12. MPEF-PA 822 (97/36.6).
1834 13. MPEF-PA 168. 14–17. *Stellatopollis crassibaculata* (Freile) Ward 1986 emend. 14. MPEF-
1835 PA 930 (100.9/30.6). 15. MPEF-PA 628 (95.5/35.2). 16. MPEF-PA 168. 17. MPEF-PA 171. 17.
1836 Detail of sculpture. 18–20. *Striatopollis exiguus* Archangelsky and Zamaloa 1986. 18. MPEF-PA
1837 952 (96.4/26.1). 19, 20. MPEF-PA 168. 20. Detail of sculpture. 21–24. *Symplocoipollenites*

microechinatus sp. nov. 21. Holotype. MPEF-PA 454 (102.1/39.1). 22. MPEF-PA 453 (102.6/44.3). 23. MPEF-PA 580 (94.7/29.8). 24. MPEF-PA 151. 23, 24. Clumps. Note the columellate exine in 23 (arrowhead) and the microechinate sculpture in 24. 25. *Tetracolpites reticulatus* Srivastava 1966. MPEF-PA 930 (99.3/39.2). 26. *Tricolporites* sp. MPEF-PA 150. 27, 28. *Tubulifloridites lilliei* (Couper) Farabee and Canright 1986. 27. MPEF-PA 472 (112.5/42.7). 28. MPEF-PA 165. 29. *Tubulifloridites* sp. 1. MPEF-PA 972 (109.2/37.9). 30. *Volkheimerites labyrinthus* Narváez et al. 2021. MPEF-PA 388 (97.3/37.4).

Scale bars: 1–4, 10–16, 18, 19, 21–23, 25, 27–30 = 10 μm; 5, 17, 20, 24 = 2 μm; 6–9 = 5 μm; 26 = 3 μm.

