International Journal of Plant Sciences

Early Eocene spore and pollen assemblages from the Laguna del Hunco fossil-lake beds, Patagonia, Argentina

--Manuscript Draft--

Article Type:	Major Article
Manuscript Number:	44423R1
Full Title:	Early Eocene spore and pollen assemblages from the Laguna del Hunco fossil-lake beds, Patagonia, Argentina
Corresponding Author:	Viviana Barreda, Ph.D. Consejo Nacional de Investigaciones Cientificas y Tecnicas Buenos Aires, Ciudad Autónoma de Buenos Aires ARGENTINA
Corresponding Author's Institution:	Consejo Nacional de Investigaciones Cientificas y Tecnicas
Other Authors:	María del Carmen Zamaloa
	María A. Gandolfo
	Carlos Jaramillo
	Peter Wilf
Abstract:	Premise of research . The early Eocene Laguna del Hunco (LH) fossil site, northwestern Chubut Province, Argentina, holds one of the best preserved and most diverse paleofloras worldwide. The paleoflora comprises ferns, gymnosperms, and flowering plants. Despite the rapidly growing knowledge of its macrofossil record, little is known about the site's palynological content. Herein, we present the first dispersed spore-pollen assemblages recovered from Laguna del Hunco. Methodology . Palynological samples were collected from seven stratigraphic levels of the Tufolitas de Laguna del Hunco (Huitrera Formation), of which six yielded palynomorphs. We determine the botanical affinities of fossil morphotypes and provide systematic descriptions of some taxa. In addition, we establish similarities between LH and other Patagonian Eocene localities, and we compare palynological and prior megafloral records from LH. Pivotal results . We identify 56 spore and pollen species and 28 plant families, of which eight are reported from the site reliably for the first time (Cyatheaceae, Schizaeaceae, Polypodiaceae, Asteraceae, Chloranthaceae, Nothofagaceae, Rubiaceae, and Ulmaceae). Among other Eocene Patagonian palynofloras, the LH assemblage is similar to Pampa de Jones/Nahuel Huapi Este and Confluencia. Conclusions . The LH spore-pollen assemblages augment the plant fossil record for this significant Eocene locality by incorporating new taxa (e.g., Asteraceae, with one morphotype that represents the oldest record of the family in Patagonia). The new data also reinforce the presence of plant families previously reported from macrofossils, such as Juglandaceae, with pollen grains similar to the Engelhardia-Alfaroa group, and Fagaceae (Castaneoideae), complementing the macrofossil record of leaves and reproductive structures.
Author Comments:	I would like figures appear in color only in the online version of the journal
Additional Information:	
Question	**Response**

Early Eocene spore and pollen assemblages from the Laguna del Hunco fossil-lake beds, Patagonia, Argentina

Viviana D. Barreda[1], María del Carmen Zamaloa[2], María A. Gandolfo[3], Carlos Jaramillo[4,5], Peter Wilf[6]

[1] División Paleobotánica, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" - CONICET, Av. Ángel Gallardo 470, C1405DJR, Buenos Aires, Argentina. E-mail: vbarreda@macn.gov.ar

[2] Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2620, C1428EHA Buenos Aires, Argentina.

[3] Liberty Hyde Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, USA.

[4] Smithsonian Tropical Research Institute, Balboa, Ancon, AA 0843-03092, Panama.

[5]ISEM, U. Montpellier, CNRS, EPHE, IRD, Montpellier, France.

[6] Department of Geosciences, Pennsylvania State University, University Park, PA 16802, USA.

Short title. Palynology of Laguna del Hunco

Abstract

Premise of research. The early Eocene Laguna del Hunco (LH) fossil site, northwestern Chubut Province, Argentina, holds one of the best preserved and most diverse paleofloras worldwide. The paleoflora comprises ferns, gymnosperms, and flowering plants. Despite the rapidly growing knowledge of its macrofossil record, little is known about the site's palynological content. Herein, we present the first dispersed spore-pollen assemblages recovered from Laguna del Hunco.

Methodology. Palynological samples were collected from seven stratigraphic levels of the Tufolitas de Laguna del Hunco (Huitrera Formation), of which six yielded palynomorphs. We determine the botanical affinities of fossil morphotypes and provide systematic descriptions of some taxa. In addition, we establish similarities between LH and other Patagonian Eocene localities, and we compare palynological and prior megafloral records from LH.

Pivotal results. We identify 56 spore and pollen species and 28 plant families, of which eight are reported from the site reliably for the first time (Cyatheaceae, Schizaeaceae, Polypodiaceae, Asteraceae, Chloranthaceae, Nothofagaceae, Rubiaceae, and Ulmaceae). Among other Eocene Patagonian palynofloras, the LH assemblage is similar to Pampa de Jones/Nahuel Huapi Este and Confluencia.

Conclusions. The LH spore-pollen assemblages augment the plant fossil record for this significant Eocene locality by incorporating new taxa (e.g., Asteraceae, with one morphotype that represents the oldest record of the family in Patagonia). The new data also reinforce the presence of plant families previously reported from macrofossils, such as Juglandaceae, with pollen grains similar to the *Engelhardia-Alfaroa* group, and

45 Fagaceae (Castaneoideae), complementing the macrofossil record of leaves and
46 reproductive structures.

47

48 *Keywords*: Spores; pollen grains; early Eocene; Chubut Province; South America

49

Introduction

Eocene fossil sites of northwestern Patagonia have been well known in the scientific literature since the beginning of the last century (e.g., Berry 1925, 1938; Aragón and Romero 1984). These sites have yielded exceptionally well preserved fossils, including insects, frogs, fishes, and plant remains. Of special interest are the highly diverse paleofloras that include ferns, gymnosperms and flowering plants, with abundant leaves, fruits, flowers, and fossil woods; the Laguna del Hunco and Río Pichileufú floras are "among the most diverse fossil macrofloras known from any time period" (Wilf et al. 2005: p. 646). Laguna del Hunco has more than 100 leaf species reported (and more than 180 in current tallies) of dicots, monocots, conifers, ginkgophytes, cycads, and ferns and more than 20 reproductive species from these groups (e.g., Wilf et al. 2003, 2005). An equable climate, with winter temperatures warmer than 10°C and abundant, aseasonal rainfall, was suggested on the basis of floral composition, drought intolerance and niche conservatism of living relatives, and leaf-margin and leaf-area analyses (e.g., Wilf et al. 2003, 2009, 2017b; Wilf 2012; Merkhofer et al. 2015). These localities, along with others such as Pampa de Jones and Confluencia (e.g., Aragón and Romero 1984; Melendi et al. 2003), represent fossil caldera-lake beds embedded within the Huitrera Formation, which crops out in Neuquén, Río Negro and Chubut Provinces (Lage 1982; Aragón and Mazzoni 1997; Rapela et al. 1988; Iannelli et al. 2017; Butler et al. 2019). The Huitrera Formation consists mainly of tuff, mudstone, and sandstone beds of lacustrine environments.

The first publication on the paleoflora of Laguna del Hunco was by E.W. Berry (1925) based on fossils collected by B. Clark during prospecting work "in gullies of a white hill just south of an andesitic mesa known as Mirador" (Berry 1925: p.184). Berry recognized 36 species of plants and placed 22 of these within botanical families. After

75 Berry's initial work, only a few contributions on the flora were published over several
76 decades (e.g., Frenguelli and Parodi 1941; Frenguelli 1943; Romero and Hickey 1976;
77 Romero et al. 1988). However, in recent years, there have been numerous scientific
78 contributions based on renewed fieldwork efforts that have increased our systematic
79 knowledge of the Laguna del Hunco and Río Pichileufú fossil floras (e.g., Zamaloa et
80 al. 2006; González et al. 2007; Wilf et al. 2009; Barreda et al. 2010; Gandolfo et al.
81 2011; Wilf 2012; Villar de Seoane et al. 2015; Hermsen and Gandolfo 2016; Wilf et al.
82 2014, 2017a/b, 2019a). These discoveries have revealed the varied biogeographic
83 connections of ancient Patagonia, which are especially strong in relation to living
84 Australasian and Malesian floras of mesic, usually montane rainforests but also show
85 links to the Neotropics and southern Africa (for summaries see Wilf et al. 2009, 2013,
86 2019a; Kooyman et al. 2014).

87 Over the last two decades there has been a considerable increase in the
88 geochronological control of these classic Patagonian Eocene fossil sites, providing a
89 precise framework for analyzing major biotic changes during the significant early
90 Paleogene interval of climate change and biotic evolution. From Pampa de Jones (the
91 oldest, ca. 54.2 Ma) to Río Pichileufú (the youngest, ca. 47.7 Ma), they cover ca. 6 myr
92 of early-middle Eocene life history (Wilf et al. 2005, 2010), and the Laguna del Hunco
93 locality occupies an intermediate age position near 52 Ma, the time of the early Eocene
94 climatic optimum (Zachos et al. 2001) and the final stage of Gondwana (Lawver et al.
95 2011). Moreover, the Confluencia locality is considered middle Eocene or younger on
96 the basis of palynology (Melendi et al. 2003).

97 Despite the rapidly growing understanding of the paleontology and geology of
98 Laguna del Hunco and Río Pichileufú, little is still known of their palynological content
99 due, in part, to the scarcity of palynomorphs in these tuffaceous, siliceous rocks. Most

100 palynological knowledge of the Huitrera Formation comes from the Pampa de Jones
101 (also "Nahuel Huapi Este") and Confluencia localities (Báez et al. 1991; Melendi et al.
102 2003; Wilf et al. 2010), which both have limited macrofloral data; the few reports from
103 Laguna del Hunco and Río Pichileufú consist of in-situ pollen found in well-preserved
104 reproductive structures (Zamaloa et al. 2006; Barreda et al. 2010). The first attempt to
105 obtain palynomorphs from the Laguna del Hunco sediments was by Archangelsky
106 (1974), and since then, several other unsuccessful efforts were performed.

107 Here we present the first spore-pollen assemblages from the well-dated early
108 Eocene deposits of Laguna del Hunco, northwestern Chubut Province (fig. 1, ca. 52
109 Ma). We compare our palynological results with the macrofloras from the same strata
110 and discuss the position of the palynofloras in the evolutionary sequence of the Eocene
111 austral floras.

112 **Materials and Methods**

113 Spore-pollen samples were collected from seven stratigraphic levels of the
114 Tufolitas de Laguna del Hunco (an informal unit of the Huitrera Formation) in Chubut
115 Province, from the 170 m thick section of fossil lake beds described elsewhere (Wilf et
116 al. 2003; Gandolfo et al. 2011; figs. 1, 2), which contains 27 plant-megafossil localities
117 (LH01-LH27). These outcrops are remains of a fossil caldera lake emplaced in the
118 Middle Chubut River Volcanic-Pyroclastic Complex of Aragón and Mazzoni (1997).
119 Seven samples were processed using standard palynological techniques, of which six
120 yielded palynomorphs. The slides are housed in the palynological collection of the
121 Museo Paleontológico Egidio Feruglio, Trelew (MPEF-PA 305-310). Coordinates of
122 the illustrated specimens are referred to the England finder. Pollen terminology follows
123 Punt et al. (2007). Fossil spores and pollen grains were identified to species level

whenever possible (table 1). We diagnosed the modern botanical affinity of fossil morphotypes and grouped them into taxonomic categories whenever possible (i.e. classes, orders, or families). Six -hundred specimens were counted in sample C12, which came from one of very few organic-rich horizons in the whole section (bed C12 of Wilf et al. 2003; see also fig. 2), but the other samples had too few palynomorphs for counts (less than a minimum of 200 specimens).

The program Palaeontological Statistics (PAST) of Hammer et al. (2001) was used for determining similarities among the Laguna del Hunco assemblages and those reported from other localities of the Huitrera Formation (i.e., Pampa de Jones (PJ)/Nahuel Huapi Este (NHE), and Confluencia (C), Neuquén Province, Báez et al. 1991; Melendi et al. 2003; Wilf et al. 2010), and the Ligorio Márquez Formation (LM), Santa Cruz Province (Macphail et al. 2013) based on presence/absence data (table 2). The data matrix was analyzed using the Jaccard coefficient, applying the UPGMA technique. The ages of these units range from the late Paleocene to the middle Eocene based on $^{40}Ar/^{39}Ar$ geochronology of tuffs closely associated with the fossils (Pampa de Jones: $^{40}Ar/^{39}Ar$ age of 54.24 ± 0.45 Ma; Laguna del Hunco: $^{40}Ar/^{39}Ar$ age of 52.22 ± 0.22 Ma; Río Pichileufú: $^{40}Ar/^{39}Ar$ age of 47.46 ± 0.05 Ma; Wilf et al. 2005, 2010; Wilf 2012). Confluencia: only has a tentative radioisotopic age, a whole-rock K-Ar date of 52 ± 3 Ma (Rapela et al. 1983, 1984), but it is considered middle Eocene or younger on the basis of palynology (Melendi et al. 2003). The isolated Ligorio Márquez Formation exposure in Santa Cruz that yielded pollen (and macrofossils) is constrained only to the late Paleocene/early or middle? Eocene, although the most likely age is early Eocene based on the fossil content (Macphail et al. 2013; Carpenter et al. 2018).

Results

Composition and comparison of the LH spore-pollen assemblages

The palynological material recovered from Laguna del Hunco, although moderately to poorly preserved, is relatively diverse. The organic debris yielded spores, pollen grains, fungal remains and amorphous organic matter. Fifty-six spore and pollen species were identified (table 1, figs. 3-5), broken down as 14 pteridophytes, 11 gymnosperms, and 31 angiosperms. From these, 39 species were taxonomically placed within families (11 ferns, 10 gymnosperms, and 18 angiosperms); the others have doubtful or uncertain botanical affinity. Overall, we recognized 28 families, 8 of them reported reliably for the first time at LH, and 17 supporting previous megafossil records (table 3). These records, combined with those only recorded from megafossils (7 families), provide a total of 30 confidently assigned plant families for the LH locality.

Spore-pollen assemblages from sample C12 are dominated by angiosperms (ca. 45%), followed by ferns (ca. 19%) and gymnosperms (ca. 17%, table 1). Fungal spores are also well represented (ca. 19 %). Among angiosperms Juglandaceae (*Plicatopollis wodehousii*) is the most abundant family (ca. 24%, figs. 4A, 5A, D). There are also records of Nothofagaceae (*Nothofagidites*), with species related to subgenera *Fuscospora* (ca. 4.5%, fig. 3Q) and *Nothofagus* (ca. 0.5%, fig. 3S); Anacardiaceae (*Striatricolporites gamerroi*, fig. 4I; *Striatricolporites* sp. 2. fig. 5I); Proteaceae (figs. 4S, T); and other eudicots of uncertain affinity (e.g., *Rhoipites* cf. sphaerica, figs. 4D, H, 5F). Asteraceae (*Huanilipollis cabrerae*, fig. 4C) are also recorded but in trace amounts. Other minor angiosperm components in the sample are related to Myrtaceae (fig. 4N), Cunoniaceae (fig. 5J), Casuarinaceae (fig. 4O), Fabaceae (fig. 4L), Ulmaceae (fig. 4F), Malvaceae-Tilioideae (figs. 4G, 5G), Chloranthaceae (fig. 5C), and a likely Fagaceae

(Castaneoideae, figs. 4M, 5B). For ferns, spores of Cyatheaceae (ca. 9%) and Dicksoniaceae (ca. 3%, figs. 3C, D) are significant components of the assemblage. Gymnosperms are mainly represented by Podocarpaceae (ca. 10%) and Araucariaceae (ca. 6%). Podocarpaceae include pollen types comparable to extant *Podocarpus* (*Podocarpidites*, figs. 3L, P), *Dacrydium* (*Lygistepollenites florinii*) and *Dacrycarpus* (*Dacrycarpites australiensis*). Araucariaceae are well represented by three fossil species close to those of extant *Araucaria* (*Araucariacites australis*, fig. 3M) and *Wollemia/Agathis* (*Dilwynites* spp., figs. 3K, N-O).

A comparison among Eocene Patagonian palynofloras using cluster analysis shows that LH is similar to Nahuel Huapi Este and Confluencia, with less similarity to the Ligorio Márquez Formation palynoflora (fig. 6).

Systematic section

This section provides brief and informal descriptive notes and dimensions on the species recorded in the LH assemblage. Species are listed in alphabetical order within the major plant groups Pteridophytes, Gymnospermophyta, and Magnoliophyta, as in Table 1.

Pteridophytes

Genus -Baculatisporites *Pflug and Thomson in Thomson and Pflug 1953*

Type species. Baculatisporites primarius *(Wolff) Thomson and Pflug 1953*

Species -Baculatisporites comaumensis *(Cookson) Potonié 1953*

not illustrated

Dimensions (1 specimen measured). Equatorial diameter: 38-54 μm.

194 *Comments*. The species is widely recorded in southern South America since the
195 Paleocene to the Miocene. These spores resemble those produced by extant
196 Osmundaceae.

197 *Genus* -Biretisporites *(Delcourt and Sprumont) Delcourt, Dettmann and Hughes 1963*

198 *Type species*. Biretisporites potoniaei *Delcourt and Sprumont 1955*

199 *Species* -Biretisporites sp.

200 fig. 3I

201 *Dimensions* (2 specimens measured). Equatorial diameter: 26-29 µm.

202 *Comments*. The scarce and poorly preserved specimens prevent species assignation. The
203 genus is related to Schizaeaceae.

204 *Genus* -Cyathidites *Couper 1953*

205 *Type species*. Cyathidites australis *Couper 1953*

206 *Species* -Cyathidites australis *Couper 1953*

207 not illustrated

208 *Dimensions* (10 specimens measured). Equatorial diameter: 45-58 µm.

209 *Comments*. The species is well represented in the palynoassemblage. The specimens
210 show similarities with some spores of extant Cyatheaceae.

211 *Species* -Cyathidites minor *Couper 1953*

212 not illustrated

213 *Dimensions* (15 specimens measured). Equatorial diameter: 22-29 µm.

214 *Botanical affinity*. Similar spores are produced by members of several fern families such
215 as Cyatheaceae (*Cyathea*), Dicksoniaceae, and Schizaeaceae (Raine et al. 2011).

216 *Genus* -Deltoidospora *Miner 1935*

217 *Type species*. Deltoidospora hallii *Miner 1935*

218 *Species* -Deltoidospora sp.

