

EARLY CENOZOIC VEGETATION IN PATAGONIA: NEW INSIGHTS FROM ORGANICALLY PRESERVED PLANT FOSSILS (LIGORIO MÁRQUEZ FORMATION, ARGENTINA)

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Editor: Patrick S. Herendeen

Premise of research. Cenozoic macrofloras from South America are fundamental for understanding extant Southern Hemisphere biotas. The Paleogene Ligorio Márquez Formation (LMF) straddles the Chile–Argentina border; leaf fossils from its Chilean outcrops were previously assigned to >50 morphotypes and interpreted as primarily representative of tropical–subtropical lineages, with dominance by diverse Lauraceae of extant Neotropical affinities. Here, we present new collections of Argentine LMF mudstones that are thus far unique in the Patagonian region in containing organically preserved plant fossils, including leaves with cuticular preservation.

Methodology. Leaf fossils were exposed by splitting blocks of mudstone or collected by flotation from disaggregated samples. Smaller fossils, including reproductive parts, conifer needles, and isolated cuticles, were recovered from sieved slurry. Fossils were examined under light microscopy, epifluorescence, and SEM.

Pivotal results. Twenty taxa were recognized from cuticle-bearing leaf fossils or dispersed cuticles. The most abundant leaf species is a morphologically variable form that is like Lauraceae in architecture but with clearly nonlauraceous cuticular details. Four-parted flower fossils are attributable to the same species, and its eudicot affinities are indicated by adherent triaperturate pollen. Lauraceae were present but much less diverse than reported from the LMF in Chile and arguably with Gondwanan (not Neotropical) affinities. Other taxa include the conifers *Dacrycarpus chilensis* and *Coronelia molinae* and possibly Cunoniaceae and a new *Ginkgoites*. A wet mesotherm paleoclimate is inferred.

Conclusions. The new fossils complement and improve our understanding of the LMF and contribute to a greater understanding of high southern latitudes at a time when overland dispersal was possible between South America and Australasia. The fossils provide further evidence for warm and humid climates in Patagonia during the early Paleogene and for a strongly Gondwanic flora, with little conclusive evidence of taxa belonging to Neotropical and megatherm lineages.

Keywords: cuticle, Gondwana, Lauraceae, leaf fossil, Patagonia, Paleogene.

Introduction

Fossils from the Patagonian region of southern South America continue to reveal new evidence that is pivotal to understanding the biogeographic history of the Southern Hemisphere (reviewed, e.g., by Wilf et al. 2013). The early Paleogene (Paleocene–Eocene) is of particular interest because of very warm global climates and a largely ice-free and vegetated Antarctica, with opportunities for direct interchange of terrestrial organisms between South America and Australia via Antarctica during the terminal phase of Gondwana. Indeed, there are numerous well-known examples of distinctly southern plant (and animal) lineages for which

Gondwanic biogeographic histories have been proposed; the antiquity of many of these lineages is increasingly being demonstrated by notable fossil discoveries, particularly from Patagonia and Australia (see review by Kooyman et al. 2014). These studies, and the rarity of Patagonian fossils with well-demonstrated Neotropical or New World affinities (Wilf et al. 2017a, 2017b), challenge the classical view of the early Paleogene vegetation of southern South America as having a significant or dominant component of extant Neotropical taxa (e.g., Berry 1938; Romero 1978, 1986; Hinojosa and Villagrán 2005).

One South American Eocene flora that is thought to have an almost entirely Neotropical composition is that from the Ligorio Márquez Formation (Suárez et al. 2000; hereafter LM and LMF), which crops out on both sides of the border between XI Región, Chile, and Santa Cruz Province, Argentina. Troncoso et al. (2002) determined that a Chilean collection of LMF fossils comprised 19 angiosperm leaf taxa, mostly belonging to Neotropical genera and including 14 species of Lauraceae, *Myrcia* DC. (Myrta-

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Manuscript received June 2017; revised manuscript received September 2017; electronically published January 5, 2017.

ceae), *Cupania* L. (Sapindaceae), Bignoniaceae, and Melastomataceae. This perceived elevated diversity of Neotropical Lauraceae and a high proportion of entire-margined leaf taxa led Troncoso et al. (2002) to propose that a very warm and wet climate prevailed in the LM region, as also supported by a physiognomic analysis based on the same 19 angiosperm taxa (Hinojosa 2005).

However, a limiting factor in furthering our knowledge of Patagonian Cenozoic floras is that with few exceptions, notably the ginkgoalean leaves described from other sites by Traverso (1964) and Villar de Seoane et al. (2015), well-preserved leaf cuticle is very rare. Cuticular evidence is important for at least two reasons. First, details of stomatal type and distribution, trichomes, glands, and inner and outer surface ornamentations can enable accurate identification of fossil leaves, even below family level (e.g., Carpenter 2012). These features can be used to complement or test identifications and diversity estimates based on leaf architectural features. Second, with respect to reconstructions of past environments and climates, leaf cuticles can provide new data and proxy evidence that complement more widely used approaches based on leaf physiognomy (see Jordan 2011 for a review). For instance, stomatal size and index have commonly been used to estimate past carbon dioxide concentrations, and recent studies have argued that amphistomatic leaves (Jordan et al. 2014) and low cell wall sinuosity (Dunn et al. 2015) in the fossil record are indicative of open vegetation structure.

More studies of the LMF macroflora are required because the principal previous assessment was limited by few and usually poorly preserved specimens (Troncoso et al. 2002), with no cuticle and little evidence of diagnostic foliar characters that could be used to justify the taxonomic determinations. Similar limitations could apply for more recent studies of the LMF flora (Hinojosa et al. 2006b, 2010, 2016) that used larger fossil collections and revised the total number of angiosperm leaf taxa from 19 to 55. Also, in contrast to several reports derived from other collections of LMF material (Troncoso et al. 2002; Quezada-Arriagada et al. 2003; Macphail et al. 2013), *Nothofagus* Blume leaves and pollen have been shown to occur in LMF sediments from the type locality in Chile (Okuda et al. 2006; Hinojosa et al. 2016), implying cooler temperatures than did the initial studies by Troncoso et al. (2002) and Hinojosa (2005).

Here, we provide an overview of the first Argentine macrofossils from the LMF that is also the first assessment of a Paleogene flora with organically preserved organs in the Patagonian region. This study furthers our knowledge of the floristics, paleoclimate, and biogeography of middle southern paleolatitudes, and it demonstrates the importance and potential of incorporating cuticular evidence.