Figure 1

Click here to access/download;Figure;FIGURE 1.tif

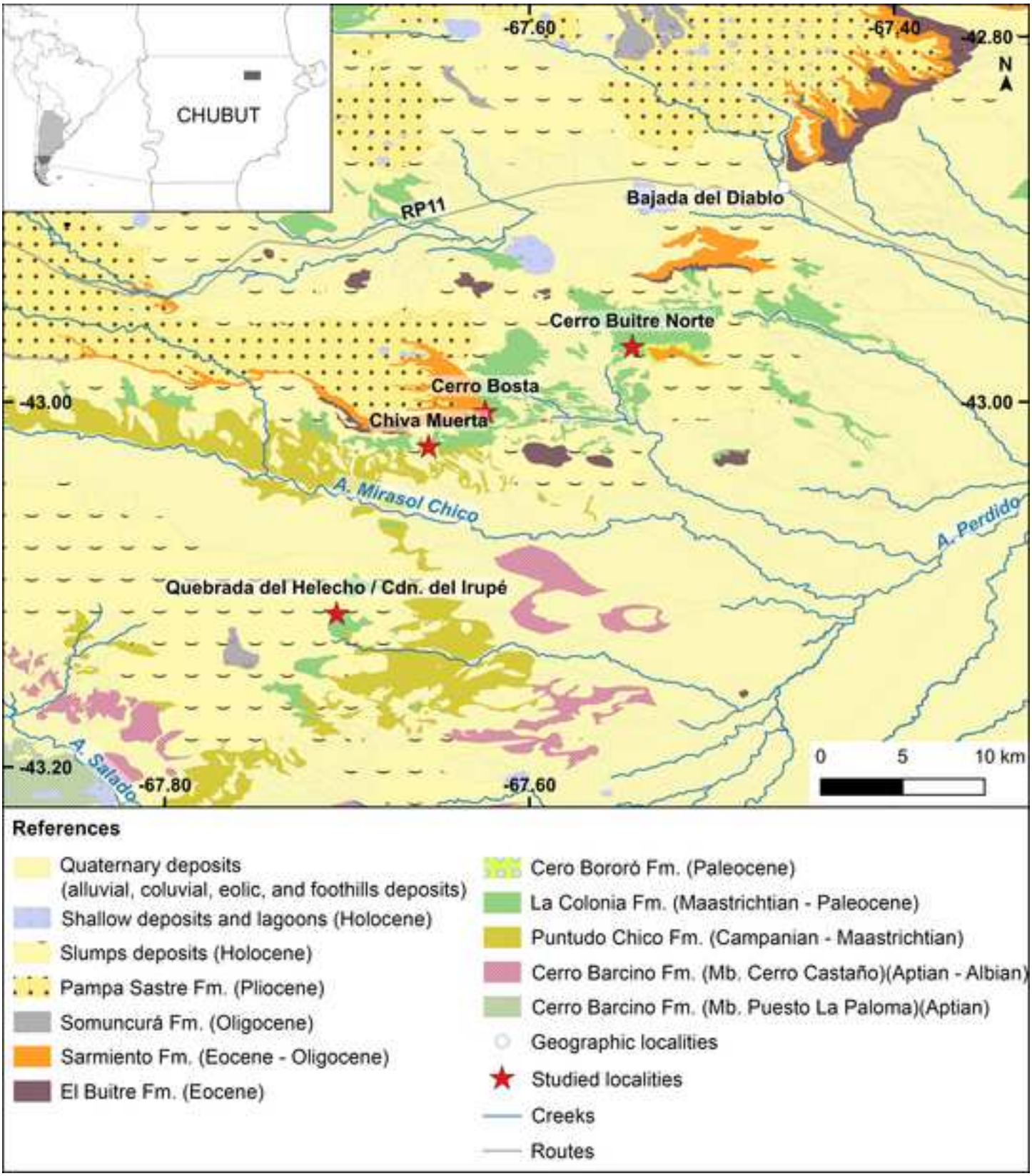


Plate 1