219 not illustrated

220 *Dimensions* (10 specimens measured). Equatorial diameter: 37-48 µm.

221 *Botanical affinity*. Several families of living Pteridophyte produce spores similar in
222 morphology and size to *Deltoidospora* sp.

223 *Genus* -Gleicheniidites *Ross 1949 ex Delcourt and Sprumont 1955 emend. Dettmann*
224 *1963*

225 *Type species*. Gleicheniidites senonicus *Ross 1949*

226 *Species* -Gleicheniidites senonicus *Ross 1949*

227 fig. 3H

228 *Dimensions* (4 specimens measured). Equatorial diameter: 35-37 µm.

229 *Botanical affinity*. Species related to Gleicheniaceae.

230 *Genus* -Ischyosporites *Balme 1957*

231 *Type species*. Ischyosporites crateris *Balme 1957*

Species -Ischyosporites areapunctatis *(Stuchlik) Barreda 1997*

fig. 3C

Dimensions (15 specimens measured). Equatorial Diameter: 49-65 µm.

Botanical affinity. Probably related to Dicksoniaceae.

Species -Ischyosporites sp.

fig. 3E

Dimensions (1 specimen measured): Equatorial diameter: 57 µm.

Comments. This spore is scarce and only recorded in one sample. Probably related to Dicksoniaceae.

Genus -Laevigatosporites *Ibrahim 1933*

Type species. Laevigatosporites vulgaris *(Ibrahim) Ibrahim 1933*

Species -Laevigatosporites ovatus *Wilson and Webster 1946*

not illustrated

Dimensions (5 specimens measured). Length: 29-44 µm.

Comments. Monolete psilate spores are common among polypods. These spores may be as well representing ornamented perisporate spores that loosed the perispore during fossilization process.

Genus -Polypodiaceoisporites *Potonié 1951 ex Potonié 1960*

Type species. Polypodiaceoisporites speciosus *Potonié 1951 ex Potonié 1960*

Species -Polypodiaceoisporites sp.

figs. 3A, 3B, 5L

Description. Spore free, anisopolar, amb subtriangular, apices rounded, sides convex; trilete, cingulate; distal face convex, proximal face pyramidal. Lesurae ondulate to straight, extending to the inner margin of cingulum. Cingulum 3-4.3 µm thick. Proximal face with small verrucae and rugae mainly in the area of each contact faces; distal face with irregular muri and rugae, sculptural elements occasionally fused giving an uneven to almost irregular distal reticulum.

Dimensions (7 specimens measured). Equatorial diameter: 34-39 µm.

Botanical affinity. These specimens show broad similarities with spores of extant Pteridaceae (Tryron and Lugardon 1990).

Genus -Polypodiidites *Ross ex Couper 1953*

Type species. Polypodiidites senonicus *Ross 1949*

Species -Polypodiidites sp.

fig. 3J

Dimensions (1 specimen measured). Length: 29 µm.

Botanical affinity. Unknown fern.

Species -Polypodiidites speciosus *(Harris) Archangelsky 1972*

fig. 3G

Dimensions (1 specimen measured). Length: 34 µm.

Botanical affinity. Related to Polypodiaceae.

Genus -Todisporites *Couper 1958*

Type species. Todisporites major *Couper 1958*

Species -Todisporites major *Couper 1958*

fig. 3F

Dimensions (1 specimen measured). Equatorial diameter: 61 µm.

Comments. This trilete spore is characterized by the large size and globose shape. Closely related to Osmundaceae.

Genus -Trilites *Erdtman ex Couper emend. Dettmann 1963*

Type species. Trilites tuberculiformis *Cookson emend. Dettmann 1963*

Species -Trilites tuberculiformis *Cookson emend. Dettmann 1963*

fig. 3D

Dimensions (2 specimens measured). Equatorial diameter: 39-45 µm.

Botanical affinity. These spores closely resemble those produced by members of the genus *Dicksonia* in the Dicksoniaceae.

Gymnospermophyta

Genus -Araucariacites *Cookson and Couper 1953*

Type species. Araucariacites australis *Cookson 1947*

289 *Species* -Araucariacites australis *Cookson 1947*

290 fig. 3M

291 *Dimensions* (19 specimens measured). Diameter: 61-80 µm.

292 *Comments*. These relatively large inaperturate and densely
293 microgranulate/microechinate pollen grains are frequent in LH sediments. They are
294 closely related to *Araucaria* of the Araucariaceae.

295 *Genus* -Cycadopites *(Wodehouse, Wilson and Webster) Herbst 1965*

296 *Type species.* Cycadopites follicularis *Wilson and Webster 1946*

297 *Species* -Cycadopites sp.

298 not illustrated

299 *Dimensions* (1 specimen measured). Length: 17 µm.

300 *Botanical affinity*. Members of the Cycadales and Ginkgoales produce pollen similar to
301 this type.

302 *Genus* -Dacrycarpites *Cookson and Pike 1953*

303 *Type species.* Dacrycarpites australiensis *Cookson and Pike 1953*

304 *Species* -Dacrycarpites australiensis *Cookson and Pike 1953*

305 not illustrated

306 *Dimensions* (1 specimen measured). Diameter: 44.5 µm.

307 *Botanical affinity*. Podocarpaceae (*Dacrycarpus*)

Genus -Dilwynites *Harris 1965*

Type species. Dilwynites granulatus *Harris 1965*

Commens. *Dilwynites* has affinity with pollen of the extant genera *Agathis* and *Wollemia* of the Araucariaceae (Macphail and Carpenter 2014). This family has an abundant macrofossil record during the Mesozoic and early Cenozoic; however, most of these records correspond to *Araucaria* (e.g., Kunzmann 2007; Panti et al. 2012). Two basal agathiods are known from the Cretaceous of Australia and New Zealand (see Cantrill and Raine 2006; Dettmann et al. 2012; Escapa and Catalano 2013), but *Wollemia* has no definite fossil record. *Agathis* fossils are scarce and had come mainly from Australia and New Zealand (Hill et al 2008; Pole 2008). However, Wilf et al. (2014) reported the first fossils of *Agathis* in Patagonia from the Eocene Laguna del Hunco and Río Pichileufú localities of the Huitrera Formation, extending the past distribution of the genus to South America (Wilf et al. 2014). Escapa et al. (2018) later reported leaves related to *Agathis* from the uppermost Maastrichtian Lefipán Formation, which represents the oldest potential record of *Agathis* in Patagonia, and multiple reproductive and vegetative organs of a basal *Agathis* from the early Danian Salamanca Formation. Pollen of *Dilwynites* was previously reported in Patagonia in the Early Cretaceous Baqueró Group (Villar de Seoane and Archangelsky 2014), in the late Paleocene/early-middle Eocene Ligorio Márquez Formation (Macphail et al. 2013) and in the early Danian Salamanca Formation (Escapa et al. 2018), where it was found in situ within pollen sacs of *Agathis*.

Species -Dilwynites granulatus *Harris 1965*

fig. 3K

331 *Dimensions* (2 specimens measured). Diameter: 47-52 µm.

332 *Comments*. These specimens fit well with the diagnosis of the type material defined
333 from Australia (Harris 1965). This species has an extensive record in Australia and New
334 Zealand since the Cretaceous to Neogene. In Patagonia it was only previously recorded
335 in the early Cretaceous of Santa Cruz Province (Villar de Seoane and Archangelsky
336 2014).

337 *Species* -Dilwynites cf. tuberculatus *Harris 1965*

338 figs. 3N, 3O

339 *Dimensions* (5 specimens measured). Diameter: 46-51 um.

340 *Comments*. These pollen grains are spheroidal, but usually folded, isopolar, inaperturate,
341 and densely ornamented with irregularly-spaced verrucae (1–2 µm in diameter and
342 height), and apparently with psilate areas between the sculptural elements. This species
343 was previously reported in the late Paleocene/early-middle Eocene Ligorio Marquez
344 Formation of southern Patagonia (Macphail et al. 2013). In-situ specimens of *Dilwynites*
345 in *Agathis* pollen cones from the early Danian Salamanca Formation, Chubut province
346 (Escapa et al. 2018) are smaller (19-35 µm) than the ones reported here.

347 *Genus* -Gamerroites *Archangelsky 1988*

348 *Type species.* Gamerroites volkheimeri *Archangelsky 1988*

349 *Species* -Gamerroites psilasaccus *(Archangelsky and Romero) Archangelsky 1988*

350 not illustrated

351 *Dimensions* (1 specimen measured). Total length: 45µm.

352 *Botanical affinity*. Podocarpaceae.

353 *Genus* -Lygistepollenites *Stover and Evans 1973*

354 *Type species.* Lygistepollenites balmei *(Cookson) Stover and Evans 1973*

355 *Species* -Lygistepollenites florinii *(Cookson and Pike) Stover and Evans 1973*

356 not illustrated

357 *Dimensions* (4 specimens measured). Total length: 43-47 µm.

358 *Botanical affinity*. Podocarpaceae (*Dacrydium*).

359 *Genus* -Microcachryidites *Cookson 1947*

360 *Type species.* Microcachryidites antarcticus *Cookson 1947 ex Couper 1953*

361 *Species* -Microcachryidites antarcticus *Cookson 1947 ex Couper 1953*

362 not illustrated

363 *Dimensions* (2 specimens measured). Diameter: 35-37 µm.

364 *Botanical affinity.* Podocarpaceae *(Microcachrys).*

365 *Genus* -Podocarpidites *Cookson 1947*

366 *Type species.* Podocarpidites ellipticus *Cookson 1947 ex Couper 1953*

367 *Species* -Podocarpidites elegans *Romero 1977*

368 fig. 3P

369 *Dimensions* (12 specimens measured): Total length: 29-41 µm.

370 *Comments*. This is a frequent species of bisaccate pollen grains found in LH. Related to
371 Podocarpaceae (*Podocarpus*).

372 *Species* -Podocarpidites ellipticus *Cookson 1947*

373 fig. 3L

374 *Dimensions* (15 specimens measured). Total length: 43-55 µm.

375 *Comments*. These pollen grains are the most frequently found among the gymnosperms
376 in LH sediments. They are related to Podocarpaceae (*Podocarpus*).

377 *Species* -Podocarpidites marwickii *Couper 1953*

378 not illustrated

379 *Dimensions* (1 specimen measured). Total length: 70 µm.

380 *Botanical affinity*. Podocarpaceae (*Podocarpus*).

381 Magnoliophyta

382 *Genus* -Clavatipollenites *Couper 1958*

383 *Type Species.* Clavatipollenites hughesii *Couper 1958*

384 *Species* -Clavatipollenites sp.

385 fig. 5C

386 *Dimensions* (1 specimen measured). Diameter: 16 µm.

Comments. Only one specimen of this distinctive pollen type was recorded in the LH assemblage during SEM analysis. Resemble pollen of extant *Ascarina* of the Chloranthaceae.

Genus -Cupuliferoipollenites *Potonié 1951 ex Potonié 1960*

Type species. Cupuliferoipollenites pusillus *Potonié 1951 ex Potonié 1960*

Species -Cupuliferoipollenites sp. 1

figs. 4M, 5B

Description. Pollen grain free, isopolar, small, subprolate, with oval outline. Tricolporate, colpi long extending 4/5 of the polar diameter, ora small. Exine 0,8-1.1 µm thick, stratification obscure, striate/rugulate (observed under SEM) the rugulae are flattened and smooth in appearance, and partially fused (rodlike fused).

Dimensions (3 specimens measured). Polar diameter: 11-16 µm

Comments. Patagonian specimens fit in size (very small), shape, and external morphological features (striate/rugulate) with pollen of Fagaceae (Castaneoideae), particularly with the specimens illustrated from the middle Eocene of North America (*Castaneoideae puryearensis*, Figs. 19-20; Crepet and Daghlian 1980) and from the Eocene of Greenland (Castaneoideae, aff. *Castanopsis* Fig. 7 g-l; Grimsson et al. 2015). The LH material is not well preserved, but under SEM it is possible to observe the striate/rugulate sculpture. Dispersed fossil pollen with morphological similarities to pollen of extant Castaneoideae has commonly been assigned to the form-genus *Cupuliferoipollenites* (Potonié 1960).

Fagaceae, the family of beeches and oaks, are trees and shrubs that are ecologically important from temperate forests of the Northern Hemisphere (North America, Europe and Asia) to the tropics, especially the SE Asian tropics. Until recently, no fossil members of Fagaceae had been found in the Southern Hemisphere; however, Wilf et al. (2019a) discovered two fossil infructescences and hundreds of leaves of Fagaceae (*Castanopsis*) in the Laguna del Hunco flora. These records suggest that *Castanopsis* evolved in Gondwana from an ancestor that had probably dispersed earlier from North America (Wilf et al. 2019a, b; see also Denk et al. 2019).

Genus -Haloragacidites *Couper 1953*

Type species. Haloragacidites trioratus *Couper 1953*

Species -Haloragacidites harrisii *(Couper) Harris 1971*

fig. 4O

Dimensions (2 specimens measured). Equatorial diameter: 22-24 µm.

Comments: The species was previously found in situ in male inflorescences of *Gymnostoma*, Casuarinaceae, derived from locality LH6 (Zamaloa et al. 2006). In this study only a few dispersed pollen grains were recovered from the same levels bearing megafossils. *H. harrisii* was recorded in Patagonia in the late Cretaceous (Barreda et al. 2012a), Paleocene and Eocene (e.g. Zamaloa et al. 2006), and Oligocene (Barreda et al. 2009).

Genus -Huanilipollis *Barreda and Palazzesi 2008 (in Barreda et al., 2008)*

Type species. Huanilipollis cabrerae *Barreda and Palazzesi 2008*

Species -Huanilipollis cabrerae *Barreda and Palazzesi 2008*

fig. 4C

Remarks. *H. cabrerae* assemble tricolporate, micro-echinate pollen grains, characterized by having the sexine formed by two ramified columellate sublayers (endosexine and ectosexine), with delicate columellae separated by an internal tectum (Barreda et al. 2008). The LH specimen conforms closely to *H. cabrerae*, defined from the Miocene of central Patagonia (Barreda et al. 2008), although being slightly smaller.

Dimensions (1 specimen measured). Polar diameter: 20 µm.

Comments. *H. cabrerae* is similar to pollen of extant *Holocheilus*, *Jungia*, and *Proustia* of the Nassauvieae (Mutisioideae, Asteraceae) (Barreda et al. 2008). This tribe comprises 25 genera and ca. 320 species of vines, shrubs and low trees endemic to America being an important component of the flora at the central and southern Andean region (Katinas et al. 2008). This is the oldest finding of Asteraceae in Patagonia and one of the oldest of non-Barnadesioideae Asteraceae worldwide. The family was previously known in the region from a capitulum with in-situ pollen of the Mutisioideae/Carduoideae type from the early middle Eocene at Río Pichileufú (Barreda et al. 2010, 2012b). Moreover, pollen with affinity to the basalmost branch of Asteraceae (subfamily Barnadeioideae) was reported for the latest Cretaceous of Antarctica (Barreda et al. 2015, Huang et al 2016). Previous records of the tribe Nassauvieae were from the Miocene of central Patagonia (Barreda et al. 2008).

Genus -Intratriporopollenites *Thomson and Pflug 1953 emend. Mai 1961*

Type species. Intratriporopollenites instructus *(Potonié) Thomson and Pflug 1953*

Species -Intratriporopollenites sp.

figs. 4G, 5G

Description. Pollen grain tricolporate, oblate, with circular amb. Colpi short, extending slightly beyond the margins of the ora. Ora circular (ca. 2 µm in diameter). Exine 1.5 um thick, nexine thinner than sexine (ca. 1 µm thick) except around the ora where the nexine is thickened. Sexine columellate, reticulate. Reticulum with small lumina (0.5-0.7 µm in diameter) irregular in shape, muri simplibaculate, very thin (ca. 0.1-0.2 µm thick).

Dimensions (2 specimens measured). Equatorial diameter: 24-35 µm.

Comments. These specimens are comparable to those described from the Eocene Río Turbio Formation, Santa Cruz Province, Argentina (Romero and Zamaloa 1985). They have a similar exine pattern and size. This genus has an affinity with Malvaceae (Tilioideae similar to extant *Tilia* (Mai 1961).

Genus -Malvacipolloides *Anzótegui and Garralla 1985*

Type species. Malvacipolloides densiechinata *Anzótegui and Garralla 1985*

Species –Malvacipolloides? sp.

not illustrated

Dimensions (1 specimen measured). Equatorial diameter: 20 µm.

Comments. A single strongly echinate tricolporate pollen grain was recovered from these assemblages that slightly resembles pollen of the Malvaceae.

Genus -Margocolporites *Ramanujam ex Srivastava 1969 emend. Pocknall and Mildenhall 1984*

Type species. Margocolporites tsukadai *Ramanujam 1966 ex Srivastava 1969*

Species -Margocolporites sp.

fig. 4L

Description. Pollen grain tricolporate, oblate, amb subcircular. Colpi long, extending almost to poles, bordered by a narrow margo, ora small, circular. Exina 1.5 µm thick, stratified. Nexine and sexine of the same thickness, sexine microreticulate. Lumina subcircular to irregular 0.3- 0.5 µm in diameter.

Dimensions (1 specimen measured). Equatorial diameter: 18 µm.

Comments. This form resembles *M. tenuireticulatus* Barreda 1997. However, as only one specimen was recovered in the LH assemblage and it is not clear the reduction in the lumina size towards colpi and poles observed in the type material (Barreda 1997), this specimen was provisionally left in open nomenclature. It shows similarities with pollen of extant Fabaceae (Mimosoideae).

Genus -Mytaceidites *Cookson and Pike 1954 ex Potonié 1960*

Type species. Myrtaceidites mesonesus *Cookson and Pike 1954 ex Potonié 1960*

Species -Myrtaceidites sp.

fig. 4N

Dimensions (6 specimens measured). Equatorial diameter: 22-25 µm.

491 *Comments*. Only a few, bad preserved specimens of the Myrtaceae family were
492 recovered in the LH assemblage.

493 *Genus* -Nothofagidites *Erdman 1947 ex Potonié 1960*

494 *Type species*. Nothofagidites flemingii *(Couper 1953) Potonié 1960*

495 *Species* -Nothofagidites flemingii *(Couper 1953) Potonié 1960*

496 fig. 3S

497 *Dimensions* (2 specimens measured). Equatorial diameter: 38-42 µm.