Material and Methods

Material

The fossils reported here came from the same stream-cut outcrop (fig. 1A) of the LMF that was described by Macphail et al. (2013), who reported the first record of *Wollemlia* W.G. Jones, K.D. Hill & J.M. Allen-like pollen (*Dilwynites* W.K. Harris: Araucariaceae) in South America and several other palynotaxa. This outcrop (lat. 46°50'01.6"S, long. 71°51'20.3"W) lies at the foot of the Andean Cordillera in Santa Cruz Province, Pata-

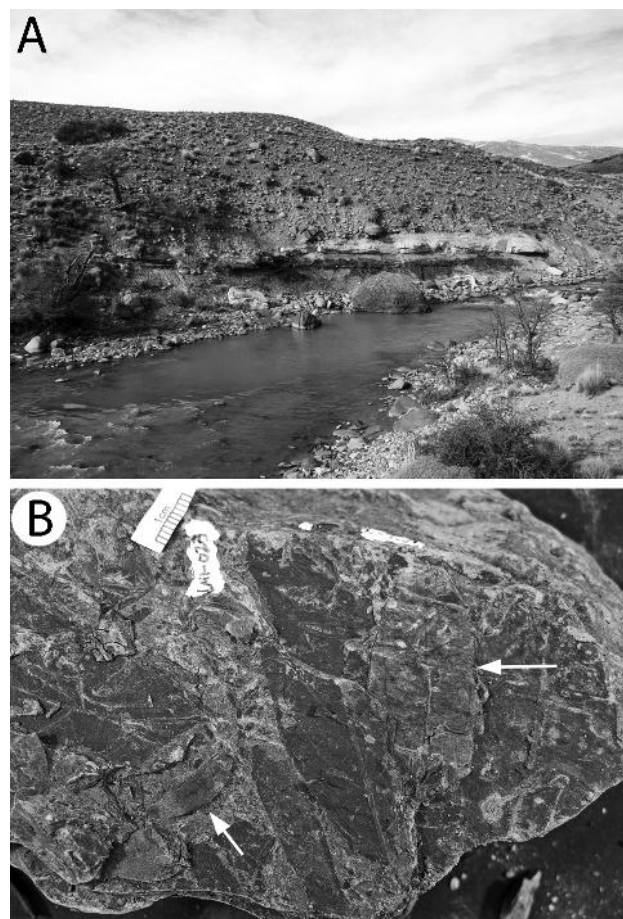


Fig. 1 Ligorio Márquez Formation exposure at the Río Zeballos fossil locality (see Macphail et al. 2013), Argentina (A), and an example of its fossiliferous mudstone (B). The large leaf near the center in B is probably of Lauraceae, and the leaves to its left and right (arrows) belong to an abundant, morphologically similar, but unrelated leaf type (angiosperm sp. 7). A color version of this figure is available online.

gonia, Argentina, located along the east bank of the Río Zeballos and 36 km south-southwest of the town of Los Antiguos. The fossils were recovered from a 0.5-m-thick carbonaceous shale bed that probably formed in a coastal swamp embedded in a suite of fluvial paleoenvironments (Suárez et al. 2000). Recently, Hinojosa et al. (2016) proposed that the age of the LMF in its Chilean type locality (~3 km away) was restricted to the early Eocene, based on a $^{40}\text{K}/^{39}\text{Ar}$ date of 47.6 ± 0.78 Ma of overlying basalts by Yabe et al. (2006), new evidence from a U-Pb zircon analysis (younger than 59.9 ± 1.1 Ma), and microfossil chronostratigraphy. However, it is problematic to determine whether the new Argentine Río Zeballos LMF material is coeval with that studied by Hinojosa et al. (2016), most notably because in contrast to the Chilean sediments (Okuda et al. 2006), our samples do not contain *Nothofagus* pollen (Macphail et al. 2013). We therefore follow Macphail et al. (2013) in interpreting the age of the fossils studied here to be probably early Eocene, but we allow that it could fall anywhere within the late Paleocene to early middle Eocene interval.

Methods

Approximately 70 kg of field-collected blocks of fossiliferous sediment (fig. 1B) were processed at Museo Paleontológico Egidio Feruglio (MEF), Trelew, Argentina. Foliar specimens and coniferous shoots were exposed by splitting blocks or collected as complete or near-complete specimens floated from sediment samples disaggregated in a large bath of water and hydrogen peroxide. The remaining slurry was sieved with a 200- μ m mesh sieve, and smaller fossils including reproductive parts, individual conifer needles, and isolated cuticles were recovered by searching subsamples of the residue in a large petri dish under binocular microscopy. Other small sediment samples (each of ~500 g) were soaked in 30% HF over several days to remove silicates, and the resultant residue of organic matter was then rinsed in water, sieved, and searched as above.

Whole and partial leaves recovered from the water bath were mounted on glass slides in Cytoseal 280 High Viscosity Mounting Medium (Richard Allen Scientific, Kalamazoo, MI) between large glass plates. Small areas (~25 mm²) of leaf blade from some of these specimens were cut for cuticular analysis. Leaf architectural descriptions follow Ellis et al. (2009). All cuticles were prepared for examination by soaking leaf fragments in household bleach (sodium hypochlorite 42 g/L) or 10% chromium trioxide to remove any adherent mesophyll tissues. The cleared and rinsed cuticles were then stained with safranin O and mounted on glass slides in glycerine jelly for viewing and photography with transmitted light microscopy using a Nikon (Tokyo) Eclipse 50i compound microscope attached to a Nikon (Tokyo) DS-Fi1 camera. Some images were stacked and uniformly adjusted for brightness and contrast using Adobe (San Jose, CA) Photoshop CS6 or Photoshop Elements software. The Eclipse 50i microscope was also used to examine specimens under epifluorescence using an Endow GFP Longpass Emission green filter: exciter HQ470/40, dichroic Q495LP BS, emitter HQ500LP, Chroma Technology number 41018 (Chroma Technology, Rockingham, VT), which in many cases allowed improved vision of cuticular details. Pieces of cuticle and assorted other fossils (reproductive parts, conifer shoots, etc.) were placed on aluminium stubs and carbon or platinum coated for SEM using a Philips (Eindhoven, Netherlands) XL 30 SEM operated at 10 kV. Specimens, including material on microscope slides, and untreated sediment blocks are housed at the Museo Padre Molina, Río Gallego, Santa Cruz Province, Argentina (MPM-Pb).

