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First Evidence for Wollemi Pine-type Pollen (*Dilwynites*: Araucariaceae) in South America

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Abstract

We report the first fossil pollen from South America of the lineage that includes the recently discovered, extremely rare Australian Wollemi Pine, *Wollemia nobilis* (Araucariaceae). The grains are from the late Paleocene to early middle Eocene Ligorio Márquez Formation of Santa Cruz, Patagonia, Argentina, and are assigned to *Dilwynites*, the fossil pollen type that closely resembles the pollen of modern *Wollemia* and some species of its Australasian sister genus, *Agathis*. *Dilwynites* was formerly known only from Australia, New Zealand, and East Antarctica. The Patagonian *Dilwynites* occurs with several taxa of Podocarpaceae and a diverse range of cryptogams and angiosperms, but not *Nothofagus*. The fossils greatly extend the known geographic range of *Dilwynites* and provide important new evidence for the Antarctic region as an early Paleogene portal for biotic interchange between Australasia and South America.

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Introduction

The Southern Hemisphere monkey-puzzle tree family, Araucariaceae, was long believed to comprise two living genera: *Araucaria* Juss., with about 19 species endemic to the southwest Pacific and South America, and *Agathis* Salisb., with about 20 species distributed from Sumatra to New Zealand but absent in South America. Remarkably, a third araucarian genus was discovered in 1994 in New South Wales, Australia, whose sole species is *Wollemia nobilis* W.G. Jones, K.D. Hill & J.M. Allen, common name Wollemi Pine [1].

With fewer than 40 adult specimens known to survive in the wild, *W. nobilis* is one of the world's rarest trees. Adding to the spectacular nature of the discovery was the location of the stands, in a remote gorge within 150 km of Sydney, Australia's largest city; the large stature of the trees (up to 40 m tall); and the apparent similarity of the foliage to that of the Jurassic species "*Agathis*" *jurassica* M.E. White [2] and the Cretaceous to early Cenozoic genus *Araucarioides* [3–6]. So far, none of the similar macrofossils has been convincingly demonstrated to belong to *Wollemia* [6,7], and indeed "*A.*" *jurassica* differs from foliage of *Wollemia* in details of venation, leaf arrangement and leaf shape [8]. However, the presumed close relationship quickly led to *W. nobilis* being given the status of a "living fossil from the age of dinosaurs" in the popular press (e.g. [9]).

In contrast, once pollen was made available, it was quickly recognized that the *Wollemia* clade had a well-established fossil history provided by the morphogenus *Dilwynites* W.K. Harris [10], comprising *D. granulatus* W.K. Harris and *D. tuberculatus* W.K. Harris [6,11,12]. For example, in southern Australia, *D. granulatus*,

the morphospecies that most closely resembles modern *Wollemia* pollen, can be traced back as far as the Turonian Age (89.8 to 93.9 Ma) of the Late Cretaceous [11–13]. So far, *Dilwynites* has been identified in Paleogene to Neogene deposits of western, central, and northern Australia (references in [14]), in Cretaceous to Neogene deposits of New Zealand [15], and in late Eocene deposits of East Antarctica [16]. However, apart from a possible record from the Paleogene of Seymour Island [17], no *Dilwynites* pollen has previously been recognized from West Gondwana.

Since 2000, the first author has also recognized that at least one species of *Agathis* produces pollen that is morphologically consistent with *Dilwynites*, and thus the nearest extant relatives of the plants that produced *Dilwynites* pollen are best regarded as both *Wollemia* and *Agathis* (e.g., [14]). This observation is consistent with the results of many recent molecular studies indicating that *Wollemia* and *Agathis* are sister taxa [18–23], along with several characteristics of the seed cones of the two genera that may be synapomorphic, especially the condition of the seeds being winged and nearly free from the fused bract and scale [24]. By contrast, in *Araucaria*, the seeds are embedded in the bract/scale complex.

We here present microfossil evidence that araucarians producing *Dilwynites* pollen were growing in southern Patagonia during the late Paleocene to early middle Eocene. This discovery greatly augments evidence for the past range of *Wollemia* and/or *Agathis* conifers that produce this pollen type and adds to the growing paleobotanical evidence for extensive trans-Antarctic interchange between Patagonia and Australia during the globally warm early Paleogene.