Click here to access/download;Figure;PLATE I.tif

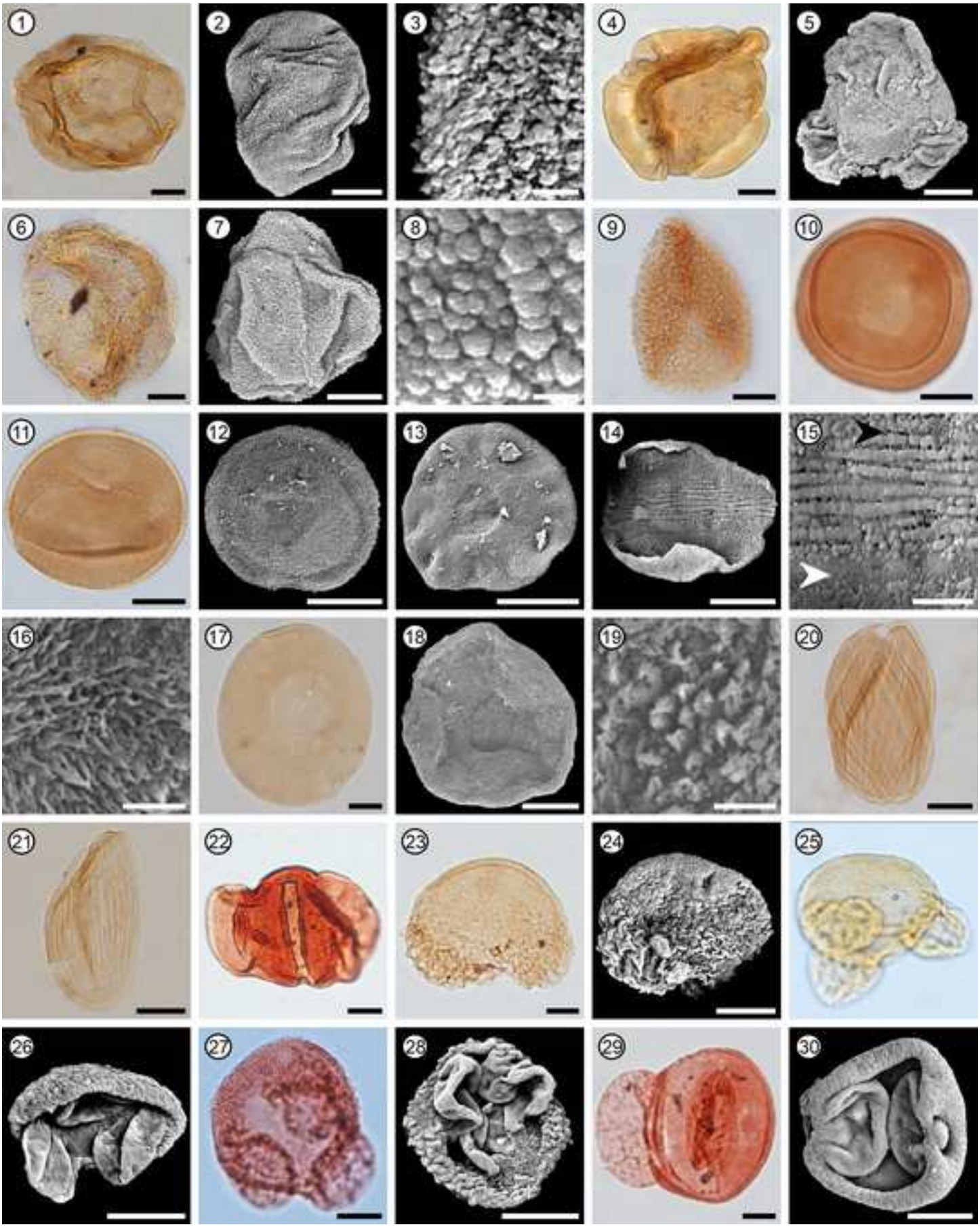
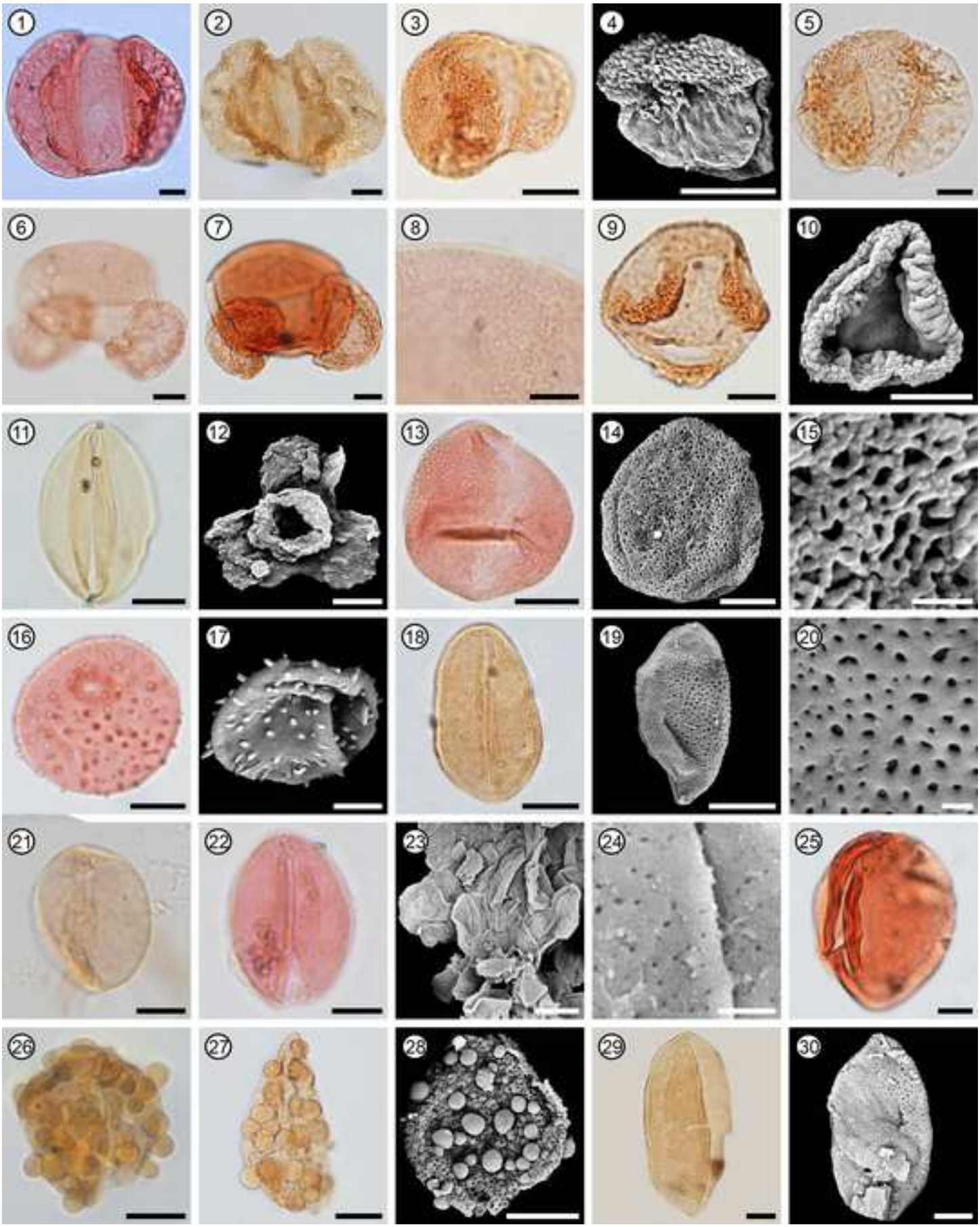