Results

Ten leaf-fossil taxa are here recognized, comprising a probable ginkgoalean, two conifers, and seven dicots. Ten more cuticle morphotypes were recovered from the sieved residues. These taxa are briefly described as follows.

Gymnosperms

?Order—*Ginkgoales* Gorozh.

?*Ginkgoites* sp. (Fig. 2A–2I)

Specimens examined. Cuticle specimens MPM-Pb-18734 (fig. 2B, 2C, 2H), MPM-Pb-18735 (fig. 2G), and other uncat-

aloged cuticles recovered from sieved residue (fig. 2A, 2D–2F, 2I).

No complete foliage specimens have been found, but several well-preserved cuticle fragments were recovered. One fragment is very slightly tapering but shows a full width of ~4 mm, and another is interpreted as a rounded foliar apex (fig. 2A). The fossils show several (~7) more or less parallel veins with intercostal randomly aligned stomata (fig. 2B–2D), which are confined to one (presumably lower = abaxial) surface with the exception of a few individual stomata on the other (upper = adaxial) surface. The stomata (fig. 2E–2G) have narrow, slit-like surface apertures (fig. 2D) and typically four to seven subsidiary cells. The guard cells are sunken and typically have polar cuticular extensions. Lateral flanges are also variably present (e.g., fig. 2F). Venous cells are narrow and straight walled with tapering end walls, whereas normal epidermal cells on the adaxial surface and within the abaxial intercostal regions are shorter and may be tightly but not prominently sinuous (fig. 2H, 2I). The cuticle surface (fig. 2D) lacks both stomatal rims and papillae associated with the subsidiary cells that overhang the stomatal apertures. No evidence of trichomes was observed.

The fossil cuticles are treated as belonging to an extinct ginkgoalean, but some fossil cycad foliage is similar, and we note that previous authors did not explicitly differentiate Ginkgoales and Cycadales solely on the basis of cuticular characters. However, the known fossil cycad foliage, including that of Mesozoic–Paleogene sediments of southern South America, typically has much wider leaflets with acute apices and evidence of trichomes (e.g., Villar de Seoane 2005; Cúneo et al. 2010; Passalia et al. 2010; Wilf et al. 2016). Also, extinct Paleogene cycads with relatively well-preserved cuticles and similarly positioned stomata to those of the LM fossils (notably *Pterostoma* R.S. Hill, *Dioonopsis* Horiuchi & Kimura, and *Pseudodioon* Erdei) are characterized by the presence of not only trichome bases but also highly sinuous epidermal cell walls and, in many cases, prominently ridged cuticular surfaces (Hill 1980; Horiuchi and Kimura 1987; Hill and Pole 1994; Erdei et al. 2010, 2012). The stomata of these cycads also differ from the LM fossils in featuring coronal rims around their apertures and in usually having prominent lateral cuticular flanges between the guard cells and subsidiary cells. At least the Zamiaceae s.l. can also be excluded because the fossil cuticles lack the clusterings of both thick- and thin-walled cells that are typical of that cycad group (Greguss 1968).

Resolution of the true affinities of the LM fossils awaits the recovery of more complete specimens. However, for the present, the fossil cuticles are interpreted as being derived from a ginkgoalean and probably from narrow lobe segments of *Ginkgoites* Seward leaves not unlike those of *Ginkgoites patagonicus*, which has been discussed and illustrated in detail based on well-preserved specimens from the early Eocene Laguna del Hunco and early/middle Eocene Río Pichileufú sites in Patagonian Argentina (Berry 1935a; Traverso 1964; Villar de Seoane et al. 2015).

In contrast to the LMF material, most fossil ginkgophytes, including *G. patagonicus*, are reported as having papillae overhanging the stomatal apertures. Nevertheless, such papillae are lacking in ginkgophytes such as *Eretmophyllum obtusum* (Velen.) J.Kvaček from the Cenomanian of the Czech Republic