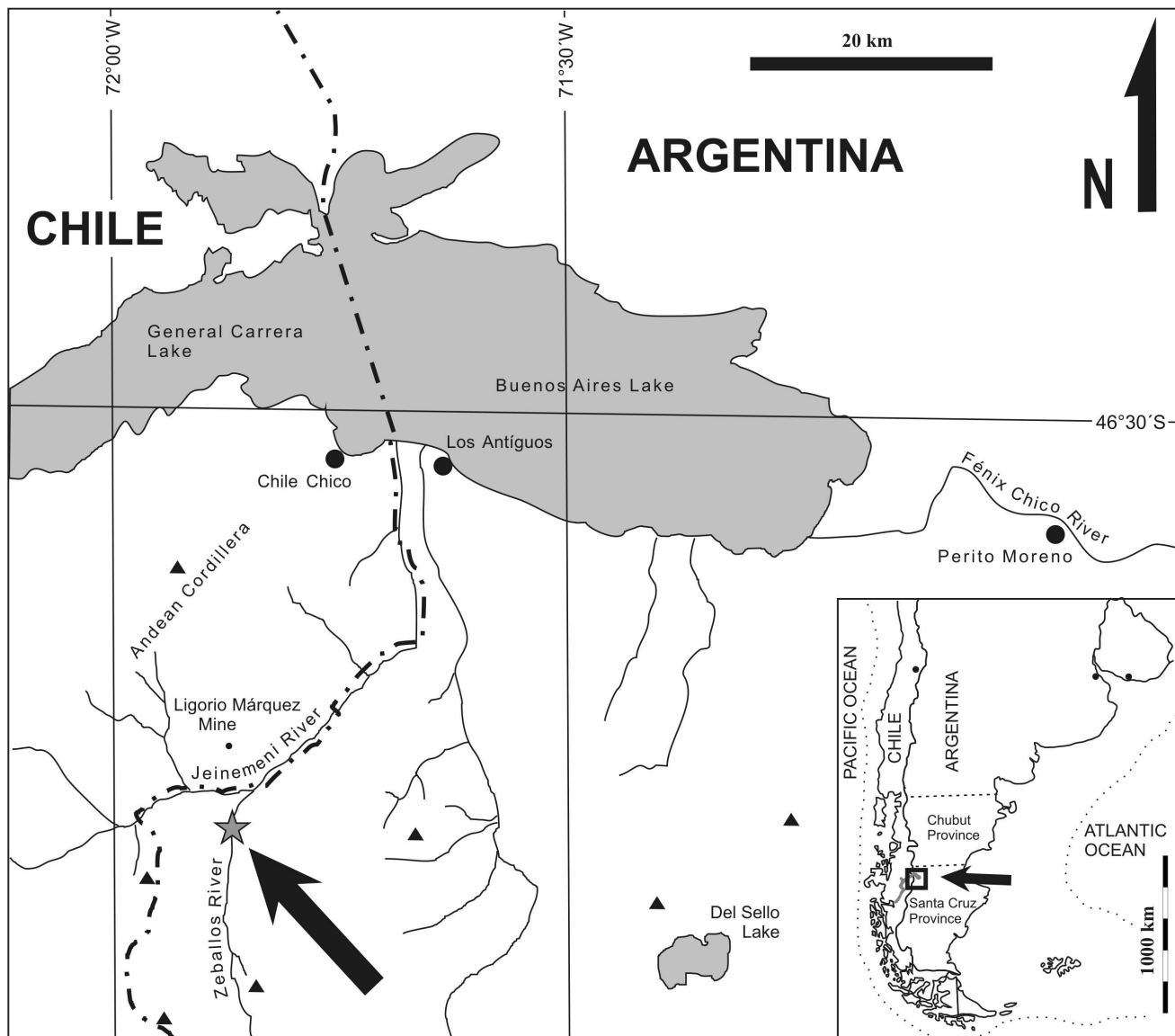


Figure 1. Map of study area. The new fossil plant locality occurs along the Río Zeballos (arrow, star) in Santa Cruz Province, Argentina. Also shown is the previously reported type locality of the Ligorio Márquez Formation [26], the Ligorio Márquez coal mine in XI Región, Chile. doi:10.1371/journal.pone.0069281.g001

Geological Setting and Age Control

Ethics Statement

All necessary permits were obtained for the described study, which complied with all relevant regulations. Permits were issued by the Secretaría de Estado de Cultura de la Provincia de Santa Cruz, Argentina.

The *Dilwynites* specimens reported here came from an isolated, newly recognized, streamcut outcrop of the Ligorio Márquez Formation in Santa Cruz Province, Patagonia, Argentina, located along the Río Zeballos and 36 km south-southwest of the town of Los Antiguos (Fig. 1). Precise locality data are available on request from AI, PW, or Museo Padre Jesús Molina, Río Gallegos, Santa Cruz, Argentina (MPM), where material is stored. The Ligorio Márquez Formation, previously studied only on the Chilean side of the nearby border [25–27], comprises a sequence of coastal floodplain, fluvial and mire facies deposited in a foreland basin (the

Ligorio Márquez Basin) that subsequently was uplifted by compressional Andean tectonic activity during and since the early Miocene [28,29]. The material studied here was derived from a ~0.5 m thick carbonaceous shale bed containing abundant fossil leaves (under separate study), from a probable coastal swamp.