498 *Botanical affinity*. Nothofagaceae (*Nothofagus* (*Nothofagus*))

499 *Species* -Nothofagidites saraensis *Menéndez and Caccavari 1975*

500 fig. 3Q

501 *Dimensions* (10 specimens). Equatorial diameter: 24-31 µm.

502 *Botanical affinity.* Nothofagaceae (*Nothofagus* (*Fuscospora*))

503 *Species* -Nothofagidites sp.

504 fig. 3R

505 *Dimensions* (6 specimens measured). Equatorial diameter: 21-27 µm.

506 *Botanical affinity.* Nothofagaceae (*Nothofagus*, extinct brassi type)

507 *Genus* -Palaeocoprosmadites *Ramanujam 1966*

508 *Type species*. Paleocoprosmadites areotense *Ramanujam 1966*

Species -Palaeocoprosmadites sp.

fig. 4E

Description. Pollen grain tricolporate, oblate to subspheroidal. Colpi short, resulting in a large polar area, narrow; ora lalongate, not clearly discernible. Exine 1 µm thick, scabrate, microgranulate, sexine columellate.

Dimensions (1 specimen measured). Equatorial diameter: 23 µm.

Comments. This specimen is comparable with *Paleocoprosmadites zelandiae* Pocknall 1982 defined from the Oligocene of New Zealand (Pocknall 1982), but the LH specimen is smaller with a considerably thinner exine. This specimen shows broad similarities with pollen of extant *Coprosma* (Rubiaceae). Berry (1938) reported leaves of two different species of *Coprosma* in the Río Pichileufú flora, but this material is pending of revision (Graham 2009). *Coprosma* is a large (more than 100 species) and widespread genera distributed from Australia and Indonesia, east through the Pacific islands and with a high diversity in New Zealand (Heads 2017), but it does not grow today in South America.

Genus -Plicatopollis *Potonié 1934*

Type species. Plicatopollis plicatus *(Potonié 1934) Krutzsch 1962*

Species -Plicatopollis wodehousei *(Nichols) Frederiksen and Christopher 1978*

figs. 4A, 5A, 5D

Remarks. These pollen grains are small, isopolar, triporate with vestibulate-aspidate apertures, oblate in shape with sub-triangular amb. The pores are circular to oval and the

530 exine is tectate with a spinulate sculpture observed under SEM. A three branched
531 thickening is commonly observed in the polar region of these grains.

532 *Dimensions* (14 specimens measured). Equatorial diameter: 20-25.5 μm.

533 *Comments*. Small vestibulate-aspidate pollen with spinules may be linked to
534 Casuarinaceae, Myricaceae and Juglandaceae. These three families have pollen with a
535 broadly similar morphology that hinders their differentiation under the light microscope.
536 However, they present subtle but clear differences under SEM. Both *Myrica* and
537 *Casuarina* present an exine sculpture with supratectal elevations where the spinules are
538 located; however, in the case of *Casuarina* the exine sculpture consists of short ridges,
539 with a linear organization, each of them bearing a row of spinules, and, in *Myrica*,
540 supratectal elevations are not arranged in a linear system, but grouped in an insular
541 pattern or remain single (Coetzee and Praglowski 1984). Juglandaceae, on the other
542 hand, have no ridges, and the spinules are distributed directly on the tectal surface.
543 Pollen grains reported here clearly belong to Juglandaceae, and within the family, these
544 pollen grains resemble the *Engelhardia-Alfaroa* group (small, isopolar, triporate) of
545 Whitehead (1965) and Nichols (1973).

546 Juglandaceae, the walnut family, is a family of trees and shrubs, centered in the
547 Americas, Eurasia and Southeast Asia. Juglandaceae have an extensive fossil record
548 (e.g., Manchester 1987), particularly in the Northern Hemisphere, where the family is
549 thought to have originated and diversified. The oldest records are pollen grains from the
550 Late Cretaceous (*Normapolles* complex), and numerous macrofossils have been
551 reported from the Paleocene onwards (e.g., Manchester 1987, and references therein). In
552 South America, fossils of Juglandaceae are scarce, but the family's presence in
553 Patagonia was first reported from pollen grains in the early Paleocene Salamanca and

554 Eocene Huitrera (Pampa de Jones site) formations (Zamaloa and Andreis 1995; Melendi
555 et al. 2003). More recently, fruits related to Engelhardioideae -one of the two
556 subfamilies of Juglandaceae- were described from the Laguna del Hunco flora (Huitrera
557 Fm.; Hermsen and Gandolfo 2016).

558 *Genus* -Propylipollis *Martin and Harris 1974*

559 *Type species*. Propylipollis reticuloscabratus *(Harris) Martin and Harris 1974*

560 *Species* -Propylipollis sp.

561 fig. 4T

562 *Description*. Pollen grain triporate, oblate, amb triangular, sides straight or nearly so.
563 Exine 1.5 µm thick. Nexine and sexine of about equal thickness. Nexine thickening at
564 the pore margins. Sexine reticulate, lumina irregular, small (ca. 0.5 µm).

565 *Dimensions* (1 specimen measured). Equatorial diameter: 42 µm.

566 *Comments*. This specimen shows broad similarities with *P. ivanhoensis* (Martin) Milne
567 1988 reported from the Eocene/Oligocene of Australia (e.g. Martin 1973, Milne 1988).
568 They share the presence of a very fine reticulate sculpture and comparable apertural
569 features. However, we only found one specimen, which is larger. *P. concretus* (Harris)
570 Martin and Harris 1974 is also similar, but it has a thicker exine with scabrate rather
571 than microreticulate sculpture. This species is common in the Eocene of Australia (e.g.
572 Milne 1988) and it was reported from the Huitrera Formation at Confluencia (Melendi
573 et al. 2003).

574 *Genus* -Proteaceidites *Cookson 1950 ex Couper 1953, emend. Dettmann and Jarzen*
575 *1996*

576 *Type species*. Proteacidites adenanthoides *Cookson 1950*

577 *Species* -Proteacidites sp.

578 fig. 4S

579 *Description*. Pollen grain triporate, oblate, amb triangular, sides slightly concave. Exine
580 thin, ca. 1 µm thick, thinning toward the pore margins. Nexine and sexine of about
581 equal thickness. Sexine micro-reticulate.

582 *Dimensions* (2 specimens measured). Equatorial diameter: 22-24 µm.

583 *Botanical affinity*. Proteaceae

584 *Genus* -Psilatricolporites *Van der Hammen 1956 ex Van der Hammen and Wijmstra*
585 *1964*

586 *Type species*. Psilatricolporites operculatus *Van der Hammen and Wijmstra 1964*

587 *Species* -Psilatricolporites sp. 1

588 fig. 4B

589 *Description*. Pollen grain small, tricolporate, psilate (LM), subprolate. Colpi relatively
590 long, ora lalongate. Exine tectate (1.5 µm thick), with the sexine thicker than the nexine.
591 Columellae indistinct. Nexine thickened at the colpi margin and around the ora.

592 *Dimensions* (14 specimens measured). Polar diameter: 18-22 µm.

593 Comments. These specimens show broad similarities with *P. protundens* Palazzesi and
594 Barreda defined to assemble pollen grains similar to pollen of extant Calyceraceae
595 (Palazzesi et al. 2010). In the LH specimens the nexine is thickened along the colpi and

596 towards ora, however it is not clear the wall protrusion on the external surface near the
597 ora that characterized the species. Moreover, it was not possible to observe the
598 specimens under SEM to determine if they have or not a faintly microechinate exine
599 under SEM.

600 *Botanical affinity*. Possibly Calyceraceae

601 *Species* -Psilatricolporites sp. *of Clyde et al. 2014*

602 not illustrated

603 *Dimensions* (1 specimen measured). Polar diameter: 26 µm.

604 *Comments*. A medium size, tricolporate, subprolate, psilate pollen grain with colpi
605 costae is similar to that illustrated from the Danian Salamanca Formation (Fig. 4R, in
606 Clyde et al. 2014).

607 *Botanical affinity*. Unknown eudicot.

608 *Genus* -Rhoipites *Wodehouse 1933*

609 *Type species.* Rhoipites bradleyi *Wodehouse 1933*

610 *Species* -Rhoipites baculatus *Archangelsky 1973*

611 fig. 4Q

612 *Dimensions* (2 specimens measured). Polar diameter: 20-22 µm.

613 *Botanical affinity*. Possibly Rutaceae

614 *Species* -Rhoipites cf. sphaerica *(Cookson) Pocknall and Crosbie 1982*

615 figs. 4D, 4H, 5F

616 *Description*. Pollen grain free, isopolar, subprolate; tricolporate, colpi long extending to
617 ⅔ of the polar diameter, margins straight, ora distinct, lalongate, 1-1.5 wide and up to
618 2.5 long, protruding. Exine clearly stratified. Nexine 0.4-0.5 µm thick. Sexine reticulate
619 thickened at the intercolpia and apocolpia (1.9-2 µm thick) and thinning gradually
620 towards colpi (0.8-0.8 µm thick); lumina of maximum diameter at the poles and
621 intercolpal regions (0.7-1.1 µm in diameter) diminishing in size towards colpi and poles
622 (0.16-0.26 µm in diameter); lumina subpolygonal to subcircular, muri 0.4-0.6µm wide
623 underlain by a single row of columelae.

624 *Dimensions* (10 specimens measured). Polar diameter: 22.3-34 µm.

625 *Comments.* The LH specimens fit well with the diagnosis of *R. sphaerica*, mainly
626 considering the variability of the species in shape, size of the mesh of the reticulum and
627 thickening of the exine (Stover and Partridge 1973). The Patagonian specimens present
628 thinner nexine and smaller and more protruding ora than the type material.

629 *Botanical affinity*. Unknown eudicot.

630 *Genus* -Simpsonipollis *Srivastava 1975*

631 *Type species*. Simpsonipollis mullensis *(Simpson) Srivastava 1975*

632 *Species* -Simpsonipollis sp.

633 not illustrated

634 Dimensions (1 specimen measured). Equatorial diameter: 21.5 µm.

635 *Comments*. A single, badly preserved, tricolporate, oblate and striate pollen grain was
636 provisionally placed within *Simpsonipollis*. Striate tricolporate grains are produced by
637 many modem families of dicot angiosperms (Muller 1968).

638 *Botanical affinity*. Unknown eudicot.

639 *Genus* -Striatricolporites *(van der Hammen 1956) Leidelmeyer 1966*

640 *Type species.* Striatricolporites pimulis *Leidelmeyer 1966*

641 *Species* -Striatricolporites gamerroi *Archangelsky 1973*

642 fig. 4I

643 *Dimensions* (11 specimens measured). Polar diameter: 24-28 µm.

644 *Botanical affinity*. Similar to pollen of the Anacardiaceae.

645 *Species* -Striatricolporites sp. 1

646 fig. 4K

647 *Description*. Pollen grain tricolporate, oblate to spheroidal with circular amb. Colpi
648 extending ⅔ of equatorial diameter, ora small, obscure. Exine 1µm thick, infra-
649 reticulate and supra-striate. Striae formed by elongate rugulae.

650 *Dimensions* (2 specimens measured). Equatorial diameter: 16-17 µm.

651 *Comments*. These specimens differ from the other types of *Striatricolporites* reported
652 from the LH assemblages in being oblate to spheroidal rather than prolate to subprolate.
653 The affinity with Anacardiaceae is doubtful.

654 *Species* –Striatricolporites sp. 2

fig. 5I

Dimensions (1 specimen measured): Polar diameter: 18 µm.

Comments. This small tricolporate, subprolate, infra-reticulate and supra-striate pollen grain is similar to *S. gamerroi* here reported, but differs in being smaller.

Botanical affinity. Anacardiaceae

Genus -Tetracolporites *Couper 1953 emend. Pocknall and Mildenhall 1984*

Type species. Tetracolporites oamaruensis *Couper 1953*

Comments. We accepted the emendation of the genus *Tetracolporites* (Pocknall and Mildenhall 1984) to include tricolporate and pentacolporate pollen grains with reduced sculpturing.

Species -*Tetracolporites* sp.

fig. 4P

Description. Pollen grain pentacolporate, zonaperturate, spheroidal with circular outline. Colpi short (½ of the polar diameter), ora circular, endoanulate. Exine 1.3 µm thick, psilate, stratification obscure.

Dimensions (1 specimen measured). Polar diameter: 22 µm.

Comments. This specimen show broad similarities with *Tetracolporites spectabilis* Pocknall and Mildenhall 1984. They share the presence of pentacolporate apertures, short colpi and psilate exine, however, the LH specimen is considerably smaller.

Botanical affinity. Unknown eudicot.

675 *Genus* -Triatripollenites *Thomson and Pflug 1953*

676 *Type species.* Triatriopollenites rurensis *Thompson and Pflug 1953*

677 *Species* -Triatriopollenites lateflexus *Archangelsky 1973*

678 fig. 4R

679 *Dimensions* (1 specimen measured). Equatorial diameter: 16 µm.

680 *Botanical affinity*. Possibly Myricaceae

681 *Genus* -Tricolpites *Cookson ex Couper 1953*

682 *Type species*. Tricolpites reticulatus *Cookson 1947*

683 *Species* -Tricolpites angululuminosus *Anderson 1960*

684 fig. 4J

685 *Dimensions* (2 specimens measured). Equatorial diameter: 24-27 µm.

686 *Comments*. Two specimens of this distinctive pollen grain were recovered from the LH
687 locality. This species was previously reported in Argentina from the Paleocene and
688 Eocene (e.g., Archangelsky 1973, Romero and Zamaloa 1985, Melendi et al. 2003).

689 *Botanical affinity*. Unknown eudicot.

690 *Genus* -Tricolporites *Cookson 1947*

691 *Type species.* Tricolporites sphaericus *Cookson 1947*

692 *Species* -Tricolporites sp. 1

693 fig. 5E

694 *Description.* Pollen grain tricolporate, oblate to subspheroidal, with circular to
695 subcircular amb. Colpi short (less than 1/3 of the equatorial diameter), ora lalongate.
696 Exine 1 µm thick, nexine thinner than sexine. Sexine scabrate at LM and rugulate under
697 SEM.

698 *Dimensions* (2 specimens measured). Equatorial diameter: 16-17 µm.

699 *Comments*. This species show broad similarities with *Cupuliferoipollenites* sp. 1 here
700 described, particularly by the presence of a slightly rugulate sculpture and small size,
701 but differs in shape and in the length of colpi.

702 *Botanical affinity*. Possibly Fagaceae.

703 *Species* -Tricolporites sp. 2

704 fig. 5J

705 *Description*. Small pollen grains, isopolar, subprolate to spheroidal. Tricolporate, colpi
706 long, ora often obscure. Exine semitectate, 1-1.1 um thick, with the sexine of the same
707 thickness than nexine. Sexine reticulate, lumina sub-polygonal slightly increasing in
708 size on the intercolpal region reaching 0.6 µm in diameter.

709 *Dimensions* (3 specimens measured). Polar diameter: 12-14 µm

710 *Comments*. These small tricolporate reticulate pollen grains with coarser reticulum in
711 the intercolpal area are comparable to those produced by extant *Weinmannia* of the
712 Cunoniaceae.

713 This family of woody plants, mostly found in tropical regions of the Southern
714 Hemisphere, has a rich fossil record in Australia, but some microfossils and
715 macrofossils have been reported from the Paleogene of southern South America,
716 including spectacular flowers with in-situ pollen from the Danian Salamanca Formation
717 (Jud et al 2018a). At Laguna del Hunco (Huitrera Formation), Gandolfo and Hermsen
718 (2012, 2017) described fossil winged fruits of Cunoniaceae (*Ceratopetalum*).

719 *Species* -Tricolporites sp. 3

720 fig. 5K

721 *Description*. Pollen grain tricolporate, subprolate, with oval outline. Colpi long, almost
722 reaching poles. Apocolpia small. Ora obscure. Exine 1-1.5 µm thick, thinning toward
723 apertures. Nexine thinner than sexine. Sexine coarsely reticulate, reticulum
724 heterobrochate, lumina poligonal to irregular, largest on mesocolpia (1-2 µm in
725 diameter), floor of lumina composed of reduced columelae, smaller lumina concentrated
726 near margins of colpi (less than 0.5 µm). Muri underlain by a single row of columelae
727 with fused heads.

728 *Dimensions* (2 specimens measured). Polar diameter: 18-20 µm.

729 *Botanical affinity*. This distinctive form shows broad resemblances with pollen of the
730 Rubiaceae although many other families have similar pollen.

731 *Genus* -Triporopollenites Pflug and Thomson 1953

732 Type species. Triporopollenites coryloides Pflug 1953

733 *Species* -Triporopollenites minor Couper 1953

not illustrated

Dimensions (3 specimens measured). Equatorial diameter: 18-21 µm.

Botanical affinity. Possibly Proteaceae

Genus -Ulmoideipites *Anderson 1960*

Type species. Ulmoideipites krempi *Anderson 1960*

Species -Ulmoideipites patagonicus *Archangelsky 1973*

fig. 4F

Remarks. This specimen is indistinguishable from those described for the Paleocene of the Bororó and Salamanca Formations, Chubut Province, Argentina (Archangelsky, 1973).

Dimensions (1 specimen measured): Equatorial diameter: 21 µm.

Botanical affinity. Ulmaceae.