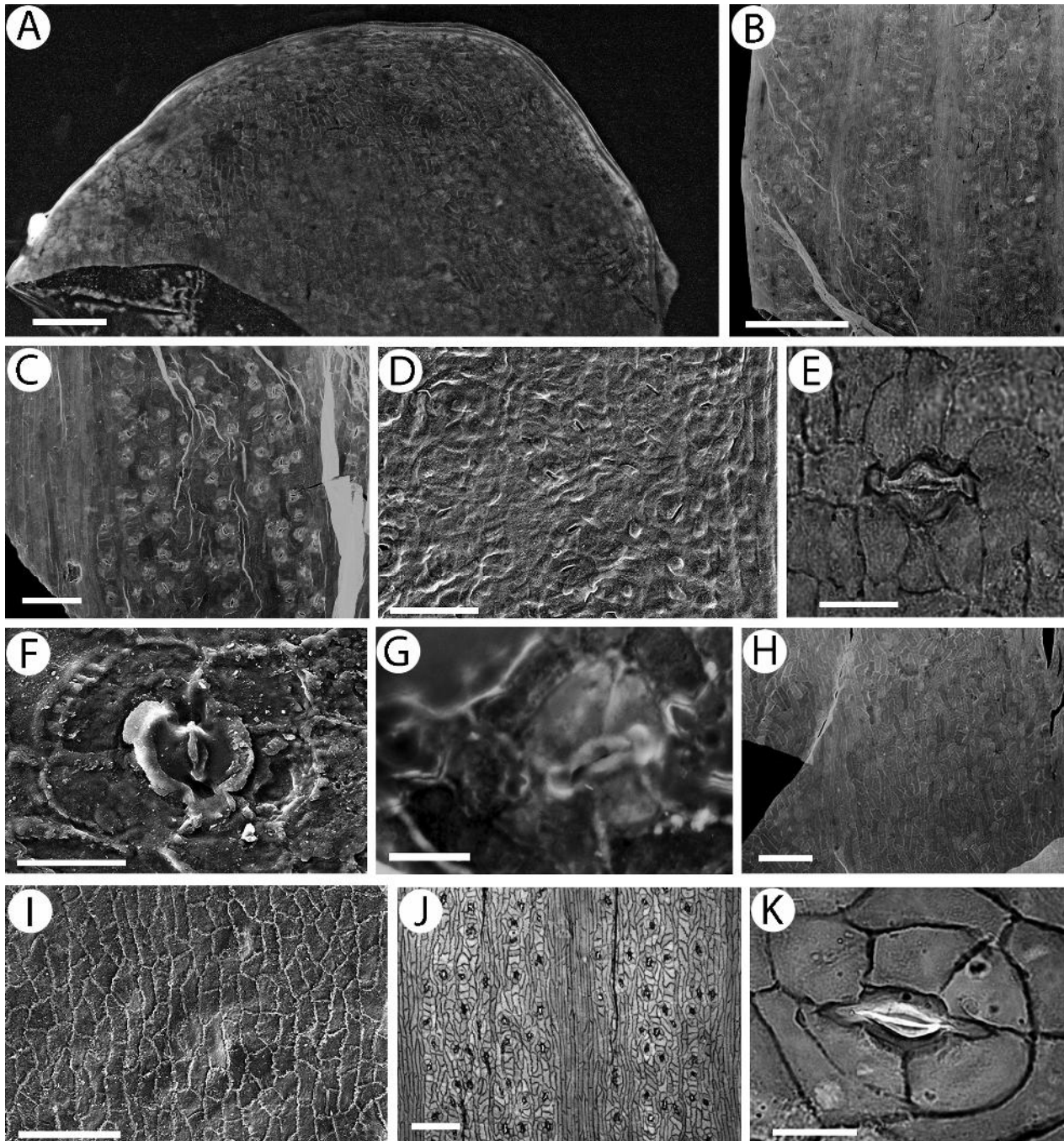


Fig. 2 *Ginkgo*-like foliar remains from the Ligorio Márquez Formation (A–I) and cuticle of specimen RP3 Mar 05, 2005 censo 527 (Museo de Paleontología de Bariloche, San Carlos de Bariloche, Rio Negro, Argentina; J, K). A, Epifluorescence microscopy (EfM) image of rounded foliage apex; uncataloged dispersed cuticle; scale bar = 200 μm . B, EfM image showing leaf margin and abaxial randomly aligned stomata between more or less parallel veins; MPM-Pb-18734; scale bar = 1 mm. C, EfM image showing a stomatal band between veins; MPM-Pb-18734; scale bar = 200 μm . D, SEM image of outer abaxial cuticle showing narrow stomatal apertures lacking both rims and overhanging papillae; uncataloged dispersed cuticle; scale bar = 200 μm . E, Light microscopy (Lm) image of single stomatal complex with eight surrounding cells; uncataloged dispersed cuticle; scale bar = 25 μm . F, SEM image of inner abaxial cuticle showing a stomatal complex with polar and pronounced lateral cuticular flanges and five surrounding cells; uncataloged dispersed cuticle; scale bar = 20 μm . G, EfM image showing an inner view of a single stomatal complex similar to that shown in E; MPM-Pb-18735; scale bar = 20 μm . H, EfM image showing sinuous adaxial cell wall cuticle; MPM-Pb-18734; scale bar = 200 μm . I, SEM image showing tightly sinuous adaxial cell wall cuticle; uncataloged dispersed cuticle; scale bar = 100 μm . J, Lm image showing two abaxial bands of randomly aligned stomata between veins. Note similarity to B, C; scale bar = 200 μm . K, Lm image showing a single stomatal complex on adaxial surface. Note similarity to E–G; scale bar = 25 μm . A color version of this figure is available online.