Plate 2

Click here to access/download;Figure;PLATE II.tif



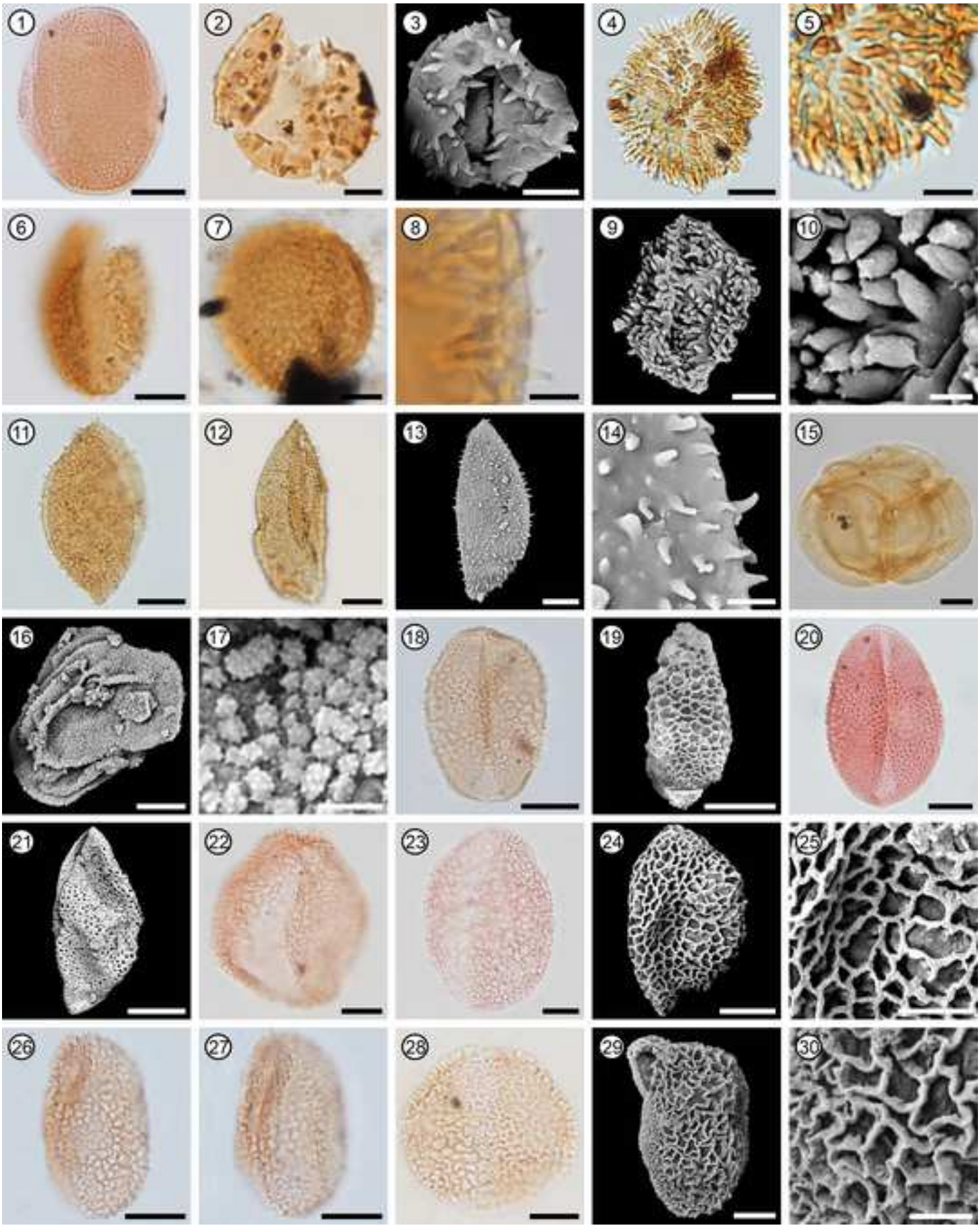


Plate 4

Click here to access/download;Figure;PLATE IV.tif