The local exposure of the Ligorio Márquez Formation lies unconformably above the Cretaceous Río Tarde Formation and is itself overlain unconformably by marine rocks of the Centinela Formation [30–32]. Stratigraphic correlation of the fossil locality is extremely difficult due to limited outcrop area and local cover. All radioisotopic ages listed below are as originally reported and would need recalibration with new constants and reanalyses with updated methods for any detailed analysis.

$^{40}\text{K}/^{39}\text{Ar}$ dates derived from ash beds at the top of the Río Tarde Formation at Lago Posadas (100 km south of our study area) were 97.1 ± 3.8 and 99.1 ± 5.6 Ma [33]. Whole-rock $^{40}\text{Ar}/^{39}\text{Ar}$ analyses of an altered ash bed from the Centinela

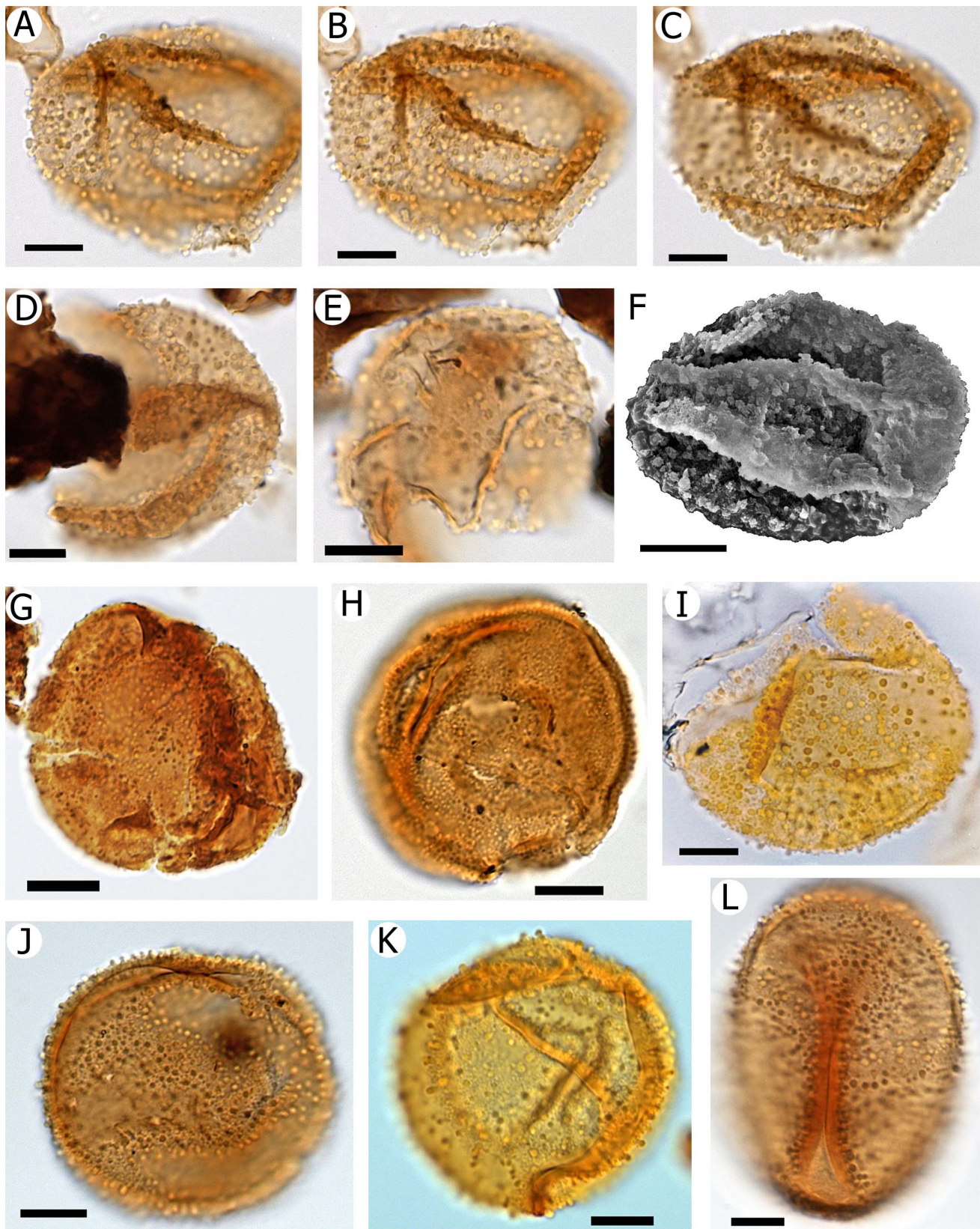


Figure 2. Microscope images of *Dilwynites* spp. (A–K) and *Agathis* pollen (L). A–F, *Dilwynites* sp. cf. *D. tuberculatus* from the Río Zeballos locality, Ligorio Márquez Formation, Santa Cruz, Argentina. A–C, single grain, showing details including clavae/gemmae at three focal planes. D–F, other specimens (F is a scanning electron microscope image). G, H, *Dilwynites granulatus* from Australia showing granulate ornamentation. G, Ti-tree Basin, Northern Territory (early Eocene). H, Frome Embayment, South Australia (Miocene). I–K, *Dilwynites tuberculatus* from Australia, showing