Discussion

The Laguna del Hunco spore-pollen assemblages both enhance the plant fossil record for this significant Eocene locality by incorporating new taxa and reinforcing the presence of many plant families previously reported from macrofossils (table 3). An outstanding member of the new taxa is the family Asteraceae, with one morphotype that represents the oldest finding of Asteraceae in Patagonia and one of the oldest of non-Barnadesioideae Asteraceae worldwide. The family was previously known in the region from a spectacular capitulum with in-situ pollen of the Mutisioideae/Carduoideae type from the early middle Eocene at Río Pichileufú (Barreda et al. 2010, 2012b). Other

755 significant angiosperm lineages first recorded here reliably for LH are Chloranthaceae,
756 Rubiaceae, Ulmaceae, and Nothofagaceae.
757 Nothofagaceae is represented by pollen grains belonging to the extant South
758 American subgenera *Fuscospora* and *Nothofagus*; subgenus *Fuscospora* is the most
759 abundant, represented today by only one species in South America (*N. alessandrii*) that
760 is confined to a small area of central Chile, whereas it is widespread in Australia and
761 New Zealand. In contrast, subgenus *Nothofagus*, now restricted to South America, is
762 more rare at LH. Comparable abundance relationships between these two subgenera
763 were observed in other palynological assemblages from Patagonia at least up to the
764 middle Miocene (Barreda obs. pers.). These records provide new evidence of ancient
765 abundances and distributions of Nothofagaceae beyond the limits of their extant ranges.
766 Interestingly, some early Oligocene leaves from Tasmania -*Nothofagus lobata* Hill-
767 were assigned to the South American subgenus *Nothofagus* (Jordan and Hill 1999).
768 Regarding Rubiaceae, Berry's (1925) "*Faramea*"*miocenica* is not considered here as a
769 valid record of that family, but the pollen occurrence reported here establishes its
770 presence. Among the ferns, Schizaeaceae and Polypodiaceae spores are the first reports
771 from LH for those families.
772 Some new palynological records representing families previously not recorded
773 in the macrofossils may be related to several factors, such as having thick walled spores
774 (Schizaeaceae, Polypodiaceae) or pollen grains (Asteraceae) that make them resistant to
775 fossilization processes and transport by biotic or abiotic agents, or high pollen
776 production associated with wind pollination as in Nothofagaceae. In addition, most of
777 the plant macrofossil diversity at Laguna del Hunco is still represented by isolated
778 angiosperm leaves that have not been diagnosed taxonomically (e.g., Wilf et al. 2005),
779 even though some of them presumably correlate to several of the palynomorphs

780 reported here. These biases in preservation between macro and microfossils are well
781 known and not unique to the Patagonian sediments (see, e.g., Davidson et al. 2005).
782 Nevertheless, several of the pollen occurrences complement macrofossil records
783 (table 3). Outstanding among these is Juglandaceae, a family of shrubs and trees mainly
784 distributed in the Northern Hemisphere. The family was known from the site from
785 winged fruits related to Engelhardioideae (Hermsen and Gandolfo 2016), here
786 supported by pollen grains similar to the *Engelhardia-Alfaroa* group (see Systematic
787 Comments). The high abundance of Juglandaceae pollen (ca. 24 %) indicates that this
788 family was a common, presumably wind-pollinated component of the flora that
789 probably was very abundant near the depocenter.
790 Rare pollen grains reported here that are similar to those of living Castaneoideae
791 complement the macrofossil record at LH of *Castanopsis* (Fagaceae: Castaneoideae;
792 leaves and infructescences, Wilf et al. 2019a), which was the first report globally of
793 Gondwanan Fagaceae. The rarity of pollen (only three grains) poses a sharp contrast to
794 the high abundance of the leaves in the same strata and could help to explain why
795 castaneoid pollen has not yet been found elsewhere in Gondwana (e.g., Denk et al.
796 2019, Wilf et al. 2019b). The low castaneoid pollen abundance at LH could be related to
797 taphonomic loss due to the very small grain size or insect-pollination syndromes as in
798 living *Castanopsis* (e.g., Nakanishi et al. 2012). *Castanopsis*/*Lithocarpus* pollen in
799 modern pollen rain samples has been found to greatly under-represent the standing
800 biomass of the source trees (e.g., Jarvis and Clay-Poole 1992). However,
801 *Castanopsis*/*Lithocarpus*pollen can be abundant in much younger (Pleistocene-
802 Holocene), unconsolidated sediments (e.g., Hope 2001).
803

804 Also, within the group -represented by both megafossils and pollen grains-, there
805 are several additional Gondwanan lineages, highlighting angiosperm families such as
806 Proteaceae, Cunoniaceae, Myrtaceae, and Casuarinaceae (table 3). Among the
807 gymnosperms, several Podocarpaceae (*Podocarpus*, *Dacrycarpus*) and Araucariaceae
808 (*Araucaria*, *Agathis*) are documented by both megafossils and pollen (table 3). The
809 ferns include Gleicheniaceae (pollen similar to *Gleichenia*, and fertile fronds of
810 Gleicheniaceae previously reported by Carvalho et al. 2013), Osmundaceae,
811 Pteridaceae, and particularly the tree fern Dicksoniaceae (pollen related to *Dicksonia*
812 and the fertile fronds mentioned by Carvalho et al. (2013).
813 Similarly, there are some records based on macrofossils that so far are not
814 known in the palynoflora, including fossils related to the families Cupressaceae,
815 Monimiaceae, Atherospermataceae, Menispermaceae, Bixaceae, Solanaceae, and
816 Akaniaceae (table 3). The absence of palynomorphs related to these families is probably
817 due to a suite of factors, among them delicate exine and therefore low fossilization
818 potential, lack of resistance to the palynological extraction treatment, low palynological
819 production (for those plants that are pollinated by insects/animals or with low standing
820 biomass) that translates into low representation in the assemblages, and the presence of
821 characters shared by several families that makes their taxonomic position difficult to
822 determine (e.g., *Tricolporites*, *Psilatricolporites*, *Rhoipites*). The lack of monocot pollen
823 is conspicuous, but monocot macrofossils, similarly, are very rare at the site (Wilf et al.,
824 2005; Carpenter et al. 2014; Wilf 2020).
825 Among Eocene Patagonian palynofloras, the LH assemblage is similar to Nahuel
826 Huapi Este and Confluencia (Fig. 6); all are characterized by the co-dominance of
827 Cyatheaceae, Polypodiaceae, Podocarpaceae, Proteaceae, and Anacardiaceae (table 2).
828 Laguna del Hunco also shows similarities with the Ligorio Márquez Formation

829 palynoflora (fig. 6), which shares the presence of *Dilwynites* (*Agathis/Wollemia*,
830 Araucariaceae), Asteraceae, and Malvaceae. The Laguna del Hunco, Pampa de Jones,
831 and Confluencia sites all belong to the Huitrera Formation, with ages ranging from ca.
832 54.2 Ma (PJ) and 52.2 Ma (LH), to middle Eocene or younger (C). Besides the
833 significant number of species shared among the three assemblages, the LH assemblages
834 share with Pampa de Jones the presence of the thermophilic Dicksoniaceae, tropical
835 groups of Juglandaceae, and Casuarinaceae, and with Confluencia, the presence of
836 Pteridaceae, ?Myricaceae, and temperate groups of the southern beech Nothofagaceae.
837 The observed turnover in the composition of the spore-pollen assemblages from the
838 early to the middle Eocene might be related to climatic change towards cooler and drier
839 conditions (Zachos et al. 2001; Dunn et al. 2015). In this context, palynological study of
840 additional floras, such as Río Pichileufú (ca. 47 Ma), would provide a better
841 understanding of Eocene plant community changes through time across the Patagonian
842 landscape.

843 **Acknowledgements**

844 This work was supported by NSF grants DEB-0919071, DEB-0918932, DEB-0345750,
845 DEB-1556666, DEB-1556136, EAR-1925755, and EAR-1925481; CONICET grant PIP
846 2014-0259, and ANPCyT grant PICT 2017-0671. Jason Hicks and Kirk Johnson first
847 recognized the pollen-bearing potential of the C12 bed and collected it. We thank the
848 Editor, Patrick Herendeen, and an anonymous reviewer for their helpful comments, and
849 Sarah Ivory for discussion. For additional field and lab assistance, we thank Marcelo
850 Krause, Elizabeth Hajek, Pablo Puerta, and many others. Palynological samples were
851 processed by Sebastian Mirabelli and Orlando Cárdenas, and drawings were done by
852 Amalia González.

853 **Literature cited**

854 Andruchow-Colombo A, P Wilf, IH Escapa 2019 A South American fossil relative of
855 *Phyllocladus*: *Huncocladus laubenfelsii* gen. et sp. nov. (Podocarpaceae), from
856 the early Eocene of Laguna del Hunco, Patagonia, Argentina. Aust Syst Bot 32:
857 290-309.

858 Aragón E, M Mazzoni 1997 Geología y estratigrafía del complejo volcánico piroclástico
859 del río Chubut medio (Eoceno), Chubut, Argentina. RAGA 52: 243-256.

860 Aragón E, EJ Romero 1984 Geología, paleoambientes y paleobotánica de yacimientos
861 Terciarios del occidente de Río Negro, Neuquén y Chubut. Actas del IX
862 Congreso Geológico Argentino, San Carlos de Bariloche 4: 475-507.

863 Archangelsky S 1973 Palinología del Paleoceno de Chubut. I. Descripciones
864 sistemáticas. Ameghiniana 10: 339-399.

865 Archangelsky S 1974 Sobre la edad de la tafoflora de la Laguna del Hunco, Prov. de
866 Chubut. Ameghiniana 11: 413-417.

867 Báez AM, MC Zamaloa, EJ Romero 1991 Nuevos hallazgos de microfloras y anuros
868 Paleógenos en el Noroeste de Patagonia: implicancias paleoambientales y
869 paleobiogeográficas. Ameghiniana *27*: 83-94.

870 Barreda VD 1997 Palynomorphs assemblage of the Chenque Formation, Late
871 Oligocene-Miocene from Golfo San Jorge basin, Patagonia, Argentina.
872 Polycolpate and tricolporate pollen. Ameghiniana 34: 131-143.

873 Barreda VD, NR Cúneo, P Wilf, ED Currano, RA Scasso, H Brinkhuis 2012a
874 Cretaceous/Paleogene floral turnover in Patagonia: drop in diversity, low
875 extinction, and a *Classopollis* spike. PLOS ONE 7: e52455.

876 Barreda V, L Palazzesi, S Marenssi 2009 Palynological record of the Paleogene Río
877 Leona Formation (southernmost South America): stratigraphical and
878 paleoenvironmental implications. Rev Palaeobot Palynol 154: 22-33.

879 Barreda V, L Palazzesi, MC Tellería 2008 Fossil pollen grains of Asteraceae from the
880 Miocene of Patagonia: Nassauviinae affinity. Rev Palaeobot Palynol 151: 51-58.

881 Barreda VD, L Palazzesi, MC Tellería, L Katinas, JV Crisci, K Bremer, MG Passalia, R
882 Corsolini, R Rodríguez Brizuela, F Bechis 2010 Eocene Patagonia fossils of the
883 daisy family. Science 329: 1621-1621.

884 Barreda VD, L Palazzesi, MC Tellería, L Katinas, JV Crisci, K Bremer, MG Passalia, R
885 Corsolini, R Rodríguez Brizuela, F Bechis 2012b An extinct Eocene taxon of the
886 daisy family (Asteraceae): evolutionary, ecological and biogeographical
887 implications. Ann Bot 109: 127-134.

888 Barreda VD, L Palazzesi, MC Tellería, EB Olivero, JI Raine, F Forest 2015 Early
889 evolution of the angiosperm clade Asteraceae in the Cretaceous of Antarctica.
890 PNAS 112: 10989-10994.

891 Berry EW 1925 A Miocene flora from Patagonia. Johns Hopkins University Studies in
892 Geology 6: 183-251.

893 Berry EW 1938 Tertiary flora from the Rio Pichileufú, Argentina. Geol Soc Am. Spec
894 Pap 12: 1-149.

895 Bippus AC, IH Escapa, P Wilf, AMF Tomescu 2019 Fossil fern rhizomes as a model
896 system for exploring epiphyte community structure across geologic time:
897 evidence from Patagonia. Peer J 7:e8244. https://doi.org/10.7717/peerj.8244

898 Bomfleur B, I Escapa 2019 A silicified *Todea* trunk (Osmundaceae) from the Eocene of
899 Patagonia. PalZ: 1-6.

900 Butler KL, BK Horton, A Echaurren, A Folguera, F Fuentes 2019 Cretaceous-Cenozoic
901 growth of the Patagonian broken foreland basin, Argentina: Chronostratigraphic
902 framework and provenance variations during transitions in Andean subduction
903 dynamics. J S Am Ear Sci https://doi.org/10.1016/j.jsames.2019.102242

904 Cantrill DJ, JI Raine 2006 *Wairarapaia mildenhallii* gen. et sp. nov., a new araucarian
905 cone related to *Wollemia* from the Cretaceous (Albian-Cenomanian) of New
906 Zealand. Int J Plant Sci 167: 1259-1269.

907 Carpenter RJ, A Iglesias, P Wilf 2018 Early Cenozoic vegetation in Patagonia: New
908 insights from organically preserved plant fossils (Ligorio Márquez Formation,
909 Argentina). Int J Plant Sci 179: 115-135.

910 Carpenter RJ, P Wilf, JG Conran, NR Cúneo 2014 Early Eocene *Ripogonum*. Palaeontol
911 Elect 17: 1-39.

912 Carvalho MR, P Wilf, EJ Hermsen, MA Gandolfo, NR Cúneo, KR Johnson 2013 First
913 record of *Todea* (Osmundaceae) in South America, from the early Eocene
914 paleorainforests of Laguna del Hunco (Patagonia, Argentina). Am J Bot 100:
915 1831-1848.

916 Clyde WC, P Wilf, A Iglesias, RL Slingerland, T Barnum, PK Bijl, TJ Bralower, H
917 Brinkhuis, EE Comer, BT Huber, M Ibañez-Mejia, BR Jicha, JM Krause, JD
918 Schueth, BS Singer, MS Raigemborn, MD Schmitz, A Sluijs, MC Zamaloa 2014
919 New age constraints for the Salamanca Formation and lower Río Chico Group in
920 the western San Jorge Basin, Patagonia, Argentina: implications for Cretaceous-

921 Paleogene extinction recovery and land mammal age correlations. GSA Bull
922 126: 289-306.

923 Coetzee JA, J Praglowski 1984 Pollen evidence for the occurrence of *Casuarina* and
924 *Myrica* in the Tertiary of South Africa. Grana 23: 23-41.

925 Crepet WL, CP Daghlian 1980 Castaneoid inflorescences from the middle Eocene of
926 Tennessee and the diagnostic value of pollen (at the subfamily level) in the
927 Fagaceae. Am J Bot 67: 739–757.

928 Davidson TA, CC Sayer, H Bennion, C David, N Rose, MP Wade 2005 A 250 year
929 comparison of historical, macrofossil and pollen records of aquatic plants in a
930 shallow lake. Freshwater Biol 50: 1671-1686.

931 Denk T, RS Hill, MC Simeone, C Cannon, ME Dettmann, PS Manos 2019 Comment on
932 "Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests":
933 Science 365: eeaaz2189.

934 Dettmann ME, HT Clifford, M Peters 2012 *Emwadea microcarpa* gen. et sp. nov.-
935 anatomically preserved araucarian seed cones from the Winton Formation (late
936 Albian), western Queensland, Australia. Alcheringa 36: 217-237.

937 Dunn RE, CAE Strömberg, RH Madden, MJ Kohn, AA Carlini 2015 Linked canopy,
938 climate, and faunal change in the Cenozoic of patagonia. Science 347: 258-261.

939 Escapa IH, SA Catalano 2013 Phylogenetic analysis of araucariaceae: Integrating
940 molecules, morphology, and fossils. Int J Plant Sci 174: 1153-1170.

941 Escapa IH, A Iglesias, P Wilf, SA Catalano, MA Caraballo-Ortiz, NR Cúneo 2018
942 *Agathis* tree of Patagonia´s Cretaceous-Paleogene death landscapes and their
943 evolutionary significance. Am J Bot 105:1345-1368.
944 Frenguelli J 1943 Restos de *Casuarina* en el Mioceno de El Mirador, Patagonia central.
945 Notas del Museo de La Plata 8: 349-354.

946 Frenguelli J, LR Parodi 1941 Una *Chusquea* fósil de El Mirador (Chubut). Not Mus La
947 Plata, Paleontol 6: 235-238.

948 Gandolfo MA, MC Dibbern, EJ Romero 1988 *Akania patagonica* n. sp. and additional
949 material on *Akania americana* Romero and Hickey (Akaniaceae), from
950 Paleocene sediments of Patagonia. Bull Torrey Bot Cb: 83-88.

951 Gandolfo MA, EJ Hermsen 2012 The emerging Patagonian fossil record of
952 Cunoniaceae and its biogeographical significance. Jap J Palynol 58: 66-67.

953 Gandolfo MA, EJ Hermsen 2017 *Ceratopetalum* (Cunoniaceae) fruits of Australasian
954 affinity from the early Eocene Laguna del Hunco flora, Patagonia, Argentina.
955 Ann Bot doi:10.1093/aob/mcw283

956 Gandolfo MA, EJ Hermsen, MC Zamaloa, KC Nixon, CC González, P Wilf, KR
957 Johnson 2011 Oldest known *Eucalyptus* macrofossils are from South America.
958 PLoS One 6: e21084.

959 González CC 2008 Revisión taxonómica y biogeográfica de las familias de
960 angiospermas dominantes de la “Flora del Hunco” (Eoceno temprano), Chubut,
961 Argentina. PhD diss. Universidad de Buenos Aires, Buenos Aires.

962 González CC, MA Gandolfo, MC Zamaloa, NR Cúneo, P Wilf, KR Johnson 2007
963 Revision of the Proteaceae macrofossil record from Patagonia, Argentina. Bot
964 Rev 73: 230-235.

965 Graham A 2009 Fossil record of the Rubiaceae. Ann Miss Bot Gard 96: 90-108.

966 Grímsson F, R Zetter, GW Grimm, GK Pedersen, AK Pedersen, T Denk 2015 Fagaceae
967 pollen from the early Cenozoic of West Greenland: Revisiting Engler's and
968 Chaney's Arcto-Tertiary hypotheses. Plant Syst Evol 301: 809–832.
969 Hammer Ø, DA Harper, PD Ryan 2001 PAST: paleontological statistics software
970 package for education and data analysis. Palaeontol Elect 4: 9.

971 Harris WK 1965 Basal Tertiary microfloras from the Princetown area, Victoria,
972 Australia. Palaeontographica B 115: 75–106.

973 Heads MJ 2017 Biogeography and evolution in New Zealand. CRC Press. Taylor and
974 Francis Group. Boca Raton, FL, USA.