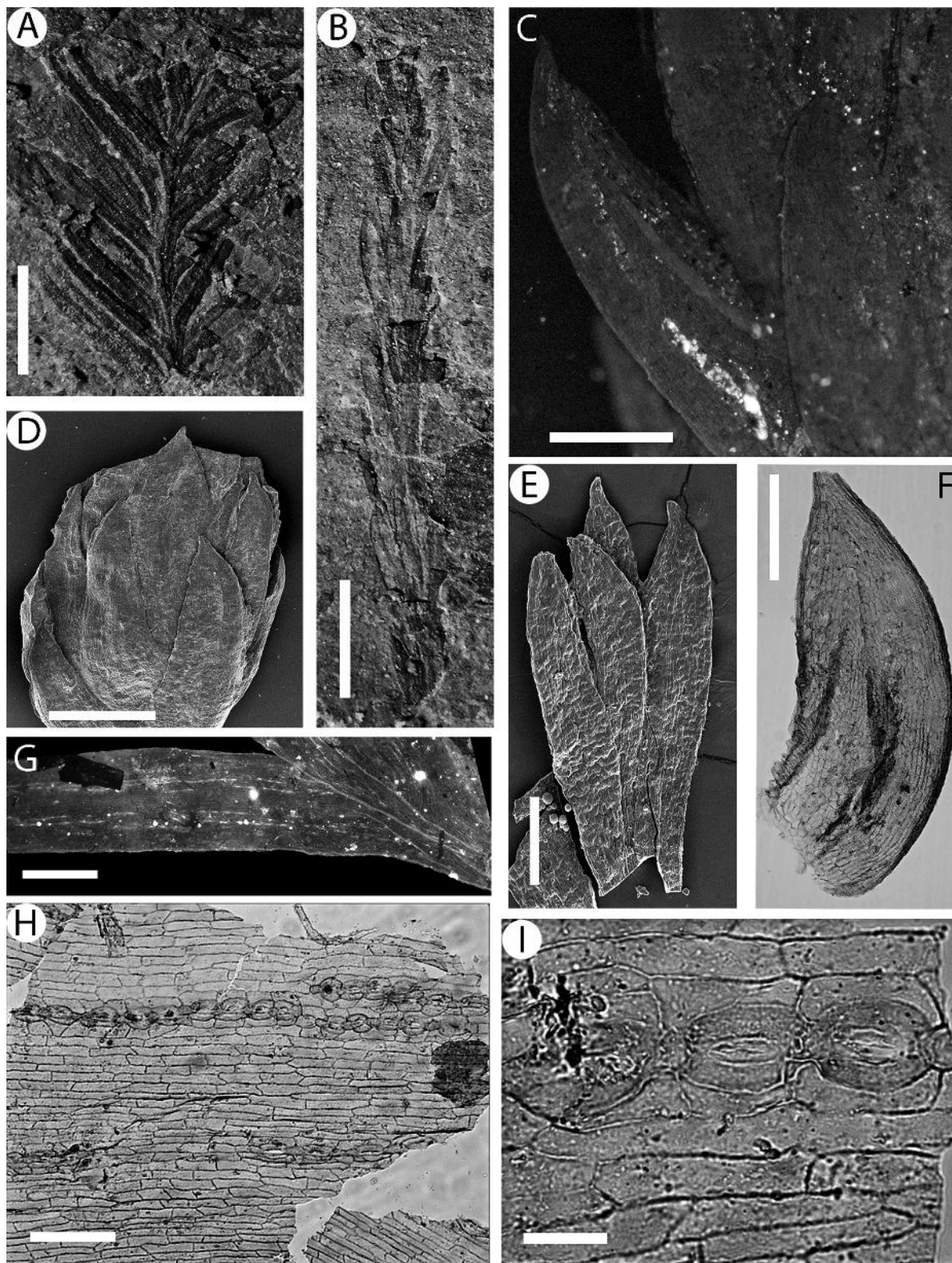


Fig. 3 *Dacrycarpus chilensis* foliar remains from the Ligorio Márquez Formation. *A*, Juvenile foliage shoot; MPM-Pb-18738; scale bar = 2 mm. *B*, Adult foliage shoot; MPM-Pb-18742; scale bar = 2 mm. *C*, Epifluorescence microscopy (EfM) image of foliage showing strong fluorescence of resin within a duct associated with the midvein of a leaf; uncataloged specimen recovered from sieved residue; scale bar = 200 μm . *D*, SEM image of resting bud (see Wilf 2012); uncataloged specimen recovered from sieved residue; scale bar = 500 μm . *E*, SEM image showing adult foliage; uncataloged specimen recovered from sieved residue; scale bar = 500 μm . *F*, Light microscopy (Lm) image of a small, scale leaf, showing frill cells near the base at lower left; uncataloged specimen recovered from sieved residue; scale bar = 500 μm . *G*, EfM image of part of a leaf showing fluorescence of stomata within two variably continuous stomatal rows on each side of the midvein; MPM-Pb-18741; scale bar = 200 μm . *H*, Lm image showing stomatal rows on each side of a midvein. Note that epidermal walls are straight, and polar cells are usually shared; uncataloged specimen recovered from sieved residue; scale bar = 100 μm . *I*, Enlargement of part of *H* showing stomatal detail; scale bar = 25 μm . A color version of this figure is available online.