sculptural elements that are similar to those of the Río Zeballos specimens (A–F), and which are more pronounced and more widely spaced than in *D. granulatus* (G, H). I, Cethana, Tasmania (early Oligocene). J, Ti-tree Basin, Northern Territory (early Eocene). K, Lowana Rd, Tasmania (early Eocene). L, *Agathis ovata* recent specimen from Mts. des Koghis (Queensland Herbarium specimen AQ 391532: W.G. Ziarnik 34), New Caledonia. Note strong similarity to *Dilwynites* spp. Scale bars: 10 μm . doi:10.1371/journal.pone.0069281.g002

Formation south of Calafate (420 km to the south) yielded a range of ages with large scatter, from which the authors suggested a best estimate of 46 ± 2 Ma [34]. This suggests a middle Eocene minimum age for the Centinela transgression in western Santa Cruz and thus of the fossil flora studied here. However, it is not certain that the Centinela exposures in our study area are correlative with those dated [34]. Our attempts to date basaltic intrusions superposed above the Río Zeballos locality did not yield informative analytical results (B. Jicha, pers. comm. 2012), although some basic intrusions in the area are associated with the Los Antiguos Teschenite and the Posadas Formation. The Los Antiguos Teschenite intrudes the Río Tarde Formation and yielded early–middle Eocene $^{40}\text{K}/^{39}\text{Ar}$ ages of 46 ± 3 and 48 ± 4 Ma [35–38]. The basalts from the Posadas Formation were dated on the Argentinean side to 43.5 ± 7 Ma [33]. At the Chilean type locality [26], the Ligorio Márquez coal mine (Fig. 1), the Ligorio Márquez Formation comprises a c. 55 m thick succession of alternating subhorizontal beds of mudstones, quartz-rich sandstones and thin coals, unconformably underlain by Lower Cretaceous tuffs, the Flamencos Tuffs, and overlain by basalts with a $^{40}\text{K}/^{39}\text{Ar}$ age on plagioclase of 47.6 ± 0.78 Ma above the mine [27] but which elsewhere range in age from c. 57 Ma to c. 41 Ma [26,27,38,39].

In summary, all the geochronologic evidence, while greatly in need of revision, is most consistent with an early middle Eocene (Lutetian) minimum age for the fossil flora at Río Zeballos. This inference is best supported by the recent $^{40}\text{K}/^{39}\text{Ar}$ dates of 47.6 ± 0.78 Ma, analyzed from units that immediately overlie the type strata of the Ligorio Márquez Formation in Chile [27].

The palynoflora so far studied at the Río Zeballos site comprises a total of 25–30 taxa of cryptogam spores and gymnosperm and angiosperm pollen (Figs. 2A–F, 3, 4). Podocarpaceous gymnosperms include *Dacrycarpites australiensis* (*Dacrycarpus*; Fig. 3G), *Dacrydiumidites florinii* (*Dacrydium*; Fig. 3H), *Phyllocladidites mawsonii* (*Lagarostrobos*; Fig. 3D), *Microcachrydites antarcticus* (*Microcachrys*; Fig. 3I), and *Podosporites microsaccatus* (*Microcachrys*; Fig. 3E). In general, these taxa are indicative of regional microtherm to mesotherm rainforest vegetation [40]. Angiosperm pollen (Figs. 3J–L, 4) includes mesotherm to possible megatherm taxa such as *Proxapertites* sp. (Araceae/Arecaceae; Fig. 3L) and *Bombacacidites* (bombacoid Malvaceae; Fig. 4B). Pollen of the microtherm to mesotherm rainforest genus *Nothofagus* was not recorded. This absence of a taxon that is usually very abundant when present, from an otherwise diverse palynoflora, also implies that our samples are most likely to be early Eocene in age, an interval that in Patagonia has long been noted to lack *Nothofagus*, and certainly no younger than middle Eocene (e.g., [41–46]).

The macroflora is currently the subject of a separate study, but so far, *Dacrycarpus* (presumably corresponding to the *Dacrycarpites australiensis* pollen) has been identified as well as a possible cycad and many angiosperms, including several species of Lauraceae, a family that is also well represented in Chilean samples of the Ligorio Márquez Formation [47]. In accord with the palynological data, *Nothofagus* macrofossils are absent. *Dacrycarpus* macrofossils are otherwise known in Patagonia only from early and middle Eocene strata [48], although *Dacrycarpites australiensis* pollen is present in the region until the Miocene [49].