975 Hermsen EJ, MA Gandolfo, MC Zamaloa 2012 The fossil record of *Eucalyptus* in
976 Patagonia. Am J Bot 99: 1356-1374.

977 Hermsen EJ, MA Gandolfo 2016 Fruits of Juglandaceae from the Eocene of South
978 America. Syst Bot 41: 316-328.

979 Hill RS, T Lewis, RJ Carpenter, SS Whang 2008 *Agathis* (Araucariaceae) macrofossils
980 from Cainozoic sediments in south-eastern Australia. Aust Syst Bot 21: 162-
981 177.

982 Hope G 2001 Environmental change in the Late Pleistocene and later Holocene at
983 Wanda site, Soroako, South Sulawesi, Indonesia: Palaeogeog Palaeoclimatol
984 Palaeoecol 171;129-145.
985 Huang CH, C Zhang, M Liu, Y Hu, T Gao, J Qi, H Ma 2016 Multiple polyploidization
986 events across Asteraceae with two nested events in the early history revealed by
987 nuclear phylogenomics. Mol biol evol 33: 2820-2835.

988 Iannelli SB, VD Litvak, L Fernández Paz, A Folguera, ME Ramos, VA Ramos 2017
989 Evolution of Eocene to Oligocene arc-related volcanism in the North Patagonian
990 Andes (39–41°S), prior to the break-up of the Farallon plate. Tectonophysics
991 696–697: 70-87.

992 Jarvis DI, ST Clay-Poole 1992 A comparison of modern pollen rain and vegetation in
993 southwestern Sichuan Province, China. Rev Palaeobot Palynol 75: 239-258.

994 Jordan GJ, RS Hill 1999 The phylogenetic affinities of Nothofagus (Nothofagaceae)
995 leaf fossils based on combined molecular and morphological data. Int J Plant Sci
996 160: 1177-1188.

997 Jud NA, MA Gandolfo, A Iglesias, P Wilf 2018a Fossil flowers from the early
998 Palaeocene of Patagonia, Argentina, with affinity to Schizomerieae
999 (Cunoniaceae). Ann Bot 121: 431-442.

1000 Jud NA, A Iglesias, P Wilf, MA Gandolfo 2018b Fossil moonseeds from the Paleogene
1001 of West Gondwana (Patagonia, Argentina). Am J Bot 105: 927-942.
1002 Katinas L, J Pruski, G Sancho, MC Tellería 2008 The subfamily Mutisioideae
1003 (Asteraceae). Bot Rev 74: 1-469.

1004 Knight CL, P Wilf 2013 Rare leaf fossils of Monimiaceae and Atherospermataceae
1005 (Laurales) from Eocene Patagonian rainforests and their biogeographic
1006 significance. Palaeontol Elect 16: 26A

1007 Kooyman RM, P Wilf, VD Barreda, RJ Carpenter, GJ Jordan, JMK Sniderman, A
1008 Allen, et al 2014 Paleo-Antarctic rainforest into the modern Old World Tropics:
1009 the rich past and threatened future of the "southern wet forest survivors". Am J
1010 Bot 101: 2121-2135.

1011 Kunzmann L 2007 Araucariaceae (Pinopsida): Aspects in palaeobiogeography and
1012 palaeobiodiversity in the Mesozoic. Zool Anz 246: 257-277.

1013 Lage J 1982 Descripción geológica de la hoja 43c, Gualjaina. Provincia del Chubut.
1014 Boletín del Servicio Geológico Nacional Nº 189. Subsecretaría de Minería.
1015 Buenos Aires.

1016 Lawver LA, LM Gahagan, IWD Dalziel 2011. A different look at gateways: Drake
1017 Passage and Australia/Antarctica. Pages: 5-33 *in* JB Anderson, JS Wellner, eds.
1018 Tectonic, Climatic, and Cryospheric Evolution of the Antarctic Peninsula. Am
1019 Geoph Union, Washington, DC.

1020 Mai D H 1961 Über eine fossile Tiliaceen-Blute und tilioiden Pollen aus dem deutschen
1021 Tertiar. Ceologie 32: 54-93.

1022 Macphail M, RJ Carpenter, A Iglesias, P Wilf 2013 First evidence for Wollemi Pine-
1023 type pollen (*Dilwynites*: Araucariaceae) in South America. PLOS ONE 8:
1024 e69281.

1025 Macphail M, RJ Carpenter 2014 New potential nearest living relatives for
1026 Araucariaceae producing fossil Wollemi Pine-type pollen (*Dilwynites*
1027 *granulatus* W.K. Harris, 1965). Alcheringa 38: 135-139.

1028 Manchester SR 1987 The fossil history of the Juglandaceae. Monographs in Systematic
1029 Botany from the Missouri Botanical Garden 21: 1–137.

1030 Martin H A 1973 The palynology of some Tertiary and Pleistocene deposits, Lachlan
1031 River Valley, New South Wales. *Aust J Bot Suppl 3*: 1-57.

1032 Melendi DL, LH Scafati, W Volkheimer 2003 Palynostratigraphy of the Paleogene
1033 Huitrera Formation in N-W Patagonia, Argentina. N. Jb. Geol. Paläont. Abh.
1034 228: 205-273.

1035 Merkhofer L, P Wilf, MT Haas, RM Kooyman, L Sack, C Scoffoni, NR Cúneo 2015
1036 Resolving Australian analogs for an Eocene Patagonian paleorainforest using
1037 leaf size and floristics. Am J Bot 102: 1160-1173.

1038 Milne LA 1988 Palynology of a late Eocene lignitic sequence from the western margin
1039 of the Eucla Basin, Western Australia. Mem Ass Australs Palaeontols 5: 285-
1040 310.

1041 Muller J 1968 Palynology of the Pedawan and Plateau Sandstone formations
1042 (Cretaceous-Eocene) in Sarawak, Malaysia. Micropaleontology 1: 1-37.

1043 Nakanishi A, H Yoshimaru, N Tomaru, M Miura, T Manabe, S Yamamoto 2012
1044 Patterns of pollen flow in a dense population of the insect-pollinated canopy tree
1045 species *Castanopsis sieboldii*. J Heredity 103: 547-556.

1046 Nichols DJ 1973 North American and European species of *Momipites* ("*Engelhardtia*")
1047 and related genera, Geosci Man 7: 103-117

1048 Palazzesi L, V Barreda, MC Tellería 2010 First fossil record of Calyceraceae
1049 (Asterales): pollen evidence from southern South America. Rev Palaeobot
1050 Palynol 158: 236-239.

1051 Panti C, RR Pujana, MC Zamaloa, EJ Romero 2012 Araucariaceae macrofossil record
1052 from South America and Antarctica. Alcheringa 36: 1–22.

1053 Pocknall DT 1982 Palynology of late Oligocene Pomahaka Estuarine Bed sediments,
1054 Waikoikoi, Southland, New Zealand. N Z J Bot 20: 263-287.

1055 Pocknall DT, DC Mildenhall 1984 Late Oligocene-early Miocene spores and pollen
1056 from Southland, New Zealand. N Z Geol Surv 51: 1-66.

1057 Pole M 2008 The record of Araucariaceae macrofossils in New Zealand. Alcheringa 32:
1058 405-426.

1059 Potonié R 1960 Synopsis der Gattungen der Sporae dispersae. III. Beih Geol Jb 39: 1–
1060 189.

1061 Punt W, PP Hoen, S Blackmore, S Nilsson, A Le Thomas 2007 Glossary of pollen and
1062 spore terminology. Rev Palaeobot Palynol 143: 1-81.

1063 Raine J I, DC Mildenhall, E Kennedy 2011. New Zealand fossil spores and pollen: an
1064 illustrated catalogue. 4th edition. Lower Hutt, New Zealand. GNS Science Ser
1065 no 4 http://data.gns.cri.nz/sporepollen/index.htm.

1066 Rapela CW, L Spalletti, J Merodio 1983 Evolución magmática y geotectónica de la
1067 “Serie Andesítica” andina (Paleoceno-Eoceno) en la Cordillera Norpatagónica.
1068 RAGA 38: 469-484.

1069 Rapela CW, LA Spalletti, JC Merodio, E Aragón 1984 El vulcanismo Paleoceno-
1070 Eoceno de la provincia volcánica Andino-Patagónica. 9° Cong Geol Arg,
1071 Relatorio 1: 189-213.

1072 Rapela CW, LA Spalletti, JC Merodio, E Aragón 1988 Temporal evolution and spatial
1073 variation of early Tertiary volcanism in the Patagonian Andes (40 S–42 30′ S). J
1074 South Am Earth Sci 1: 75-88.

1075 Romero EJ, MC Dibbern, MA Gandolfo 1988 Revisión de *Lomatia bivascularis* (Berry)
1076 Frenguelli (Proteaceae) del yacimiento de la Laguna del Hunco (Paleoceno),
1077 Provincia del Chubut. 4° Cong Arg Paleontol Bioestrat 3: 125-130.

1078 Romero EJ, LJ Hickey 1976 A fossil leaf of Akaniaceae from Paleocene beds in
1079 Argentina. Bull Torrey Bot Cb 1: 126-131.

1080 Romero EJ, MC Zamaloa 1985 Polen de angiospermas de la Formación Río Turbio
1081 (Eoceno), Provincia de Santa Cruz, República Argentina. Ameghiniana 22: 45-
1082 51.

1083 Rossetto-Harris G, P Wilf, IH Escapa, A Andruchow-Colombo 2020 Eocene *Araucaria*
1084 Sect. *Eutacta* from Patagonia and floral turnover during the initial isolation of
1085 South America. American Journal of Botany, in press

1086 Stover LE, AD Partridge 1973 Tertiary and Late Cretaceous spores and pollen from the
1087 Gippsland Basin, Southeastern Australia. Proc Roy Soc Vict 85: 237-286.

1088 Tryon AF, B Lugardon 1990 Spores of the Pteridophyta. Surface, wall structure and
1089 diversity based on electron microscope studies. Springer-Verlag.

1090 Villar de Seoane L, S Archangelsky 2014 Estudios palinológicos del Grupo Baqueró
1091 (Cretácico Inferior), provincia de Santa Cruz, Argentina. X. Polen de
1092 Gymnospermae y Apéndice Final. Rev Mus Arg Cien Nat ns 16: 33-44.

1093 Villar de Seoane L, NR Cúneo, I Escapa, P Wilf, MA Gandolfo 2015 *Ginkgoites*
1094 *patagonica* (Berry) comb. nov. from the Eocene of Patagonia, last ginkgoalean
1095 record in South America. Int J Plant Sci 176: 346-363 and Erratum p. 364.

1096 Whitehead DR 1965 Pollen morphology in the Juglandaceae, II: survey of the family. J
1097 Arnold Arb 46: 369-410.
1098 Wilf P 2012 Rainforest conifers of Eocene Patagonia: attached cones and foliage of the
1099 extant Southeast Asian and Australasian genus *Dacrycarpus* (Podocarpaceae).
1100 Am J Bot 99: 562-584.

1101 Wilf P 2020 Eocene "Chusquea" fossil from Patagonia is a conifer, not a bamboo
1102 Phytokeys, in press
1103 Wilf P, MR Carvalho, MA Gandolfo, NR Cúneo 2017b Eocene lantern fruits from
1104 Gondwanan Patagonia and the early origins of Solanaceae. Science 355: 71-75.

1105 Wilf P, NR Cúneo, IH Escapa, D Pol, MO Woodburne 2013 Splendid and seldom
1106 isolated: the paleobiogeography of Patagonia. Ann Rev Earth Planet Sci 41:
1107 561-603.
1108 Wilf P, NR Cúneo, KR Johnson, JF Hicks, SL Wing, JD Obradovich 2003 High plant
1109 diversity in Eocene South America: evidence from Patagonia. Science 300: 122-
1110 125.

1111 Wilf P, MP Donovan, NR Cúneo, MA Gandolfo 2017a The fossil flip- leaves
1112 (*Retrophyllum*, Podocarpaceae) of southern South America. Am J Bot 104:
1113 1344-1369.

1114 Wilf P, IH Escapa, NR Cúneo, RM Kooyman, KR Johnson, A Iglesias 2014 First South
1115 American *Agathis* (Araucariaceae), Eocene of Patagonia. Am J Bot 101: 156–
1116 179.

1117 Wilf P, KR Johnson, NR Cuneo, ME Smith, BS Singer, MA Gandolfo 2005 Eocene
1118 plant diversity at Laguna del Hunco and Río Pichileufú, Patagonia, Argentina.
1119 Am Nat 165: 634-650.

1120 Wilf P, SA Little, A Iglesias, MC Zamaloa, MA Gandolfo, NR Cúneo, KR Johnson,
1121 2009 *Papuacedrus* (Cupressaceae) in Eocene Patagonia: a new fossil link to
1122 Australasian rainforests. Am J Bot 96: 2031-2047.

1123 Wilf P, KC Nixon, MA Gandolfo, NR Cúneo 2019a Eocene Fagaceae from Patagonia
1124 and Gondwanan legacy in Asian rainforests. Science 364: eaaw5139.

1125 Wilf P, KC Nixon, MA Gandolfo, NR Cúneo 2019b, Response to Comment on “Eocene
1126 Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests”: Science
1127 366: eaaz2297.

1128 Wilf P, BS Singer, MC Zamaloa, KR Johnson, NR Cúneo 2010 Early Eocene
1129 40Ar/39Ar age for the Pampa de Jones plant, frog, and insect biota (Huitrera
1130 Formation, Neuquén Province, Patagonia, Argentina). Ameghiniana 47: 207-
1131 216.

1132 Wilf P, DW Stevenson, NR Cúneo 2016 The last Patagonian cycad, *Austrozamia*
1133 *stockeyi* gen. et sp. nov., early Eocene of Laguna del Hunco, Chubut, Argentina.
1134 Botany 94: 817-829.

1135 Zachos J, M Pagani, L Sloan, E Thomas, K Billups 2001 Trends, rhythms and
1136 aberrations in global climate 65 Ma to Present. Science 292: 686–693.

1137 Zamaloa MC, RR Andreis 1995. Asociación palinológica del Paleoceno temprano
1138 (Formación Salamanca) en Ea. Laguna Manantiales, Santa Cruz, Argentina. 6°
1139 Cong Arg Paleontol Bioestrat 1: 301-305.

1140 Zamaloa MC, MA Gandolfo, CC González, EJ Romero, NR Cúneo, P Wilf 2006
1141 Casuarinaceae from the Eocene of Patagonia, Argentina. Int J Plant Sci 167:
1142 1279-1289.
1143

Figure legends

Fig. 1. Location map showing the geographic position of samples, except for sample LH26 which is an isolated exposure of the lake beds, found in the road just north of the main outcrop area (42°27'2.60"S, 70° 2'45.95"W). Sample C12 is from bed C12, and the other samples are from the eponymous megafloral localities, as described in the J. Hicks reference section published in Wilf et al. (2003). "Laguna del Hunco" indicates the ephemeral local pond with that name, for which the fossil site is also named. Map data: Google Earth, Image © 2019 CNES/Airbus

Fig. 2. Stratigraphic sections of the Huitrera Formation at the Laguna del Hunco locality showing: integrated section of 180 m thickness, five local sections and correlations (pink lines), and the positions of samples used here (modified from Wilf et al. 2003); radiometrically dated sample on sanidine with 95% confidence interval (date updated in Wilf 2012); intervals of reversed and normal polarity (R1, N1, etc.); and assignment to geomagnetic polarity subchrons (also from Wilf et al. 2003). The stratigraphic position of sample LH 26 is not precise and thus not shown, but it lies within the upper part of the lake-bed section.

Fig. 3. *A, B*, *Polypodiaceoisporites* sp. *A*, MPEF-PA 307a$_1$: L55-2, *B*, MPEF-PA 307b$_2$: B42-3. *C*, *Ischyosporites areapunctatis* MPEF-PA 307a$_4$: F31. *D, Trilites tuberculiformis* MPEF-PA 307a$_6$: A59-4. *E, Ischiosporites* sp. MPEF-PA 306a: N40. *F*, *Todisporites major* MPEF-PA 305b: S52-2. *G*, *Polypodiisporites speciosus* MPEF-PA 307b$_3$: B47-2. *H*, *Gleicheniidites senonicus* MPEF-PA 307a$_1$: Q60-1. *I*, *Birestisporites* sp. MPEF-PA 306a: Y17-3. *J*, *Polypodiidites* sp. MPEF-PA 307a$_6$: H30-4. *K*, *Dilwynites granulatus* MPEF-PA 307a$_5$: Q54-4. *L*, *Podocarpidites ellipticus* MPEF-PA 306a: D51-3. *M*, *Araucariacites australis* MPEF-PA 307a$_2$: F39. *N, O, Dilwynites* cf.

tuberculatus N, MPEF-PA 307a$_5$: X48, *O*, MPEF-PA 307a$_5$: S49. *P*, *Podocarpidites elegans* MPEF-PA 306a: J39-3. *Q*, *Nothofagidites saraensis* MPEF-PA 307b$_1$: F36. *R*, *Nothofagidites* sp. MPEF-PA 307b$_4$: F37. *S*, *Nothofagidites flemingii* MPEF-PA 307a$_1$: V38-3. Scale bar in all figures equals 10 µm, except in figures *J, Q, R* where scale bar is equals 5 µm.

Fig. 4. *A, Plicatopollis wodehousi* MPEF-PA 307b$_3$: W21-4. *B, Psilatricolporites* sp. 1 MPEF-A 307b$_2$: W60-4. *C*, *Huanilipollis cabrerae* MPEF-PA 307b$_2$: E42. *D, H, Rhoipites* cf. *sphaerica*, *D*, MPEF-PA 307b$_1$: K36-4, *H*, MPEF-PA 307b$_2$: V26-1. *E*, *Palaeocoprosmadites* sp. MPEF-PA 307b$_6$: H51-3. *F*, *Ulmoideipites patagonicus* MPEF-PA 307b$_5$: F56. *G*, *Intratriporopollenites* sp. MPEF-PA 307b$_4$: J42. *I*, *Striatricolporites gamerroi* MPEF-PA 307b$_4$: R30. *J*, *Tricolpites anguloluminosus* MPEF-PA LH 307b$_2$: N34-1. *K*, *Striatricolporites* sp. 1 MPEF-PA 307b$_2$: O38-3. *L*, *Margocolporites* sp. MPEF-PA 307b$_3$: F56. *M*, *Cupuliferoipollenites* sp. 1 MPEF-PA 307b$_6$: F33-2. *N*, *Myrtaceidites* sp. MPEF-PA 307b$_6$: P45. *O*, *Haloragacidites harrisii* MPEF-PA 308$_b$: O45. *P*, *Tetracolporites* sp. MPEF-PA 307b$_2$: B62-3. *Q*, *Rhoipites baculatus* MPEF-PA 307b$_2$: J44-3. *R*, *Triatriopollenites lateflexus* MPEF-PA 307b$_1$: H49-4. *S*, *Proteacidites* sp. MPEF-PA 307b$_5$: H49. *T*, *Propylipollis* sp. MPEF-PA 308b: N44-1. Scale bar in all figures equals 5 µm.