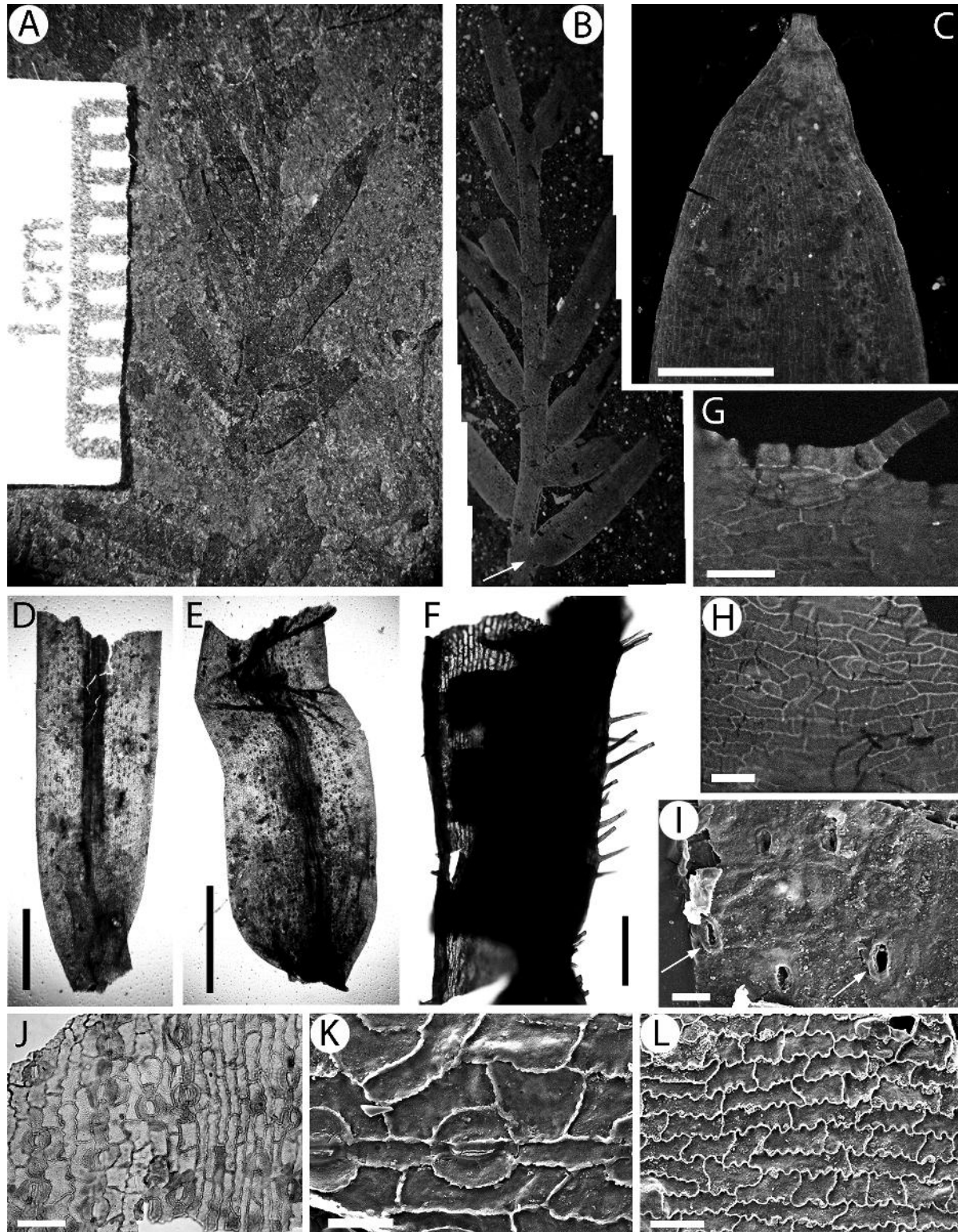


Fig. 4 *Coronelia* foliar remains from the Ligorio Márquez Formation. **A**, Part of foliage shoot showing leaves twisted into a plane; MPM-Pb-18745. **B**, Epifluorescence microscopy (EfM) image of the specimen in **A**. Note that the leaf blades are constricted into narrow petioles and that these (arrow) are decurrent down the stem axis. **C**, EfM image showing an acute and sharply pointed leaf apex; uncataloged specimen recovered from sieved residue; scale bar = 1 mm. **D**, **E**, Light microscopy (Lm) images of incomplete leaves recovered from sieved residues; MPM-Pb-18746a, 18746b. Note the stomata (black dots) within broad stomatal bands on each side of the midveins. Also note the basal constrictions of the leaf blades, with evidence of petiole twisting in MPM-Pb-18746a (**D**), and especially abrupt transition from broad leaf base to petiole in MPM-Pb-18746b (**E**); scale bars = 1 mm. **F**, Lm image of uncataloged foliage fragment from sieved residue, presumably from leaf base, showing abundant, stout trichomes along the margin at right; scale bar = 200 μm . **G**, EfM image showing a single, marginal trichome. Cell wall divisions are evident, but the apical region (?one cell) has been broken away; uncataloged specimen recovered from sieved residue; scale bar = 50 μm .

(Kvaček et al. 2005), and in others, these papillae may only correspond to little more than thickenings adjacent to the stomatal apparatus (e.g., Denk and Velitzelos 2002; Mays 2015). Interestingly, in extant *Ginkgo* L., papillar development is plastic, being related to light levels (Denk and Velitzelos 2002). Thus, although it may be of phylogenetic importance, the consistent lack of stomatal papillae in the LMF material could merely reflect derivation from shaded understory plants. In many other respects, the LMF fossils appear to conform to *G. patagonicus*. For example, leaf lobes of this species are 4–5 mm wide, and there are six to 14 veins/cm within each lobe, which all have rounded apices (Villar de Seoane et al. 2015). Also, although *G. patagonicus* cuticle has been described as being hypostomatic by Traverso (1964) and hypostomatic and striate by Villar de Seoane et al. (2015), cuticle from a Río Pichileufú leaf prepared for our study (fig. 2J, 2K) appears relatively smooth and has several isolated, adaxial stomata (fig. 2K), which are not so obviously papillate around their apertures as those on the abaxial side. This new evidence suggests that the status of *G. patagonicus* needs further assessment. Additionally, the Río Pichileufú specimen examined here shows numerous adaxial trichome bases, whereas *G. patagonicus* has been interpreted as having smooth epidermal cells (i.e., lacking hairs; Villar de Seoane et al. 2015).

Order—*Araucariales* Gorozh.

Family—*Podocarpaceae* Endl.

Dacrycarpus chilensis (Engelhardt) Wilf (Fig. 3)

Specimens examined. MPM-Pb-18736, MPM-Pb-18737, MPM-Pb-18738 (fig. 3A), MPM-Pb-18739, MPM-Pb-18740, MPM-Pb-18741 (fig. 3G), MPM-Pb-18742 (fig. 3B), MPM-Pb-18743, MPM-Pb-18744, and other uncataloged specimens recovered from sieved residue (fig. 3C–3F, 3H, 3I).

Shoots and isolated leaf specimens of *Dacrycarpus* are relatively common in our material and include many specimens with cuticular preservation. We confirm details consistent with previously reported specimens of *D. chilensis* (especially by Florin 1940 under *Podocarpus inopinatus* Florin) and with other fossil and extant *Dacrycarpus* species (e.g., Cookson and Pike 1953; de Laubenfels 1969; Wells and Hill 1989a, 1989b; Hill and Carpenter 1991; Hill and Whang 2000; Wilf 2012). Most distinctively, and unique to *Dacrycarpus* among living podocarp genera, is the combined presence of shoots with expanded, bilaterally flattened, distichous juvenile leaves (fig. 3A) and shoots with bifacially flattened adult leaves of variable size with incurved apices (fig. 3B–3F). Wilf (2012) drew particular attention to resting buds in *Dacrycarpus* that appear as loose clusters of leaves overtopping the long-shoot meristems and also

to the stomatal bands that generally occur in linear pairs at equal distance from the midvein. These features are clearly evident among our fossils (fig. 3D, 3G, 3H). Although not diagnostic for *Dacrycarpus*, we further note the same type of resin-duct casts associated with the leaf midveins (fig. 3C) as illustrated by Wilf (2012). As in other *Dacrycarpus* species, the anticlinal cell walls of the LMF specimens are not buttressed, and the stomata occur in rows on both leaf surfaces with the polar subsidiary cells typically shared (fig. 3H, 3I). Also, some marginal, finger-like frill cells have been observed near the base of one of the new LMF leaves (fig. 3F). Marginal frills in Australian *Dacrycarpus* fossils have been reported by Cookson and Pike (1953) and Wells and Hill (1989a). As shown previously by Macphail et al. (2013), the distinctive trisaccate *Dacrycarpus*-type pollen (*Dacrycarpites australiensis* Cookson & K.M. Pike) is present in the same LMF beds as our leaf fossils.

Wilf (2012) comprehensively discussed the past occurrence and taxonomic history of *Dacrycarpus* in Patagonia. He proposed the new combination *D. chilensis* to encompass Chilean material from the Eocene Concepción-Arauco flora. This material was originally named by Engelhardt (1891) as *Sequoia chilensis* and then resolved by Florin (1940), with supporting cuticular evidence, as belonging to what was then *Podocarpus* section *Dacrycarpus* (now a synonym of the genus *Dacrycarpus*) and named by him as *P. inopinatus*. *Podocarpus inopinatus* was noted to occur in the LMF by Suárez et al. (2000), and although Troncoso et al. (2002) briefly described one shoot specimen (adult foliage only; see above), this fossil was not illustrated in detail.

Wilf (2012) noted consistent differences between *D. chilensis* and a new species, *Dacrycarpus puertae* Wilf from Laguna del Hunco and Río Pichileufú. Most obviously, *D. chilensis* is set apart by its smaller leaf dimensions and appears to be limited to coastal swamp environments, in contrast to the caldera-lake environments occupied by *D. puertae*. Typical sizes of *D. chilensis* juvenile leaves are ca. 3.5–7 mm long × 0.5 mm wide, with the adult leaves being only about 2 mm long. As discussed by Wilf (2012), Florin (1940) compared *D. chilensis* (then *P. inopinatus*) most closely to *Dacrycarpus dacrydioides* (A. Rich.) de Laub., a species now confined to very wet climates in New Zealand, where it is characteristic of the swampy, lowland vegetation of the west coast of the South Island (Salmon 1980).