Although more study is clearly needed, the combined geological and paleobotanical evidence suggests an early Eocene age for the Río Zeballos material studied here, and most conservatively, its age lies within the late Paleocene to early middle Eocene interval.

Results

Systematic Paleontology

Turma: Aletes.

Subturma: Azonaletes.

Infraturma: Subpilonapiti.

Genus: *Dilwynites* W.K. Harris, 1965 [10].

Dilwynites sp. cf. *D. tuberculatus* W.K. Harris 1965 [10].

Description. Monad, apolar; inaperturate, spheroidal but usually flattened and/or folded; exine thin, less than 1 μm thick, densely ornamented with irregularly-spaced clavae c. 1–2 μm in diameter and height, areas between the sculptural elements apparently psilate; 36–(49)–52 μm in maximum diameter (10 specimens measured).

Illustrations. Figs. 2A–F.

Material and referred specimens. Ligorio Márquez Formation carbonaceous shale from the Río Zeballos locality, Santa Cruz, Argentina. Mounted specimens can be found on slide MPM-PB-14715.

Age. Late Paleocene to early middle Eocene, and most probably early Eocene.

Distribution. So far known only from the Río Zeballos locality, Santa Cruz, Patagonia, Argentina.

Affinity. *Wollemlia/Agathis* (Araucariaceae).

Remarks. The specimens from the Ligorio Márquez Formation differ from *Dilwynites granulatus* (Figs. 2G, H) and *D. tuberculatus* (Figs. 2I–K), described from the Danian to Selandian (early to middle Paleocene) Pebble Point Formation, South Australia [10], in that the coarse ornamentation of the fossils studied here consists of clavae (which may appear as gemmae in poorly preserved specimens) rather than granula and verrucae-tuberculae, respectively. The exines of the new fossils are also thinner. Pseudo-laeurae created by folding superficially resemble the trilete apertures on baculate-rugulate spores assigned to *Baculatisporites*, e.g. *B. turbioensis* Archangelsky in Argentina (see Fig. 5A in [50]). Lauraceae pollen is similar to that of Araucariaceae in being spheroidal and inaperturate, but it typically differs from *Dilwynites* in having ornamentation that consists of regularly-spaced, sharply pointed echinae, spinulae or foveolae (see e.g., Plate 33, images 391–393 in [51]). Moreover, it is well known that Lauraceae pollen is generally absent from fossil assemblages, mostly because it has only very thin exine with little sporopollenin [52], and probably very low production [53].

Here, we infer that the *Dilwynites* specimens from the Ligorio Márquez Formation potentially indicate the past presence of *Wollemlia* in Patagonia because the specimens closely resemble pollen of *W. nobilis* [6,11,12]. Alternatively, the fossil pollen could be attributed to *Agathis* because it has recently become apparent that several extant species of *Agathis* produce grains ornamented with relatively coarse granules (M.K. Macphail, unpublished data) and thus would be accommodated within *Dilwynites* if found as fossils. Examples of *Agathis* species producing this type of pollen include the New Caledonian *A. ovata* (Vieill.) Warb. (Fig. 2L) and *A. moorei* (Lindl.) Mast. Other extant Araucariaceae (and in