Fig. 5. Figs. *A, D*, *Plicatopollis wodehousi*. *B*, *Cupuliferoipollenites* sp. 1. *C*, *Clavatipollenites* sp. *E*, *Tricolporites* sp. 1. *F*, *Rhoipites* cf *sphaerica*. *G*, *Intratriporopollenites* sp. *H*, *Nothofagidites* sp. *I*, *Striatricolporites* sp. 2. *J*, *Tricolporites* sp. 2. *K*, *Tricolporites* sp. 3. *L*, *Polypodiaceoisporites* sp. Scale bar equals 2 µm.

1191 **Fig. 6**. Cluster analysis dendrogram showing the similarities of the LH assemblages
1192 with other Eocene Patagonian units based on Table 2. LH: Laguna del Hunco; NHE:
1193 Nahuel Huapi Este; C: Confluencia; LM: Ligorio Márquez.

Table 1

Species list, nearest living relatives, stratigraphic distributions and frequencies

Fossil taxon	Nearest living relatives	Samples						
		LH23	LH13	C12		LH6	LH22	LH26
				N	%			
Pteridophyte								
Baculatisporites comaumensis (Cookson) Potonié 1953	Osmundaceae		•	1	0.17			
Biretisporites sp. (Fig. 3I)	Schizaeaceae		•	1	0.17			
Cyathidites australis Couper 1953	Cyatheaceae		•	16	2.64			•
Cyathidites minor Couper 1953	Cyatheaceae/Dicksoniaceae/Schyzaeaceae			40	6.60			
Deltoidospora sp.	Unknown fern		•	10	1.65			
Gleicheniidites senonicus Ross 1949 (Fig. 3H)	Gleicheniaceae		•	4	0.66			
Ischyosporites areapunctatis (Stuchlik) Barreda 1997 (Fig. 3C)	Dicksoniaceae			15	2.48			
Ischyosporites sp. (Fig. 3E)	Dicksoniaceae					•		
Laevigatosporites ovatus Wilson and Webster 1946	Polypods			5	0.83			
Polypodiaceoisporites sp. (Figs. 3A-B, 5L)	Pteridaceae			19	3.14			
Polypodiidites sp. (Fig. 3J)	Unknown fern			1	0.17			
Polypodiidites speciosus (Harris) Archangelsky 1972 (Fig. 3G)	Polypodiaceae			1	0.17			
Todisporites major Couper 1958 (Fig. 3F)	Osmundaceae	•						
Trilites tuberculiformis Cookson emend. Dettmann 1963 (Fig. 3D)	Dicksoniaceae (*Dicksonia*)		•	2	0.33			
Spores total sum and %				115	18.98			
Gymnospermophyta								
Araucariacites australis Cookson 1947 (Fig. 3M)	Araucariaceae (*Araucaria*)		•	19	3.14			•
Cycadopites sp.	Cycadales/Ginkgolaes			1	0.17			

Dacrycarpites australiensis Cookson and Pike 1953	Podocarpaceae (Dacrycarpus)				•		
Dilwynites granulatus Harris 1965 (Fig. 3K)	Araucariaceae (*Agathis/Wollemia*)		2	0.33		•	
Dilwynites cf. *tuberculatus* Harris 1965 (Figs. 3N-O)	Araucariaceae (*Agathis/Wollemia*)		18	2.97			
Gamerroites psilasaccus (Archangelsky and Romero) Archangelsky 1988	Podocarpaceae		1	0.17			
Lygistepollenites florinii (Cookson and Pike) Stover and Evans 1973	Podocarpaceae (*Dacrydium*)	•	4	0.66	•		
Microcachryidites antarcticus Cookson 1947 ex Couper 1953	Podocarpaceae (*Microcachrys*)		2	0.33	•		
Podocarpidites elegans Romero 1977 (Fig. 3P)	Podocarpaceae (*Podocarpus*)	•	26	4.29	•		
Podocarpidites ellipticus Cookson 1947 (Fig. 3L)	Podocarpaceae (*Podocarpus*)	•	28	4.62	•		•
Podocarpidites marwickii Couper 1953	Podocarpaceae (*Podocarpus*)				•		
Gymnosperms total sum and %			101	16.67			
	Magnoliophyta						
Clavatipollenites sp. (Fig. 5C)	Chloranthaceae (*Ascarina*)		1	0.17			
Cupuliferoipollenites sp. 1 (Figs. 4M, 5B)	Fagaceae (Castaneoideae)		2	0.33			
Haloragacidites harrisii (Couper) Harris 1971 (Fig. 4O)	Casuarinaceae				•	•	
Huanilipollis cabrerae Barreda and Palazzesi 2008 (Fig. 4C)	Asteraceae (Mutisioideae (Nassauvieae))		1	0.17			
Intratriporopollenites sp. (Figs. 4G, 5G)	Malvaceae (Tilioideae)		1	0.17			
Malvacipolloides? sp.	Malvaceae?		1	0.17			
Margocolporites sp. (Fig. 4L)	Fabaceae (Mimosoideae)		1	0.17		•	
Myrtaceidites sp. (Fig. 4N)	Myrtaceae		6	0.99		•	
Nothofagidites flemingii (Couper) Potonié 1960 (Fig. 3S)	Nothofagaceae (*Nothofagus (Nothofagus*))		2	0.33		•	
Nothofagidites saraensis Menéndez and Caccavari 1975 (Fig. 3Q)	Nothofagaceae (*Nothofagus (Fuscospora*))		28	4.62	•		
Nothofagidites sp. (Fig. 3R)	Nothofagaceae (*Nothofagus,* extinct brassi*)*		9	1.49			
Palaeocoprosmadites sp. (Fig. 4E)	Rubiaceae		1	0.17			
Plicatopollis wodehousi (Nichols) Fred. Christ 1978 (Figs. 4A, 5A, D)	Juglandaceae		146	24.09		•	
Propylipollis sp. (Fig. 4T)	Proteaceae				•		
Proteacidites sp. (Fig. 4S)	Proteaceae		2	0.33			
Psilatricolporites sp. 1 (Fig. 4B)	Calyceraceae?		18	2.97			
Psilatricolporites sp. of Clyde et al. 2014	Unknown eudicot		1	0.17			

Rhoipites baculatus Archangelsky 1973 (Fig. 4Q)	Rutaceae?			2	0.33		
Rhoipites cf. *sphaerica* (Cook) Pock Crosb 1982 (Figs. 4D,H, 5F)	Unknown eudicot			14	2.31		
Simpsonipollis sp.	Unknown eudicot			1	0.17		
Striatricolporites gamerroi Archangelsky 1973 (F92) (Fig. 4I)	Anacardiaceae			11	1.82		
Striatricolporites sp. 1 (Fig. 4K)	Anacardiaceae?			2	0.33		
Striatricolporites sp. 2 (Fig. 5I)	Anacardiaceae			1	0.17		
Tetracolporites sp. (Fig. 4P)	Unknown eudicot			1	0.17		
Triatriopollenites lateflexus Archangelsky 1973 (Fig. 4R)	Myricaceae?			1	0.17		
Tricolpites angululuminosus Anderson 1960 (Fig. 4J)	Unknown eudicot			7	1.16		
Tricolporites sp. 1 (Fig. 5E)	Fagaceae?			2	0.33		
Tricolporites sp. 2 (Fig. 5J)	Cunoniaceae (*Weinmania*)		•	2	0.33	•	•
Tricolporites sp. 3 (Fig. 5K)	Unknown eudicot			2	0.33		
Triporopollenites minor (Couper) Barreda 1997	Proteaceae?			3	0.50		
Ulmoideipites patagonicus Archangelsky 1973 (Fig. 4F)	Ulmaceae			1	0.17		
Angiosperms total sum and %				270	44.55		
Algae							
Botryococcus				3	0.50		
Fungi							
Fungal spores		•	•	117	19.31	•	
Total sum of palynomorphs				606	100		

Notes. Frequencies based on a count of 606 grains, only possible in sample C12; ●: presence of a taxon in those samples with few palynomorphs.

Table 2

Presence/absence matrix of taxa of the Laguna del Hunco, Nahuel Huapi Este, Confluencia and Ligorio Márques spore-pollen assemblages

	LH	NHE	C	LM
Bryophyte				
Aytoniaceae (*Reboulisporites*)	0	0	0	1
Lycopodiaceae (*Foveotriletes*)	0	1	0	0
Pteridophyte				
Cyathidites/Deltoidospora	1	1	1	1
Dicksoniaceae *(Ischyosporites/Trilites)*	1	1	0	1
Gleicheniaceae	1	0	0	0
Osmundaceae	1	1	1	1
Polypodiaceae	1	1	1	0
Pteridaceae	1	0	1	0
Schizaeaceae	0	1	0	0
Gymnospermophyta				
Agathis/Wollemia type	1	0	0	1
Araucaria type	1	1	0	1
Cycadopites sp.	1	0	0	0
Dacrycarpus type	1	1	1	1
Dacrydium type	1	1	1	1
Lagarostrobos type	0	1	1	1
Microcachrys type	1	1	1	1
Podocarpus type	1	1	1	1
Magnoliophyta				
Agavaceae (*Luminidites*)	0	0	0	1
Anacardiaceae	1	1	1	0
Araceae (*Proxapertites*)	0	0	0	1
Asteraceae	1	0	0	1
Calyceraceae?	1	0	0	0
Casuarina type	1	1	0	0
Chenopodiaceae/Amaranthaceae	0	1	1	0
Chloranthaceae	1	0	0	0
Cupania type	0	0	1	0
Didymelaceae	0	0	0	1
Ericales	0	0	0	1
Gunnera type	0	0	1	0

Haloragaceae	0	0	0	1
Hammamelicaceae (*Liquidambar*)	0	1	0	0
Juglandaceae	1	1	0	0
Liliaceae	0	0	0	1
Loranthaceae	0	0	1	0
Malvaceae(Bombacoideae)	1	0	0	1
Myricaceae (*Triatriopollenites*)	1	0	1	0
Myrtaceae	1	0	0	0
Nothofagaceae (brassi type)	1	0	1	0
Nothofagaceae (fusca type)	1	0	1	0
Proteaceae (*Beauprea* type)	0	1	1	0
Proteaceae s.l.	1	1	1	1
Rutaceae? (*R. baculatus*)	1	1	1	1

Table 3

Palynological and most comparable megafloral records from Laguna del Hunco

Family/Genus	Microfossil	Megafossil		
	Fossil genus/species	Fossil genus/species	Type of fossil	References
Pteridophyta				
Dicksoniaceae: *Dicksonia*	*Trilites tuberculiformis, Ischyosporites areapunctatis*	*Dicksonia* sp.	Fertile pinnae	Carvalho et al. 2013
Gleicheniaceae	*Gleicheniidites senonicus*	Gleicheniaceae sp.	Fertile pinnae	Carvalho et al. 2013
Pteridaceae	*Polypodiaceoisporites* sp.	*Adiantum* sp.	Fertile pinnae	Carvalho et al. 2013
Osmundaceae	*Baculatisporites comaumensis, Todisportes major*	*Todea amissa* Carvalho	Fertile pinnae and silicified trunk	Carvalho et al. 2013; Bomfleur and Escapa 2019; Bippus et al. 2019
Cyatheaceae	*Cyathidites* spp.	----------		
Schizaeaceae	*Birestisporites* sp.	----------		
Polypodiaceae	*Polypodiidiies speciosus*	----------		
Gymnospermophyta				
Araucariaceae: *Araucaria* Sect. *Eutacta*	*Araucariacites australis*	*Araucaria* new species	Leafy branches, cone scales, pollen cones	Rossetto-Harris et al. 2020
Araucariaceae: *Agathis*	*Dilwynites* spp.	*Agathis zamunerae* Wilf	Leafy branches, single leaves, seed cones, cone scales + seeds, pollen cones	Wilf et al. 2014

Cycadaceae	*Cycadopites* sp.	*Austrozamia stockeyi* Wilf et al.	Leaves	Wilf et al. 2016
Ginkgoaceae	*Cycadopites* sp.	*Ginkgoites patagonicus* (Berry) Villar et al.	Leaves	Villar et al. 2015
Podocarpaceae: *Podocarpus*	*Podocarpidites* spp.,	*Retrophyllum oxyphyllum* (Freng. and Parodi) Wilf, *Podocarpus andiniformis*Berry	Leafy branches, peduncle of pollen cones (*Retrophyllum*); leafy branches (*Podocarpus*)	Berry 1938; Frenguelli and Parodi 1941; Wilf et al. 2017a; Wilf 2020
Podocarpaceae: *Dacrycarpus*	*Dacrycarpites australiensis*	*Dacrycarpus puertae* Wilf	Leafy branches, seed cones, pollen cones	Wilf 2012
Podocarpaceae: *Dacrydium*	*Ligistepollenites florinii*	----------		
Podocarpaceae: *Microcachyis*	*Microcachyidites antarcticus*	----------		
Podocarpaceae	*Gamerroites psilasaccus*	----------		
Podocarpaceae: Phyllocladoid clade	----------	*Huncocladus laubenfelsii* Andruchow-Colombo et al.	Foliage	Andruchow-Colombo et al. 2019
Cupressaceae	----------	*Papuacedrus prechilensis* (Berry) Wilf et al.	Foliage, seed cone	Wilf et al. 2009
Magnoliophyta				
Juglandaceae: Engelhardiodeae	*Plicatopollis wodehousi*	*Alatonucula ignis* Hermsen and Gandolfo	Fruits	Hermsen and Gandolfo 2016
Fabaceae	*Margocolporites* sp.	Fabaceae spp.	Several foliage types, rare fruits (pods)	Wilf et al. 2005
Proteaceae	*Proteacidites* sp., *Propylipollis* sp.	*Orites bivascularis*(Berry) Romero et al., *Roupala patagonica* Durango	Fruits, plus several associated leaves	Romero et al. 1988; González et al. 2007

		de Cabrera and Romero, *Lomatia preferruginea* Berry, *Lomatia occidentalis* (Berry) Frenguelli		
Anacardiaceae	*Striatricolporites gamerroi*	Sapindales spp.	Several foliage types	Wilf et al. 2005
Fagaceae: *Castanopsis*	*Cupuliferoidapollis* sp. 1	*Castanopsis rothwellii* Wilf et al. (infructescences), *Castaneophyllum patagonicum* (Berry) Wilf et al. (leaves)	Infructescences and leaves	Wilf et al. 2019a
Myrtaceae	*Myrtaceidites* sp.	*Eucalyptus frenguelliana* Gandolfo and Zamaloa (leaves), *E. caldericola* Hermsen et al. (infructescences), *E. lynchiae* Gandolfo and Hermsen (flower buds), several additional Myrtaceae spp. (leaves and fruits)	Leaves, flowers, fruits	Wilf et al. 2005; Gandolfo et al. 2011; González 2008; Hermsen et al. 2012
Cunoniaceae	*Tricolporites* sp. 2 (*Weinmania* type)	*Ceratopetalum edgardoromeroi* and others	Fruits, plus several undescribed leaf and infructescence spp. of the family	Gandolfo and Hermsen 2017
Casuarinaceae or Myricaceae	*Haloragacidites harrisii*	*Gymnostoma patagonicum (*Frenguelli) Zamaloa*, G. archangelskyi* Zamaloa and Romero*, G. argentinum* Zamaloa and Gandolfo	Branchlets + leaves + infructescences or + male inflorescence + pollen	Zamaloa et al. 2006

Malvaceae	*Intratriporopollenites* sp.	Malvaceae spp.	Infructescences	Gandolfo pers. com.
Asteraceae	*Huanilipollis cabrerae*	----------		
Chloranthaceae	*Clavatipollenites sp.*	----------		
Nothofagaceae: *Nothofagus*	*Nothofagidites saraensis, N. flemingii, N.* sp.	----------		
Rubiaceae	*Palaeocoprosmadites* sp.	----------		
Ulmaceae	*Ulmoideipites patagonicus*	----------		
Monimiaceae	----------	*Monimiophyllum callidentatum* CL Knight	Leaf	Knight and Wilf 2013
Atherospermataceae	----------	*Atherospermophyllum guinazui* (Berry) CL Knight	Leaves	Knight and Wilf 2013
Menispermaceae	----------	Menispermaceae *sp., Menispermites calderensis* Jud et al.	Endocarp, leaf	Jud et al. 2018b
Bixaceae	----------	*Bixa, Cochlospermum*	Leaves, fruits	González 2008
Solanaceae	----------	*Physalis infinemundi* Wilf	Fruits	Wilf et al. 2017b
Akaniaceae	----------	*Akania americana* Romero and Hickey, *A. patagonica* Gandolfo et al.	Leaves	Romero and Hickey 1976, Gandolfo et al. 1988

Note. First column: Botanical affinity (family, genus); second column: palynomorphs taxa here recorded (only those palynomorphs identified to genus level are listed in this table); third to fifth columns: megafossil records (fossil taxa, type of fossil, and references). Underscores indicate absence of fossil record.