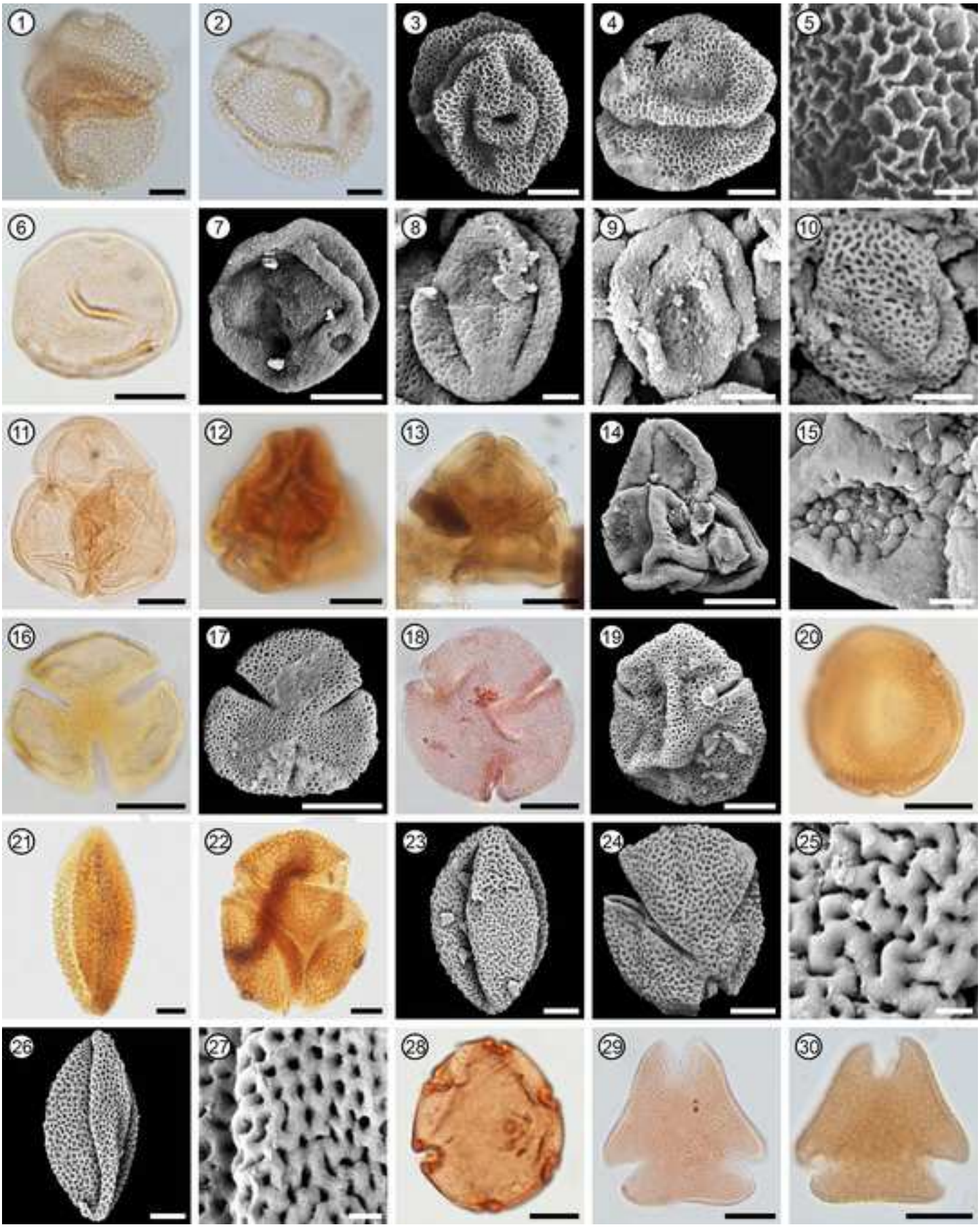


Plate 5

Click here to access/download;Figure;PLATE V.tif

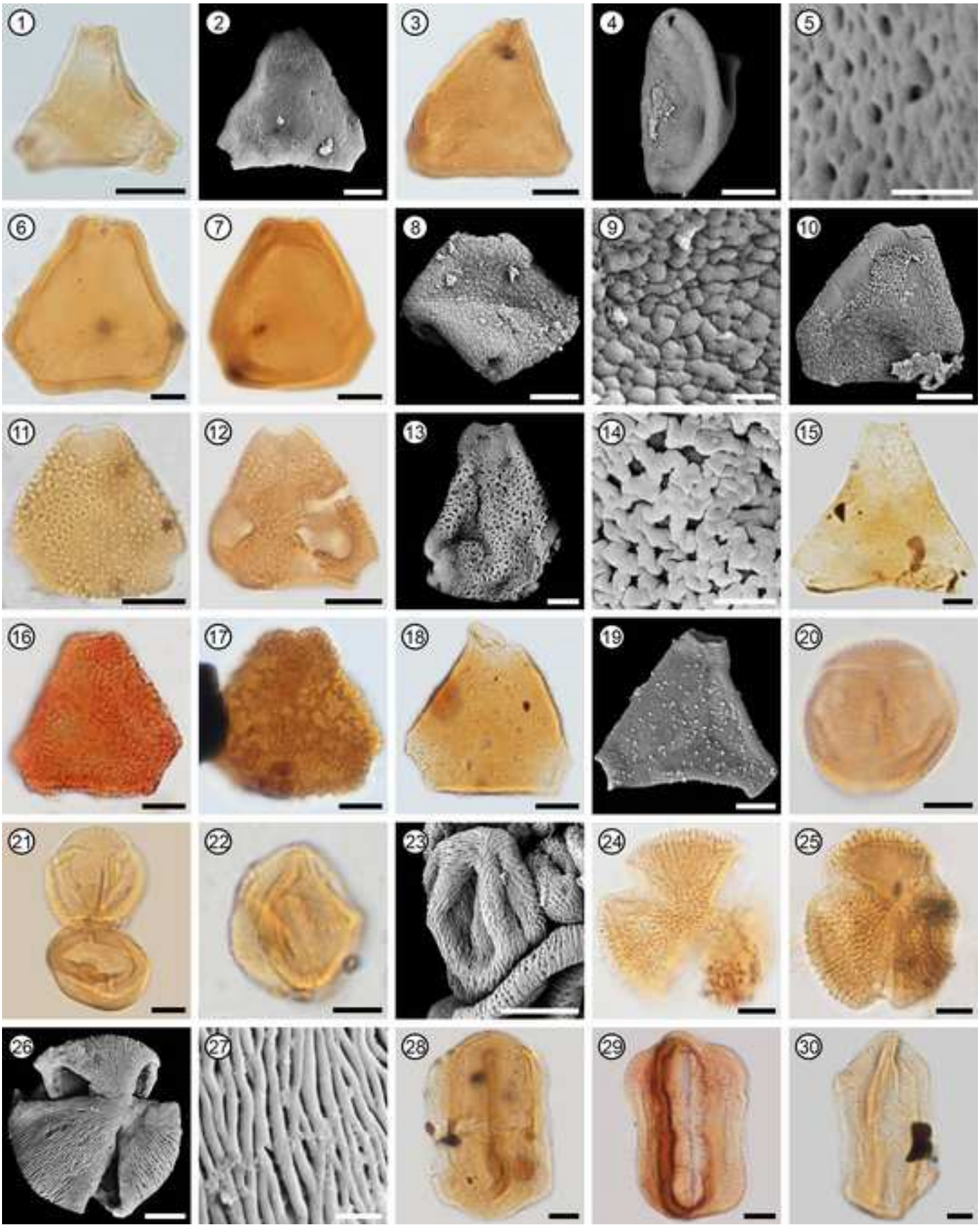


Plate 6

Click here to access/download;Figure;PLATE VI.tif