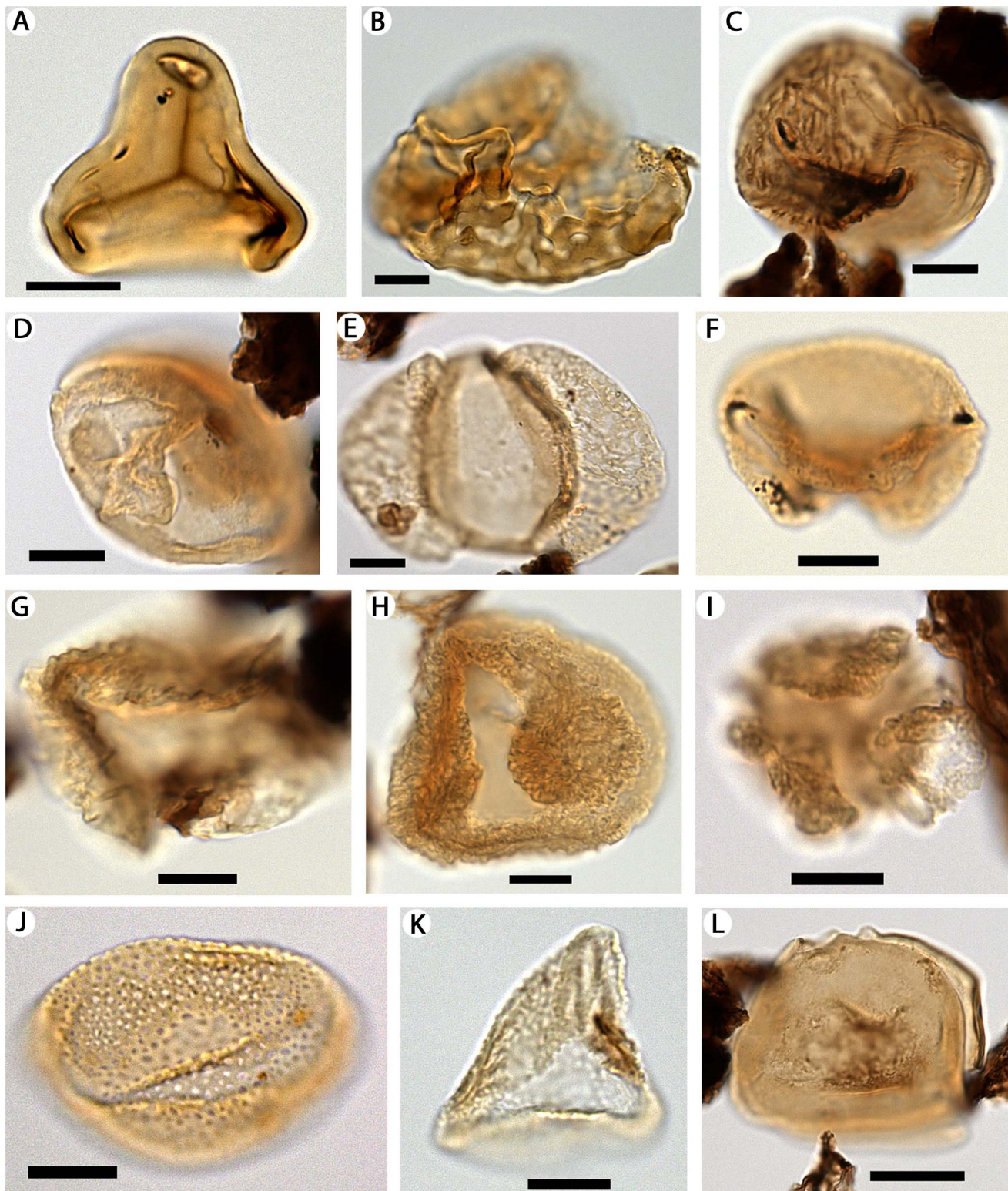


Figure 3. Microscope images of cryptogam spores (A–C), other gymnosperm pollen (D–I) and monocot pollen (J–L) from the Río Zeballos locality. Suggested extant affinities, if known, are shown in parentheses. A, *Cyathidites* sp. (Cyatheaceae). B, *Ischyosporites areapunctata* (Stuchlik) Barreda (Dicksoniaceae). C, *Reboulisporites fuegiensis* Zamalao & E.J. Romero (Aytoniaceae). D, *Phyllocladidites mawsonii* Cookson ex Couper (*Lagarostrobos*). E, *Podocarpidites marwickii* Couper (*Podocarpus/Prumnopitys*). F, *Podosporites microsaccatus* (Couper) M.E. Dettmann (*Microcachrys*). G, *Dacrycarpites australiensis* Cookson & K.M. Pike (*Dacrycarpus*). H, *Dacrydiumites florinii* Cookson & K.M. Pike var. (*Dacrydium*). I, *Microcachryidites antarcticus* Cookson (*Microcachrys*). J, *Liliacidites* cf. *L. regularis* Archangelsky (*Liliaceae*). K, *Luminidites* sp. (*Agavaceae*). L, *Proxapertites* sp. (*Araceae*). Scale bars: A–K, 10 μ m; L, 20 μ m.
doi:10.1371/journal.pone.0069281.g003