Figure 1

Click here to access/download;Figure;Fig. 1.jpg

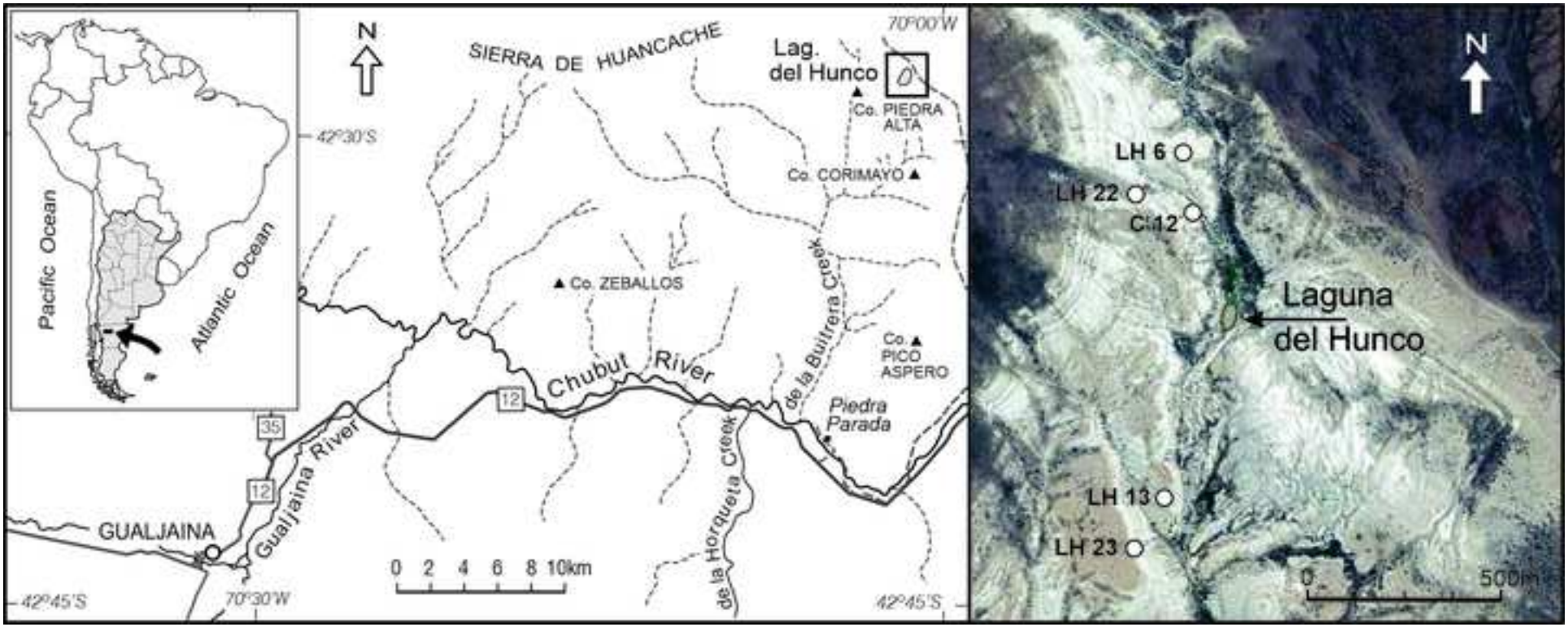

Figure 1 shades of gray

Click here to access/download;Figure;Fig. 1 shades of gray .jpg

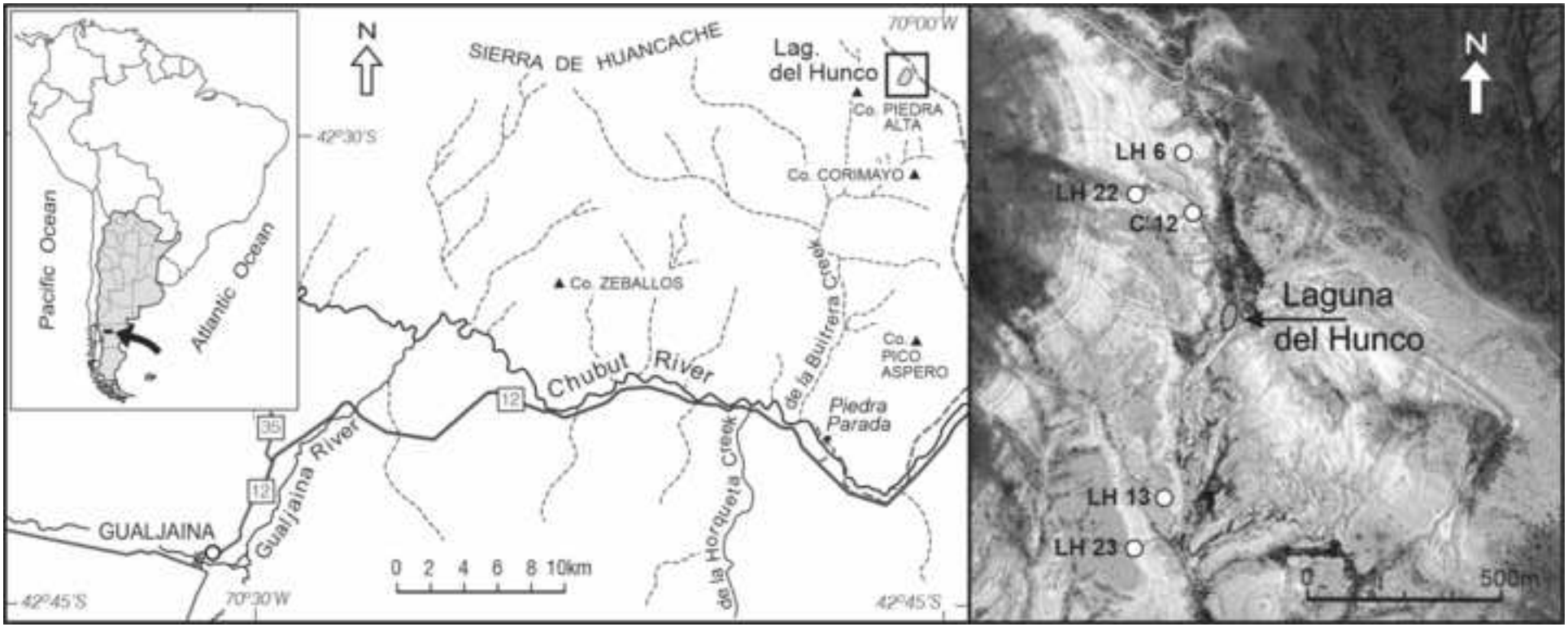

Figure 2

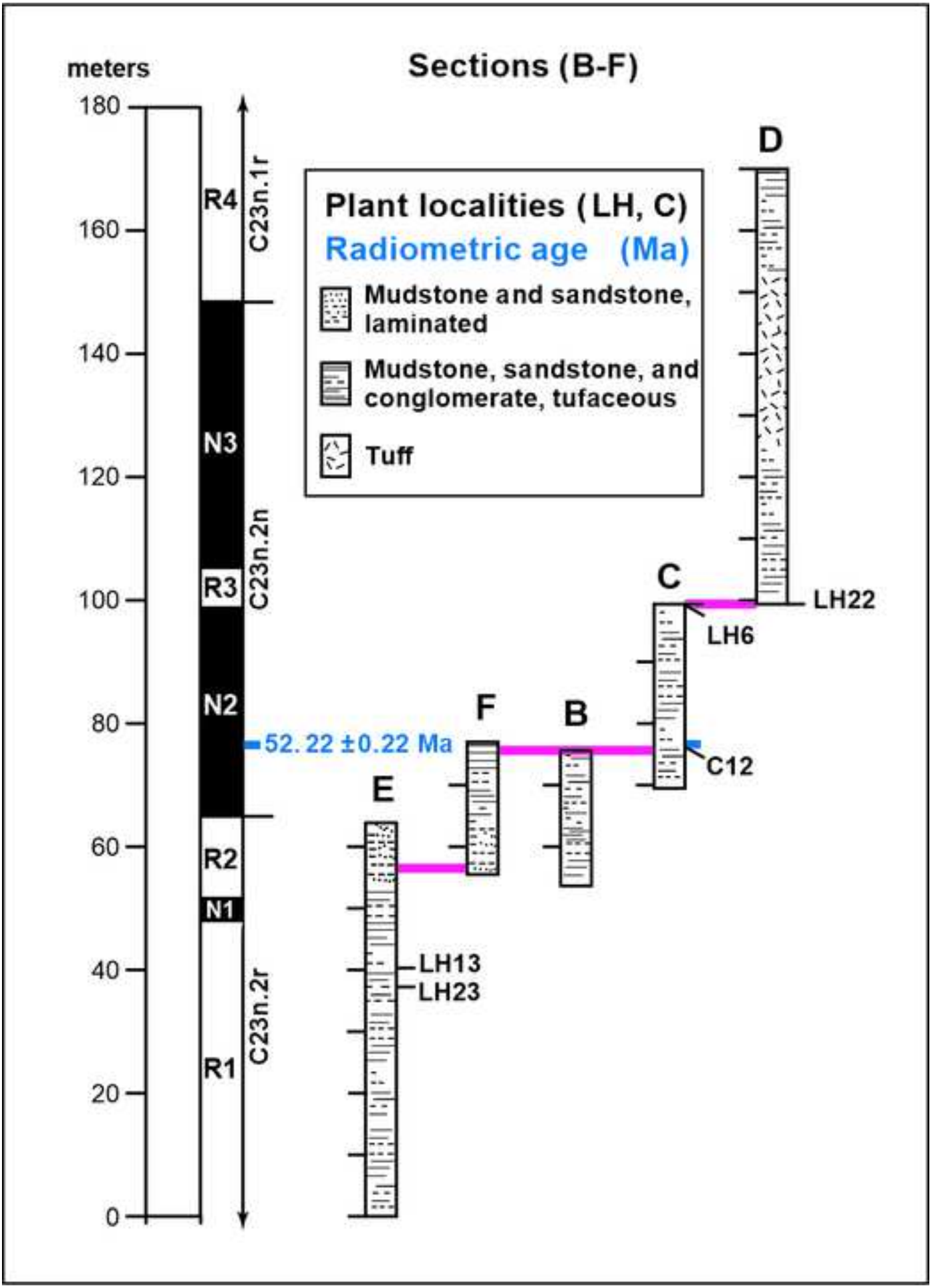

Figure 2 shades of gray

Click here to access/download;Figure;Fig. 2 shades of gray.jpg

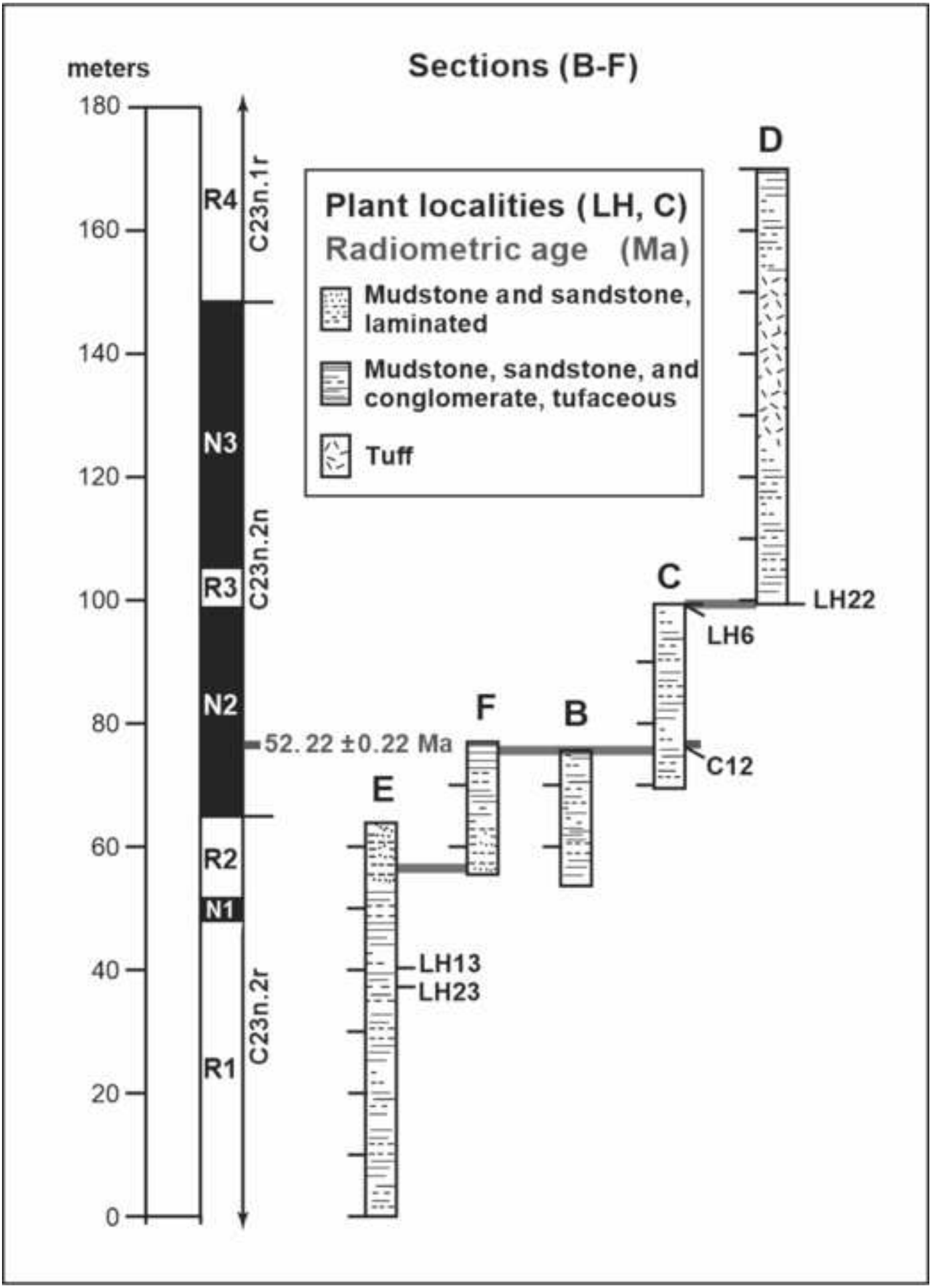

Figure 3

Click here to access/download;Figure;Figure 3.jpg

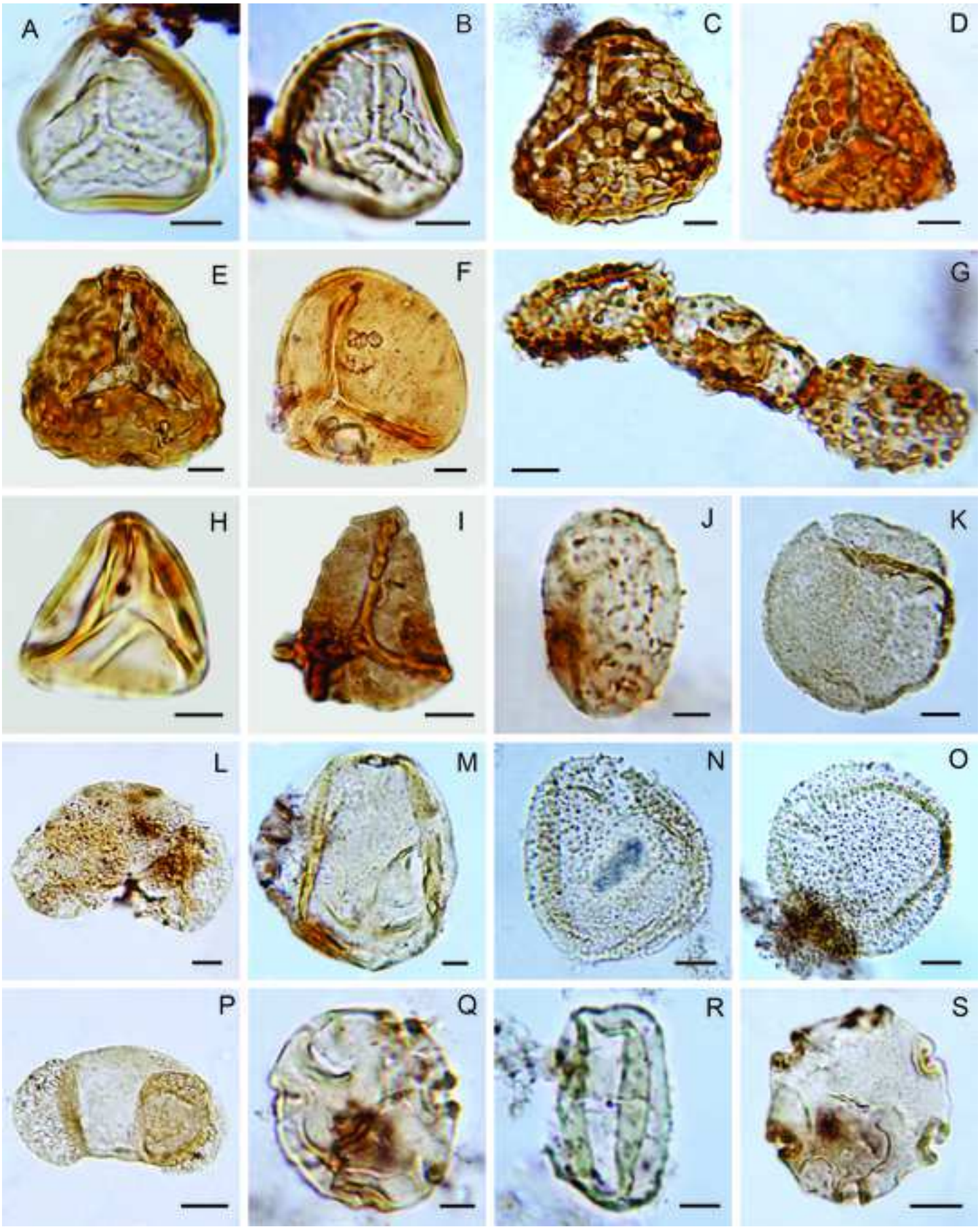

Figure 3 shades of gray