?*Podocarpaceae* Endl.

Coronelia molinae Florin (Fig. 4)

Specimens examined. MPM-Pb-18745 (fig. 4A, 4B), MPM-Pb-18747, and other specimens recovered from sieved residue including MPM-Pb-18746a (fig. 4D), MPM-Pb-18746b

H, EFM image of abaxial laminar cuticle showing a stomatal complex at left and evidence of three associated stout, multicellular trichomes, the uppermost of which appears complete; specimen recovered from sieved residue; scale bar = 50 μ m. I, SEM image of outer abaxial cuticle showing stomatal apertures and weakly and variably developed rims (the most developed marked by arrows); specimen recovered from sieved residue; scale bar = 20 μ m. J, Lm image showing files of stomata within a stomatal band. Note the (stained) rounded papillae on the cells among the stomata and pronounced sinuosity of cell walls; dispersed cuticle MPM-Pb-18748a; scale bar = 100 μ m. K, SEM image of inner abaxial cuticle showing stomata with shared polar cells; specimen recovered from sieved residue; scale bar = 50 μ m. L, SEM image of inner adaxial cuticle showing sinuous anticlinal walls; specimen recovered from sieved residue; scale bar = 50 μ m. A color version of this figure is available online.

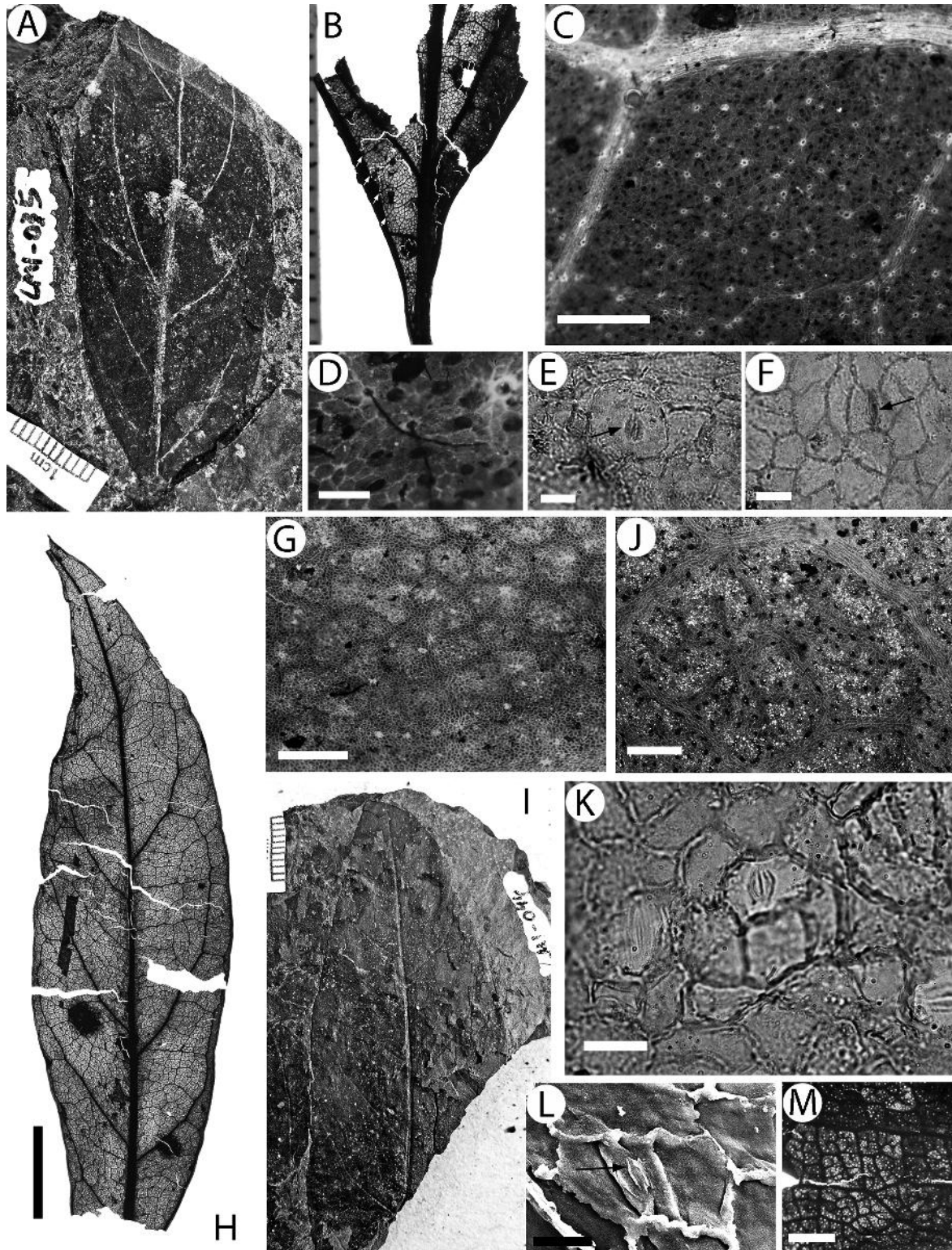


Fig. 5 Lauraceae sp. 1 (A–G) and Lauraceae sp. 2 (H–M) from the Ligorio Márquez Formation. *A*, Leaf specimen MPM-Pb-18749. *B*, Leaf specimen MPM-Pb-18750. Note the percurrent tertiary veins (arrows) and well-defined areoles; scale is in millimeters. *C*, Epifluorescence microscopy (EfM) image showing higher-order venation on abaxial leaf surface, stomata (black dots) within very small areoles, and abundant evidence of trichomes (pores surrounded by cuticular thickening that shows strong fluorescence) along veins; MPM-Pb-18749; scale bar = 200 μm . *D–G*, Lauraceae sp. 1; MPM-Pb-18750. *D*, EfM image showing stomata within an areole. Note especially the two simple, long, and thin trichomes (center left) that arise from poral bases; scale bar = 50 μm . *E*, Lm image of a single paracytic stomatal complex and a small, thickened poral

(fig. 4E), MPM-Pb-18748a (fig. 4J), and several uncataloged specimens (fig. 4C, 4F–4I, 4K, 4L).