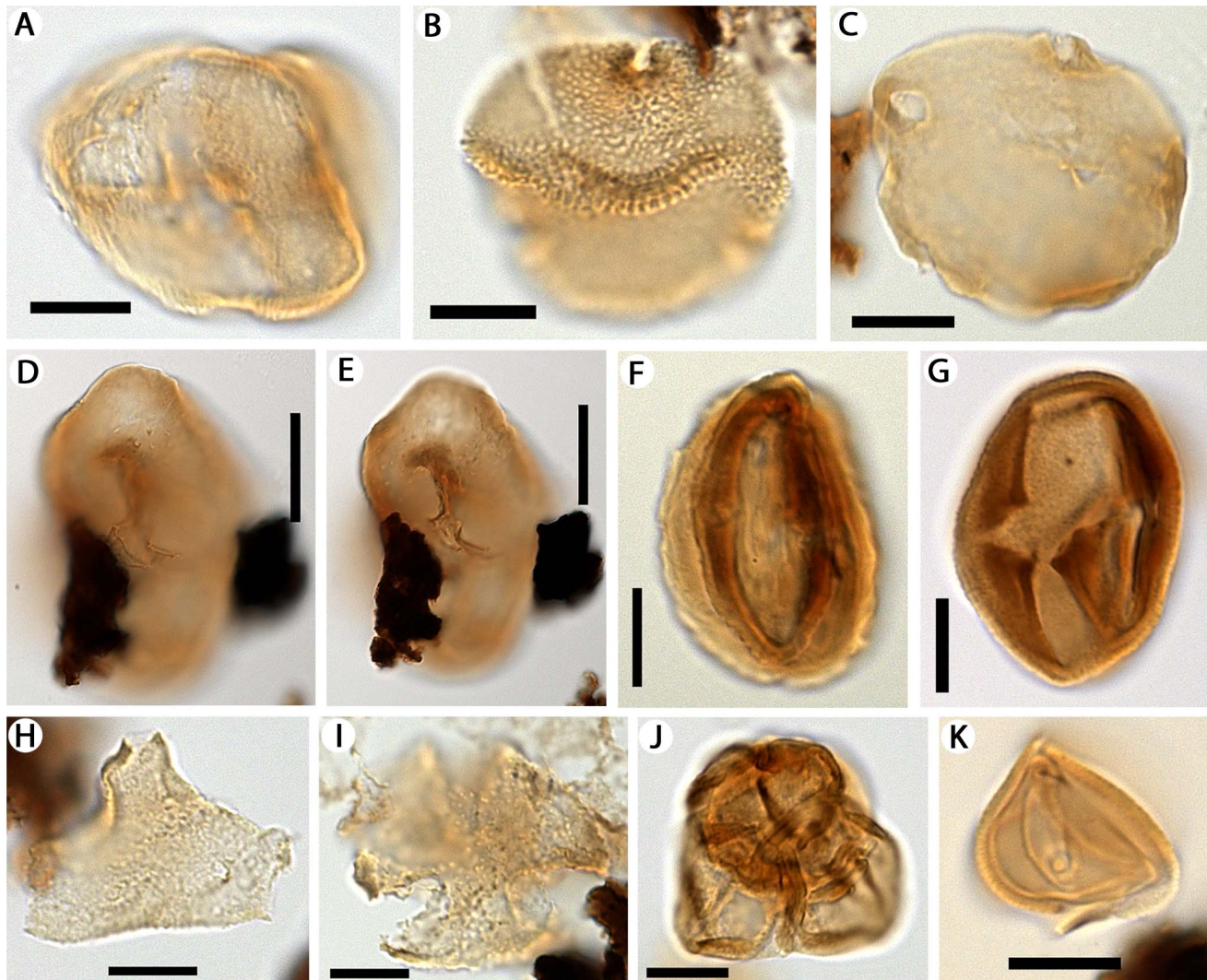


Figure 4. Microscope images of dicot pollen from the Río Zeballos locality. Suggested extant affinities, if known, are shown in parentheses. A, *Ailanthipites* sp. (Anacardiaceae). B, *Bombacacidites* sp. (bombacoid Malvaceae). C, *Stephanocolpites* sp. (cf. Haloragaceae). D, E, Triprojectacites group cf. *Integricorpus* sp. (at two focal planes). F, *Mutisiapollis* sp. (Asteraceae). G, *Tricolporites* sp. H, *Proteacidites* sp. (Proteaceae). I, *Spinitricolpites* sp. J, *Ericipites microverrucatus* (Ericales). K, *Schizocolpus* sp. (Didymelaceae). Scale bars: A–C, F–K, 10 μ m; D, E, 20 μ m. doi:10.1371/journal.pone.0069281.g004

particular *Araucaria*) pollen most obviously differ in having much less prominent surface ornamentation [12]. Further refinement of relationships between *Dilwynites* and extant taxa may be possible following more detailed comparisons.

Discussion

The Ligorio Márquez Formation specimens of *Dilwynites* are the first known record of *Wollemia*-type pollen in South America. It is uncertain whether the newly recognized Patagonian clavate morphotype of *Dilwynites* represents a new species, given the wide range of variation observed in the granulate sculptural elements characterizing *D. granulatus* and the baculate to tuberculate sculptural elements characterizing *D. tuberculatus* populations in Australia (see Figs. 2G–K). The same is true from preliminary observations of other gymnosperm pollen taxa in the Ligorio Márquez Formation sample, which differ from the ranges of morphologies observed in Australian populations and those recorded from the Falkland (Malvinas) Islands (compare

Figs. 3D–I with, e.g., Fig. 21 in [54]). A not unreasonable conclusion is that degrees of geographic differentiation occurred over the very long distances of these plants' ancient ranges.