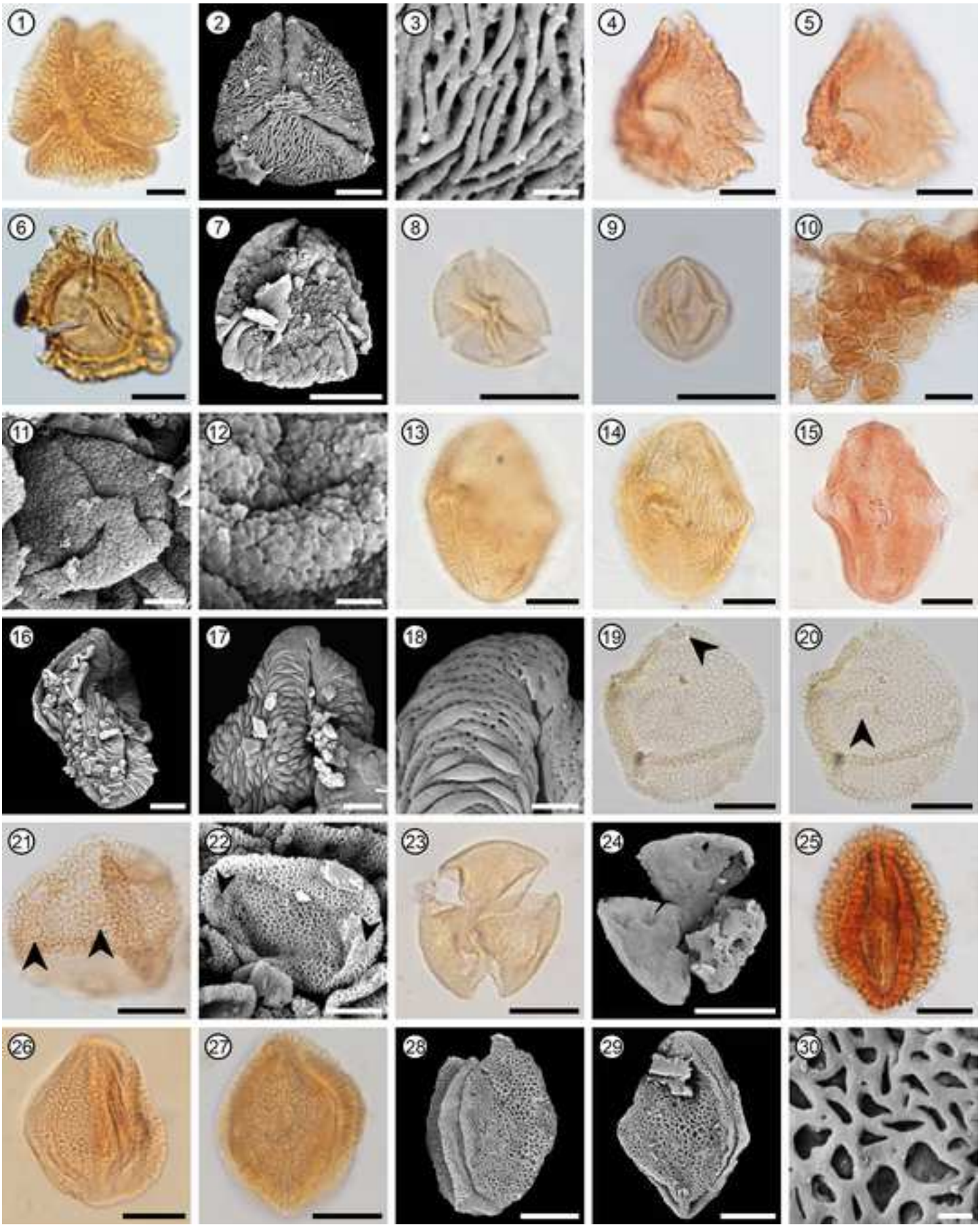


Plate 7

Click here to access/download;Figure;PLATE VII.tif

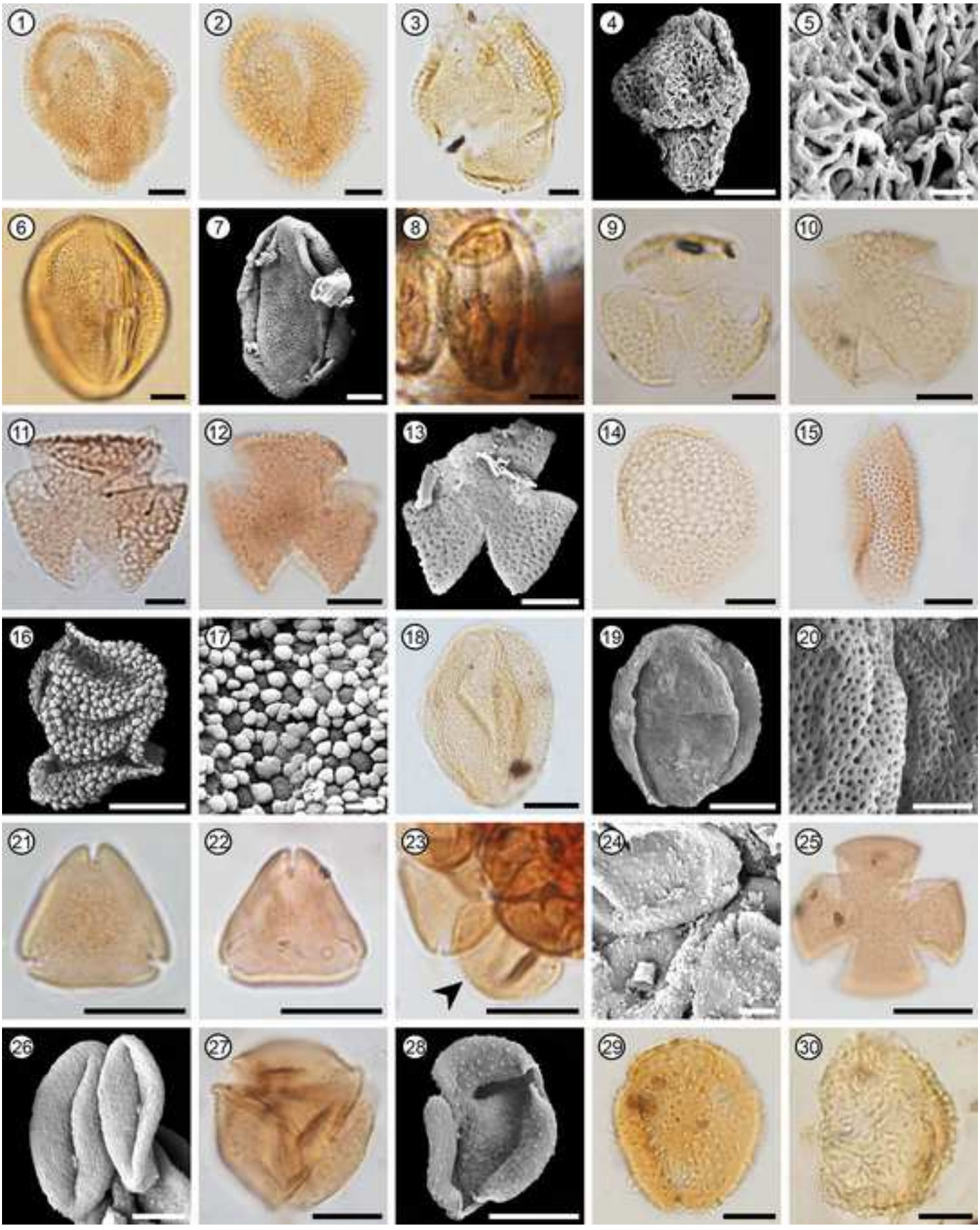


Table (Editable version)