Click here to access/download;Figure;Figure 3 shades of gray.jpg

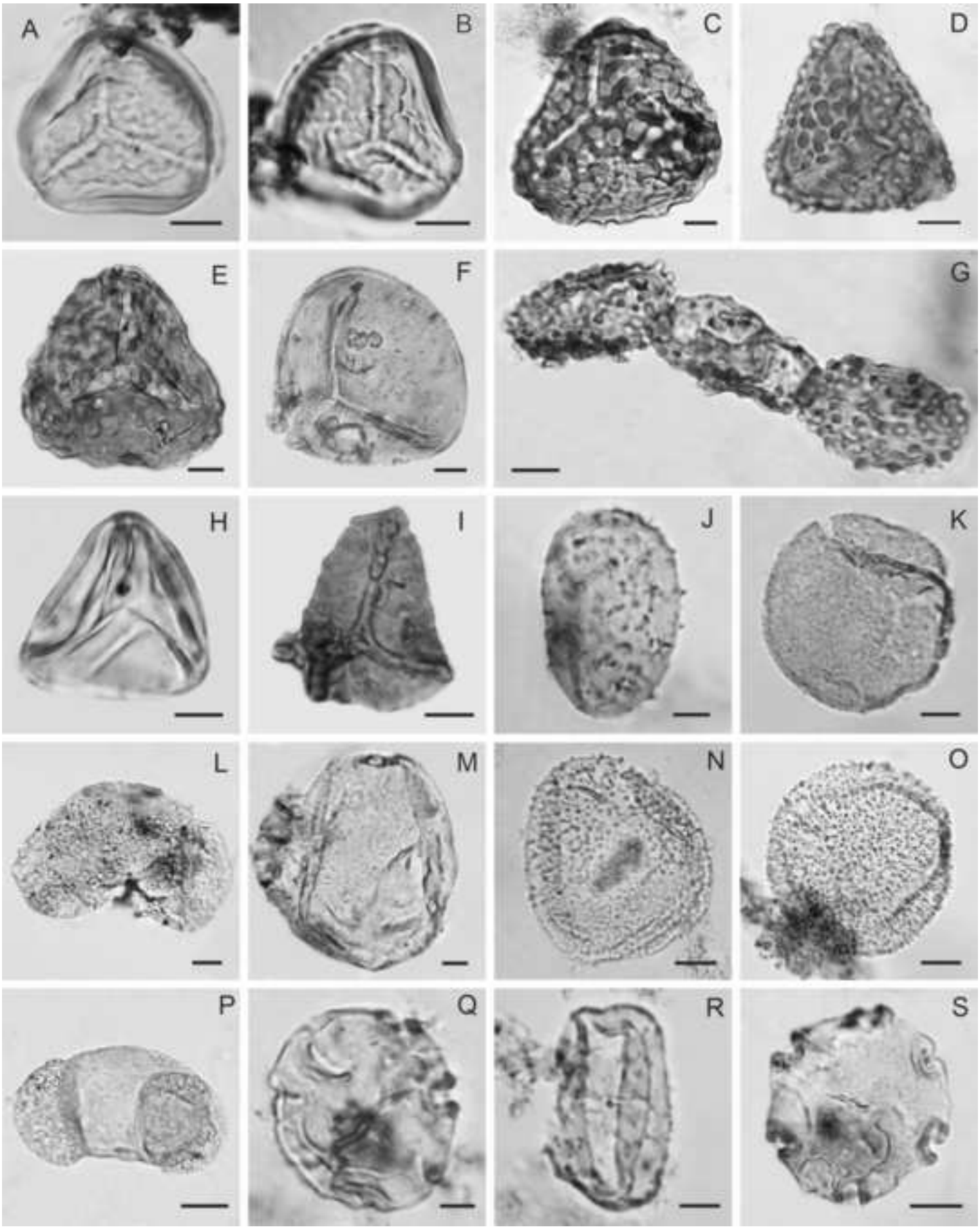

Figure 4

Click here to access/download;Figure;Figure 4.jpg

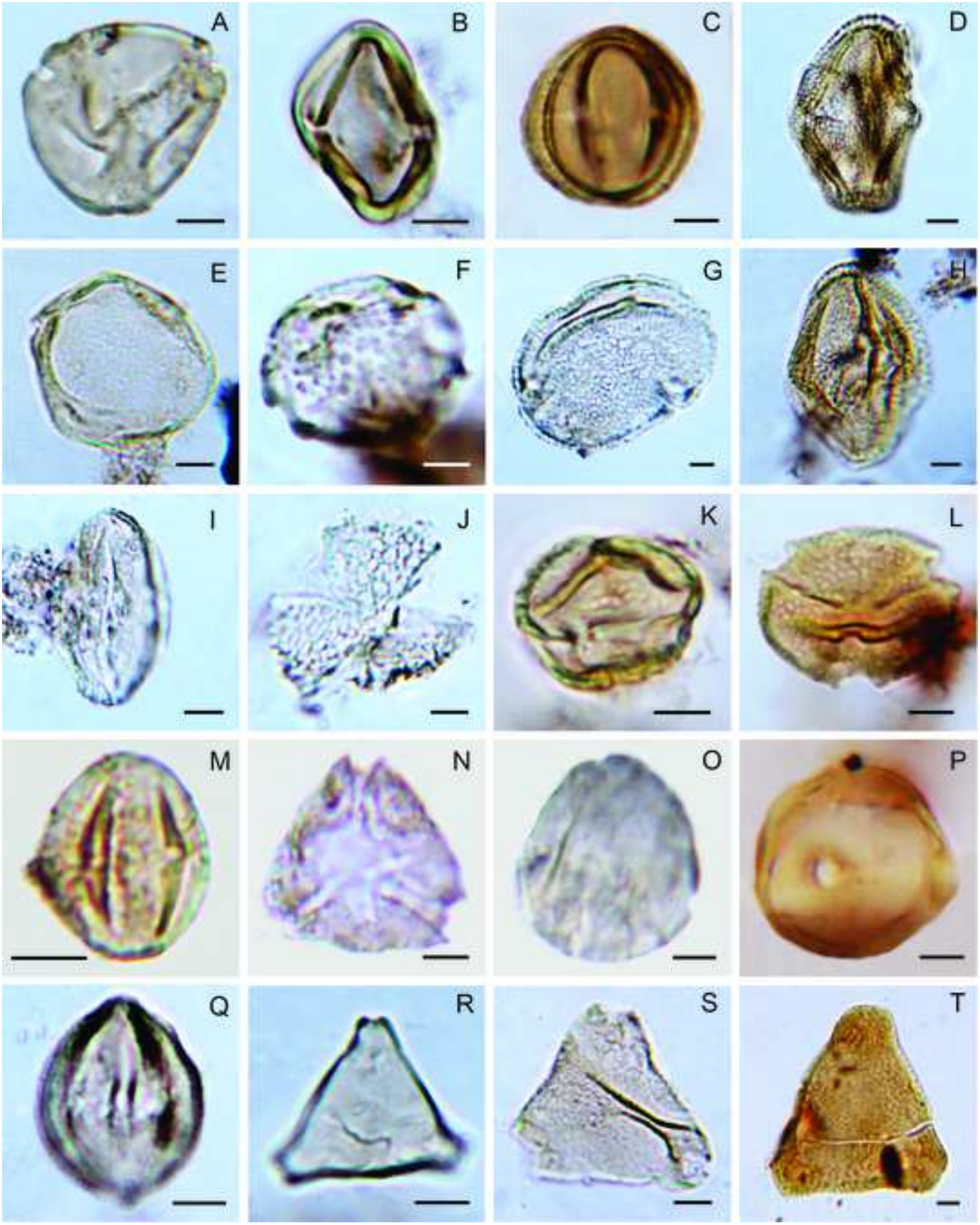

Figure 4 shades of gray

Click here to access/download;Figure;Figure 4 shades of gray.jpg

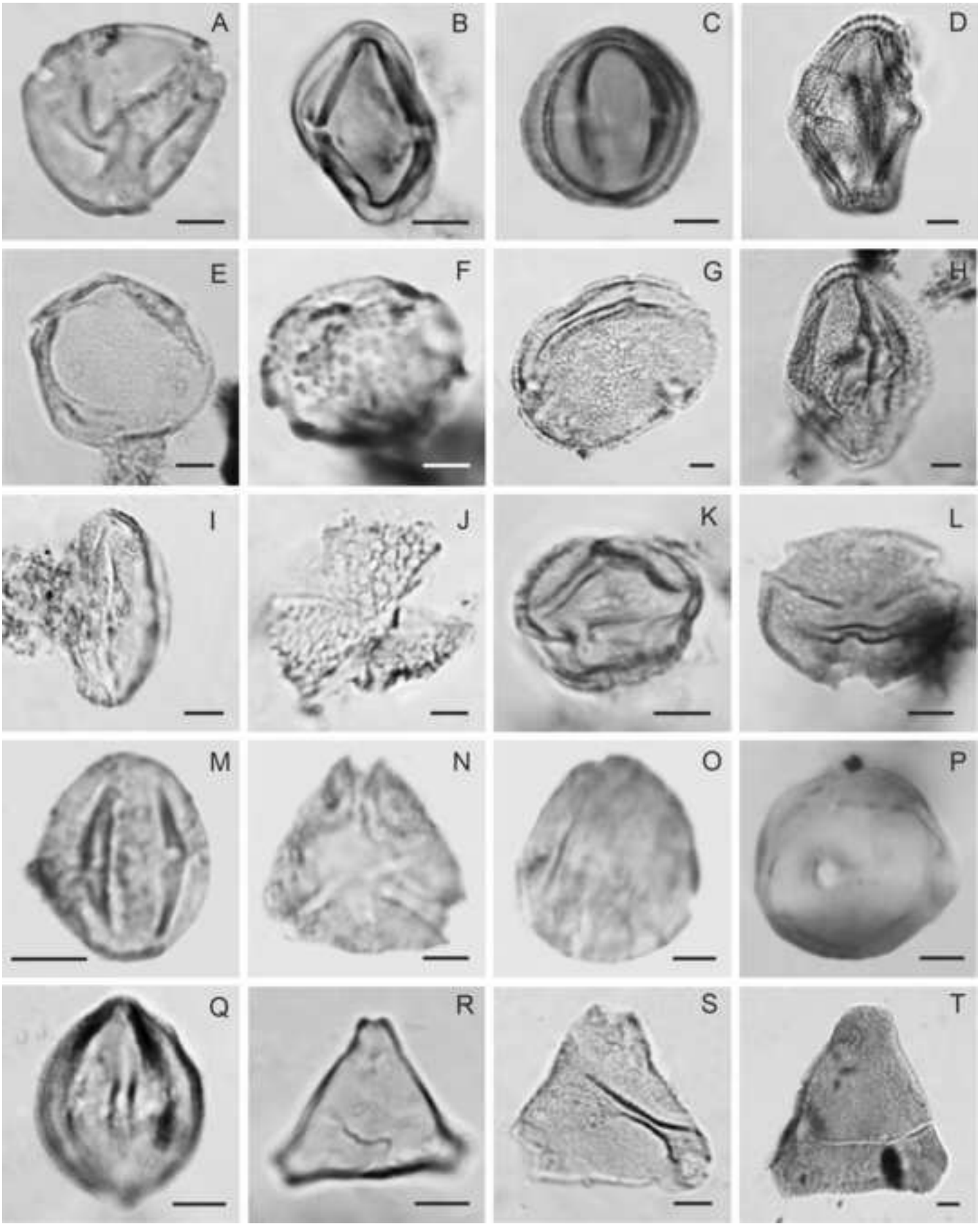

Figure 5

Click here to access/download;Figure;Figure 5.jpg

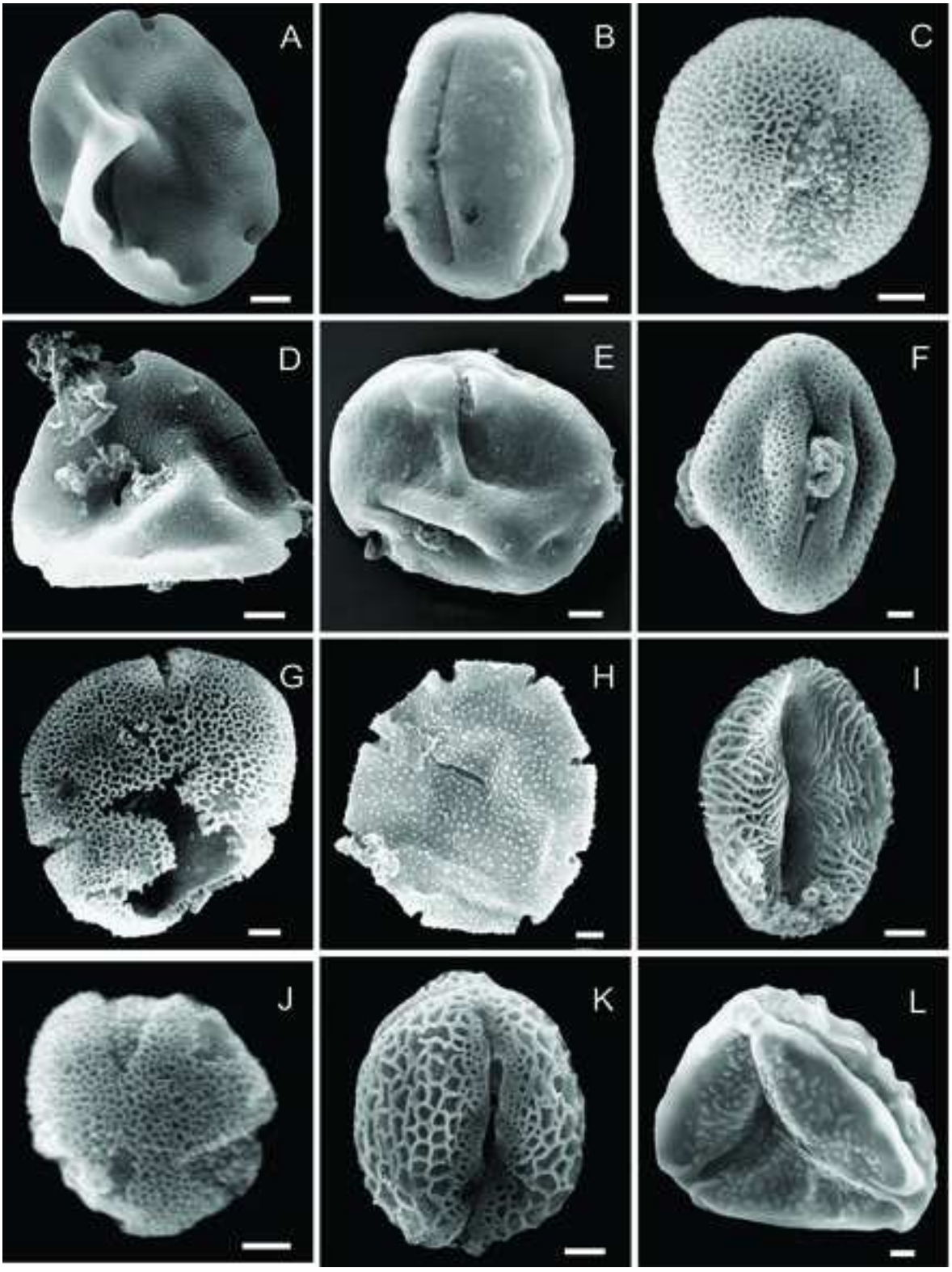

Figure 5 shades of gray

Click here to access/download;Figure;Figure 5 shades of gray.jpg

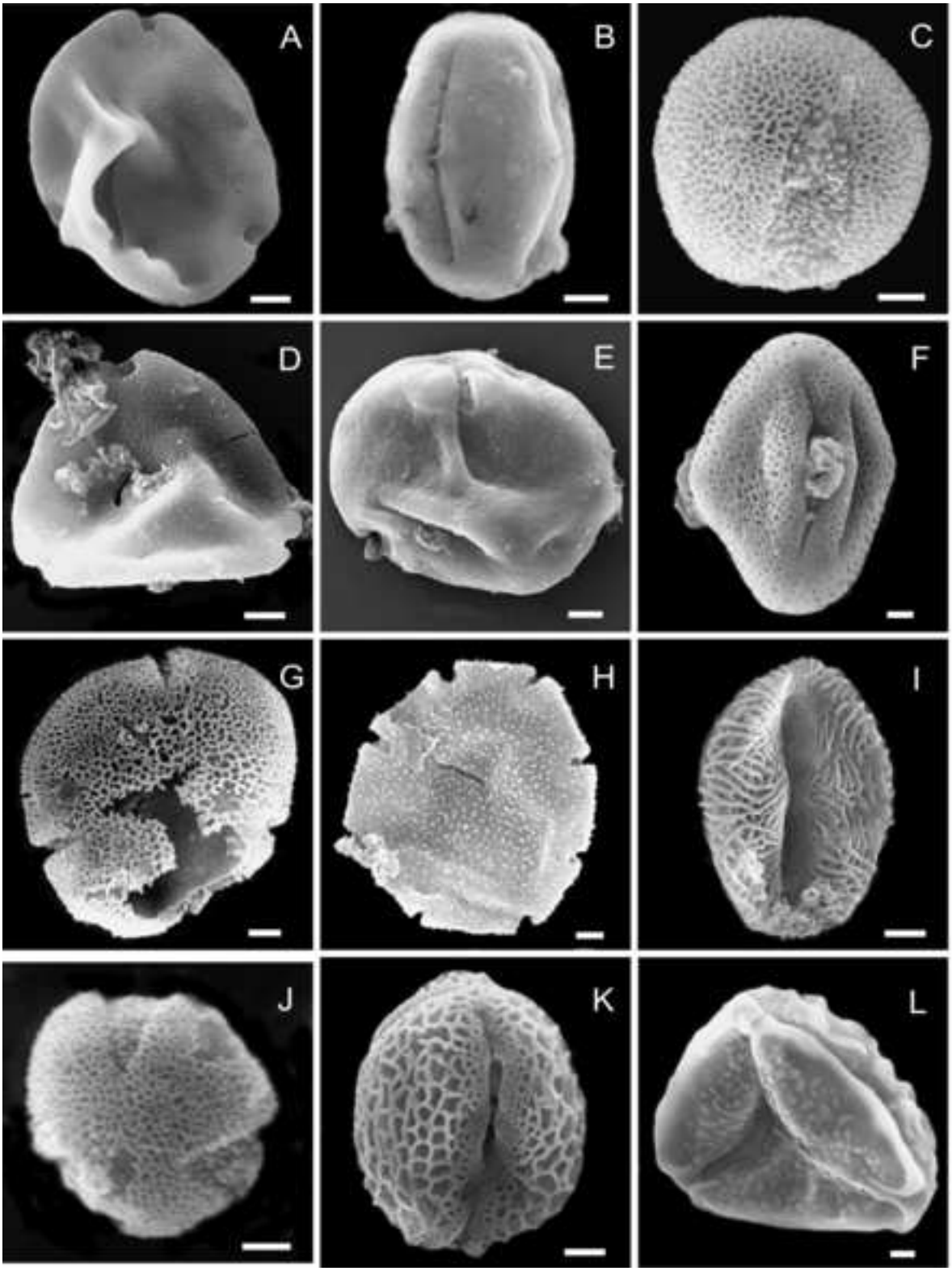

Figure 6