Both *Araucaria* and *Agathis* have substantial macrofossil records in the Southern Hemisphere, but there is no strong macrofossil evidence for *Wollemia* (reviews [55–59]). *Araucaria* occurs extensively in Patagonia from the Early Jurassic to present, in West Antarctica from the Jurassic or Early Cretaceous to Eocene, and in Australia and New Zealand from the Early Cretaceous. The much more fragmentary *Agathis* record formerly came only from Cenozoic Australia and New Zealand, but abundant macrofossil *Agathis* specimens from the early and middle Eocene of northwestern Patagonia are now being described [60]; these include pollen cones, but pollen grains are not preserved within them. Reliable macrofossil evidence for *Agathis* is so far unknown from the Mesozoic [7,55,57].

At present, the macrofossils most likely to have close affinity to *Wollemia* are leaves of *Araucariooides* from Australia and New Zealand [6], and it is especially interesting that at the early

Eocene Lowana Road site in Tasmania, these leaves co-occur with relatively abundant *Dilwynites tuberculatus* pollen [61]. As stated previously, recent molecular and reproductive data resolve *Wollemia* and *Agathis* as likely sister taxa [18–24]. This evidence, combined with the fact that *Dilwynites* first appears in the fossil record much later (Turonian: Late Cretaceous) than *Araucaria* suggests that at least some Mesozoic fossils that cannot be assigned to *Araucaria* can now be regarded as belonging to the stem lineage of the *Agathis+Wollemia* clade [24]. These fossils include winged seeds and cone scales with seed detachment scars from the Early to mid-Cretaceous in southeastern Australia [6,62], New Zealand [63] and Alexander Island, West Antarctica [64]. It should also be noted that at least some of the pollen included in the generalized, widespread form *Araucariacites australis* Cookson, which extends to the Triassic in the Southern Hemisphere, and which broadly accommodates pollen of modern *Araucaria* and many *Agathis* (e.g. [15]), could have been produced by extinct close relatives of *Agathis* and *Wollemia*.

The only extant Araucariaceae in South America are *Araucaria angustifolia* (Bertol.) Kuntze, native to southern Brazil and northeastern Argentina, where it is a dominant in temperate to subtropical rainforest, and *A. araucana* (Molina) K. Koch, native to Andean central and southern Chile and western Argentina between latitudes c. 37 to 40°S, where it associates with *Nothofagus* spp. to form mixed forests above c. 600–900 m elevation. The two species are apparently the survivors of the considerably more diverse Mesozoic araucarian flora of South America, represented by wood, foliage, cone, and pollen material (e.g., [58,65–68]). This flora reached its maximum diversity and dominance in Patagonia, where araucarians were often co-dominant with cheirolepidiaceae conifers [69,70] during the Jurassic to Early Cretaceous. By the early and early middle Eocene, *Araucaria* and *Agathis* were abundant, but not diverse in Patagonia, occurring in association with crown group Podocarpaceae and Cupressaceae conifers with Australasian affinities and very diverse angiosperms [48,60,71,72]. However, so far as is known, none of the previously reported South American fossil species is comparable to *Wollemia*.

Our evidence extends the geographic range of the araucarian lineage(s) that produced *Wollemia/Agathis* (coarsely granulate)-type pollen to South America. This is a significant contribution to the emerging biogeographic pattern for Paleogene Gondwana, where there are numerous shared extant genera known as macrofossils

(e.g., *Dacrycarpus*, *Papuacedrus*, *Gymnostoma*, *Eucalyptus*) and/or microfossils from Eocene floras of both southern South America and Australia and occasionally Antarctica (e.g., [48,60,71–79]). These trans-Antarctic distributions are increasingly comparable to the numerous examples of Holarctic floral and faunal interchange during this globally warm time interval.

Materials and Methods

Blocks of wet sediment containing abundant mummified leaves (under separate study) were collected 3–4 May, 2011 at the Argentine Ligorio Márquez Formation outcrop (Fig. 1), wrapped in plastic to minimize water loss, and temporarily stored in a large refrigerator. Sediment samples selected for palynological processing were then oven-dried. Microfossils were extracted and replicate slides prepared by M. Rueda, Paleoflora Ltd, Bucaramanga, Colombia, using standard protocols. Microfossils were examined and photographed at ANU, Canberra, Australia using a Leica Axiophot transmitted light microscope fitted with AxioVision image capturing software. Residues were also examined and microfossils photographed at La Plata University, La Plata, Argentina using a JEOL JSM-6360LV scanning electron microscope operated at 10 kV. Adobe Photoshop Elements 6.0 software was used to optimise brightness and contrast of images, and to compose figures.

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Author Contributions

Analyzed the data: MM RJC. Contributed reagents/materials/analysis tools: AI PW. Wrote the paper: MM RJC AI PW. Performed field work: AI PW.

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