Click here to access/download;Table (Editable version);TABLE 1.docx

Botanical affinity	Taxa[1]	Illustration	Sections[2]				Maast.	Dan.
			QH/CI	CBO	CBN	CHM		
GYMNOSPERMAE								
ARAUCARIACEAE *Araucaria*/*Agathis*	*Araucariacites australis* Cookson 1947	Pl. I, 1–3	x	x	x	x	x	x
	Callialasporites trilobatus (Balme) Dev 1961	Pl. I, 4, 5	x	x	x	x	x	x
Wollemia/*Agathis*	*Dilwynites granulatus* Harris 1965	Pl. I, 6–8	x	x	x	x	x	x
Wollemia/*Agathis*	*Dilwynites tuberculatus* Harris 1965	Pl. I, 9	x	x	x	x	x	x
CHEIROLEPIDIACEAE	***Classopollis patagonicus***	Pl. I, 10–16	x	x	x	x	x	x
	Classopollis sp. 1	Pl. I, 17–19	x	x	x	–	x	–
EPHEDRACEAE	*Ephedripites jansonii* (Pocock) Muller 1968	Pl. I, 20	x	x	x	–	x	x
	Ephedripites multicostatus Brenner 1963	Pl. I, 21		x	x	x	x	x
PODOCARPACEAE	*Gamerroites psilasaccus* (Archangelsky & Romero) Archangelsky 1988	Pl. I, 22	x	x	x	–	x	x
Dacrydium	*Lygistepollenites florinii* (Cookson & Pike) Stover & Evans 1973	Pl. I, 23, 24	x	x	x	x	x	x
Microcachrys	*Microcachryidites antarcticus* Cookson 1947	Pl. I, 25, 26	x	x	x	x	x	x
Microcachrys	*Microcachryidites cesariae* Llorens 2012	Pl. I, 27, 28	x		x	x	x	–
Lagarostrobos	*Phyllocladidites mawsonii* Cookson ex Couper 1953	Pl. I, 29, 30	x	x	x	x	x	x
Podocarpus	*Podocarpidites ellipticus* Cookson 1947	Pl. II, 1	x	x	x	x	x	x
Podocarpus	*Podocarpidites marwickii* Couper 1953	Pl. II, 2	x	x	x	x	x	x
Podocarpus	*Podocarpidites rugulosus* Romero 1977	Pl. II, 3, 4	x	x	x	x	x	x
Podocarpus	*Podocarpidites verrucosus* Volkheimer 1972	Pl. II, 5	x	x	x	–	x	x
Podocarpus	***Podocarpidites rectangularis***	Pl. II, 6–8	x	x	x	–	x	–
	Trichotomosulcites microsaccatus (Couper) Schrank 2010	Pl. II, 9, 10	x	x	x	x	x	x
INCERTAE SEDIS	*Cycadopites* sp.	Pl. II, 11	x	x	x	–	x	x
ANGIOSPERMAE								
ARISTOLOCHIACEAE *Lactoris*	*Rosannia manika* Srivastava emend. Srivastava & Braman 2010	Pl. II, 12	–	x	x	–	x	x
CHLORANTHACEAE	*Clavatipollenites* sp.	Pl. II, 13–15	x	x	x	–	x	x
Monocots								
ARACEAE	*Pandaniidites radicus* Leffingwell 1971	Pl. II, 16, 17	x	x	x	x	x	x
ARECACEAE	*Arecipites minutiscabratus* (McIntyre) Milne 1988	Pl. II, 18–20	x	x	x	x	x	x
	Arecipites botrus	Pl. II, 21–24	x	x	x	–	x	–
	Confertisulcites sp.	Pl. II, 25	x	x	x	x	x	–
	Gemmamonocolpites chubutensis	Pl. II, 26–28		x	x	x	x	x
	Longapertites andreisii Archangelsky 1973	Pl. II, 29, 30	x	x	x	x	x	x
	Longapertites patagonicus Archangelsky 1973	–	x	x	x	–	x	x
	Proxapertites operculatus Van der Hammen 1956	Pl. III, 1	x	x	x	–	x	x
Nypa fruticans	*Spinizonocolpites hialinus* Archangelsky & Zamaloa 1986	Pl. III, 2, 3	x	x	x	x	x	x
Nypa fruticans	*Spinizonocolpites riochiquensis* Vallati & De Sosa Tomas 2020	Pl. III, 4, 5	x	x	x	x	x	x
Nypa fruticans	***Spinizonocolpites coloniensis***	Pl. III, 6–10	–	–	x	–	x	x
	Spinizonocolpites variabilis	Pl. III, 11–14	x	x	x	x	x	x
JUNCACEAE?	*Inaperturotetradites scabratus* Tschudy 1973	Pl. III, 15–17	x	–	x	–	x	–
LILIACEAE?	*Liliacidites regularis* Archangelsky 1973	Pl. III, 18, 19	x	x	x	–	x	x
	Liliacidites variegatus Couper 1953	Pl. III, 20, 21	x	x	x	x	x	x
	Liliacidites buitrensis	Pl. III, 22–25	–	x	x	–	x	x
	Liliacidites lacunosus	Pl. III, 26–30	x	x	x	x	x	x
TYPHACEAE; *Typha*	***Sparganiaceaepollenites annulatus***	Pl. IV, 1–5	x	x	x	x	x	x
Eudicots								
CANNABACEAE	*Cricotriporites minutiporus* (Muller) Jaramillo & Dilcher 2001	Pl. IV, 6, 7	x	x	x	–	x	x
CUNONIACEAE	*Dryadopollis* sp. 1	Pl. IV, 8	–	x	x	–	x	x
	Dryadopollis sp. 2	Pl. IV, 9	–	x	–	–	x	–

	Dryadopollis sp. 3	Pl. IV, 10	–	–	x	–	–	x
ERICACEAE	*Ericipites scabratus* Harris 1965	Pl. IV, 11	–	x	x	x	x	x
	Ericipites verrucatus	Pl. IV, 12–15	–	x	x	x	x	–
GUNNERACEAE	*Tricolpites reticulatus* Cookson ex Couper emend. Jarzen & Dettmann 1989	Pl. IV, 16, 17	x	x	x	x	x	x
MALVACEAE	*Bombacacidites brevis* (Dueñas) Muller et al. 1987	Pl. IV, 18, 19	x	x	–	–	x	–
	Intratriporopollenites sp.	Pl. IV, 20	x	x	x	x	x	x
NELUMBONACEAE *Nelumbo*	***Nelumbopollenites patagonicus***	Pl. IV, 21–27	x	x	x	x	x	x
NOTHOFAGACEAE *Nothofagus*	*Nothofagidites saraensis* Menéndez & Caccavari 1975	Pl. IV, 28	–	x	x	–	x	x
PROTEACEAE	*Peninsulapollis gillii* (Cookson) Dettmann & Jarzen 1988	Pl. IV, 29	x	x	x	x	x	x
	Peninsulapollis sp. 1	Pl. IV, 30	x	x	x	–	x	x
	Propylipollis lateflexus (Archangelsky) Baldoni & Askin 1993	Pl. V, 1, 2	x	x	x	x	x	x
	Proteacidites scaboratus Couper 1960	Pl. V, 3–5	x	x	x	x	x	x
	Proteacidites baibianae	Pl. V, 6–10	x	x	x	x	x	x
	Proteacidites mirasolensis	Pl. V, 11–14	x	x	x	x	x	x
	Proteacidites sp. 1	Pl. V, 15	x	x	x	x	x	x
	Proteacidites sp. 2	Pl. V, 16	–	x	–	–	x	–
	Proteacidites sp. 3	Pl. V, 17	–	x	–	–	x	–
	Triporopollenites ambiguus Stover, in Stover & Partridge 1973	Pl. V, 18, 19	x	x	x	x	x	x
INCERTAE SEDIS	***Ailanthipites diminutus***	Pl. V, 20–23	x	x	–	–	x	–
	Ailanthipites feruglioi	Pl. V, 24–27	–	–	x	–	x	–
	Ailanthipites hexagonalis	Pl. V, 28–30	–	x	x	–	x	x
	Ailanthipites sp. 1	Pl. VI, 1–3	–	–	x	–	x	–
	Krutzschipollis argentinum	Pl. VI, 4–7	–	x	x	x	x	x
	Nyssapollenites scabratus	Pl. VI, 8–12	x	x	x	x	x	x
	Parviprojectus archangelskyi	Pl. VI, 13–18	x	x	x	–	x	x
	Periporopollenites delicatus	Pl. VI, 19–22	x	x	x	–	x	x
	Psilatricolpites psilascabratus (Norton) Archangelsky 1973	Pl. VI, 23, 24	x	x	x	x	x	x
	Quadraplanus brossus Stover in Stover & Partridge 1973	–	x	x	x	–	x	–
	Retitricolporites chubutensis Archangelsky 1973	Pl. VI, 25	–	x	x	–	x	x
	Retitricolporites ganganensis	Pl. VI, 26–30	x	x	x	–	x	x
	Retitricolporites irupensis	Pl. VII, 1–5	–	x	x	–	x	x
	Rhoipites baculatus Archangelsky 1973	Pl. VII, 6, 7	x	x	x	x	x	x
	Rhoipites sp. 1	Pl. VII, 8	–	x	–	–	x	–
	Rousea minuscula Archangelsky & Zamaloa 1986	Pl. VII, 9	x	x	x	–	x	x
	Rousea patagonica Archangelsky 1973	Pl. VII, 10	x	x	x	x	x	x
	Rousea robusta	Pl. VII, 11–13	–	–	x	–	x	x
	Stellatopollis crassibaculata (Freile) Ward 1986 emend.	Pl. VII, 14–17	x	x	x	–	x	x
	Striatopollis exiguus Archangelsky & Zamaloa 1986	Pl. VII, 18–20	x	–	x	x	x	–
	Symplocoipollenites microechinatus	Pl. VII, 21–24	x	x	x	–	x	x
	Tetracolpites reticulatus Srivastava 1966	Pl. VII, 25	x	x	x	–	x	x
	Tricolporites sp.	Pl. VII, 26	–	x	–	–	x	–
	Tubulifloridites lilliei (Couper) Farabee & Canright 1986	Pl. VII, 27, 28	x	x	x	x	x	–
	Tubulifloridites sp. 1	Pl. VII, 29	–	–	x	x	x	x
	Volkheimerites labyrinthus Narváez et al. 2021	Pl. VII, 30	x	x	–	–	x	–

[1] New species are in bold.

[2] Stratigraphic sections: QH/CI (Quebrada del Helecho/Cañadón del Irupé), CBO (Cerro Bosta), CBN (Cerro Buitre Norte), and CHM (Chiva Muerta). Presence (X); Absence (–).

Declaration of interests

☒The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Appendix A

Appendix B

Research Data

Click here to download Research Data
https://figshare.com/s/4375c5437214a0bc7d79