Shoot specimens and isolated leaves (fig. 4A–4F) were readily assigned to *Coronelia* (represented only by *C. molinae*), first described from the Chilean Concepción-Arauco Coal Measures by Florin (1940) and subsequently reported from the Eocene of Tasmania, Australia (Townrow 1965). The diagnostic features of this genus are clearly evident in the LMF material, including the spiral arrangement of the leaves, with their bases apparently twisted so that the leaves lie homofacially in the same plane (fig. 4A, 4B). The sharply pointed leaves (fig. 4C) are linear-lanceolate, with leaf bases that are decurrent along the stem axes and abruptly constricted into very short petioles (fig. 4A, 4B, 4D, 4E). Perhaps most distinctive is the presence of stout, bristlelike, multicellular trichomes along the leaf margins (fig. 4F, 4G), especially near the leaf bases, and also on the abaxial lamina (fig. 4H). As described by Florin (1940) and Townrow (1965), the leaves are hypostomatic, with the stomata lying in two bands separated by a nonstomatiferous zone over the midrib (fig. 4D, 4E). Surface rims surrounding the stomatal apertures that are consistent with weakly and variably developed Florin rings (Buchholz and Gray 1948) are evident (fig. 4I), albeit not always visible or well preserved. Such Florin rings in *Coronelia* were not reported by Florin (1940) or Townrow (1965), although the latter interpreted the subsidiary cell papillae he observed on only one of four leaves known from Tasmania as forming a grade from separate papillae to a distinct ring.

The stomata of the LMF specimens have two polar and two lateral subsidiary cells (fig. 4H, 4J, 4K), in many cases with the polar cells shared by consecutive stomata in a file. Florin (1940) reported that the stomatal bands were slightly papillate, with the papillae small and rounded. Townrow (1965), however, noted that in both the Chilean and the Tasmanian material, such papillae were variably formed and not always visible. Similarly, rounded papillae are visible only within some stomatal bands of the LM fossils as thickened (stained) regions (fig. 4J). Anticlinal walls of the epidermal cells on both leaf surfaces are mostly sinuous (fig. 4H, 4J, 4L).

For the present, we regard the cited fossil material as belonging only to *C. molinae*, but typical leaves from the LMF are smaller than those reported by Florin (1940) and Townrow (1965), being ~5 mm long and 1 mm wide at the widest point (fig. 4A–4E), compared with 12–16 mm × 2.5–3 mm for the Concepción-Arauco and Tasmanian specimens. Based mostly on the morphology of the stomata, we do not dispute the proposal by Florin (1940) and supported by Townrow (1965) that *Coronelia* probably belongs in Podocarpaceae.

Angiosperms

Order—*Laurales* Juss. ex Bercht. & J. Presl

Family—*Lauraceae* Juss.

Lauraceae sp. 1 (Fig. 5A–5G)

Specimens examined. MPM-Pb-18749 (fig. 5A, 5C), MPM-Pb-18750 (fig. 5C–5G).

These specimens are entire margined, weakly brochidodromous leaves, with five alternately inserted secondary veins on each side of the primary vein. The best-preserved specimen, MPM-Pb-18749 (fig. 5B), is incomplete at the apex, but it is 22 mm wide and estimated to be ca. 55 mm long. The tertiary veins are broadly spaced and mostly opposite percurrent. Fourth- and fifth-order venation is regular polygonal reticulate with well-developed areoles (fig. 5B–5D, 5G), within which the stomata (fig. 5C–5F) occur on the abaxial side. The stomata are paracytic with small guard cells and evidence of cuticular scales between guard and subsidiary cells (fig. 5E, 5F). This species is characterized by the presence of abundant, large-diameter (~15 μm), poral trichome bases along all veins on the abaxial surface (fig. 5C, 5D). Many simple, unicellular trichomes (>100 μm long) are preserved (fig. 5D), especially those that arise from smaller-diameter bases. Simple, unicellular trichomes are characteristic of Lauraceae (e.g., Rohwer 1993).

Lauraceae sp. 2 (Fig. 5H–5M)

Specimens examined. MPM-Pb-18751 (fig. 5H, 5J, 5K), MPM-Pb-18752 (fig. 5I, 5L, 5M), MPM-Pb-18753.

This species is similar to *Lauraceae* sp. 1, but trichomes and trichome bases are mostly restricted to the primary vein and are not evident elsewhere (fig. 5J). As in the first species, the stomata are of the typical Lauraceae type, with cuticular scales associated with small guard cells (fig. 5K, 5L). Abundant resin bodies are evident within the mesophyll (fig. 5M). The best-preserved specimen (MPM-Pb-18751) shows an acuminate apex, or “drip tip” (fig. 5H).

Lauraceae sp. 3 (Fig. 6A–6E)

Specimens examined. MPM-Pb-18754 (fig. 6A, 6B, 6D, 6E), MPM-Pb-18755 (fig. 6C).

This species is characterized by the presence of sinuous anticlinal cell walls on both leaf surfaces (fig. 6B, 6C, 6E). It shows some persistent trichomes (fig. 6B). The stomata have prominent scales associated with the guard cells (fig. 6D).

trichome base at lower left. The guard cells are very small and have associated cuticular scales (arrow); scale bar = 20 μm. F, Lm image of a single paracytic stomatal complex. The guard cells are small and have associated extremely small cuticular scales (arrow); scale bar = 20 μm. G, EFM image of adaxial surface showing the mesh of small vein areoles; scale bar = 1 mm. H, Leaf specimen MPM-Pb-18751; scale bar = 1 cm. I, Leaf specimen MPM-Pb-18752; scale bar = 1 cm. J, EFM image of higher-order venation, showing stomata (black dots) within very small areoles. Note the near absence of trichome bases; MPM-Pb-18751; scale bar = 200 μm. K, Lm image of a single paracytic stomatal complex. The guard cells are very small and have associated cuticular scales; MPM-Pb-18751; scale bar = 20 μm. L, SEM image of inner abaxial cuticle showing a stomatal complex with extremely small guard cell cuticular scales (arrow); MPM-Pb-18752; scale bar = 10 μm. M, EFM image showing areolate higher-order venation. Note especially the abundant, small, round resin bodies within the leaf matrix; MPM-Pb-18752, scale bar = 1 mm. A color version of this figure is available online.

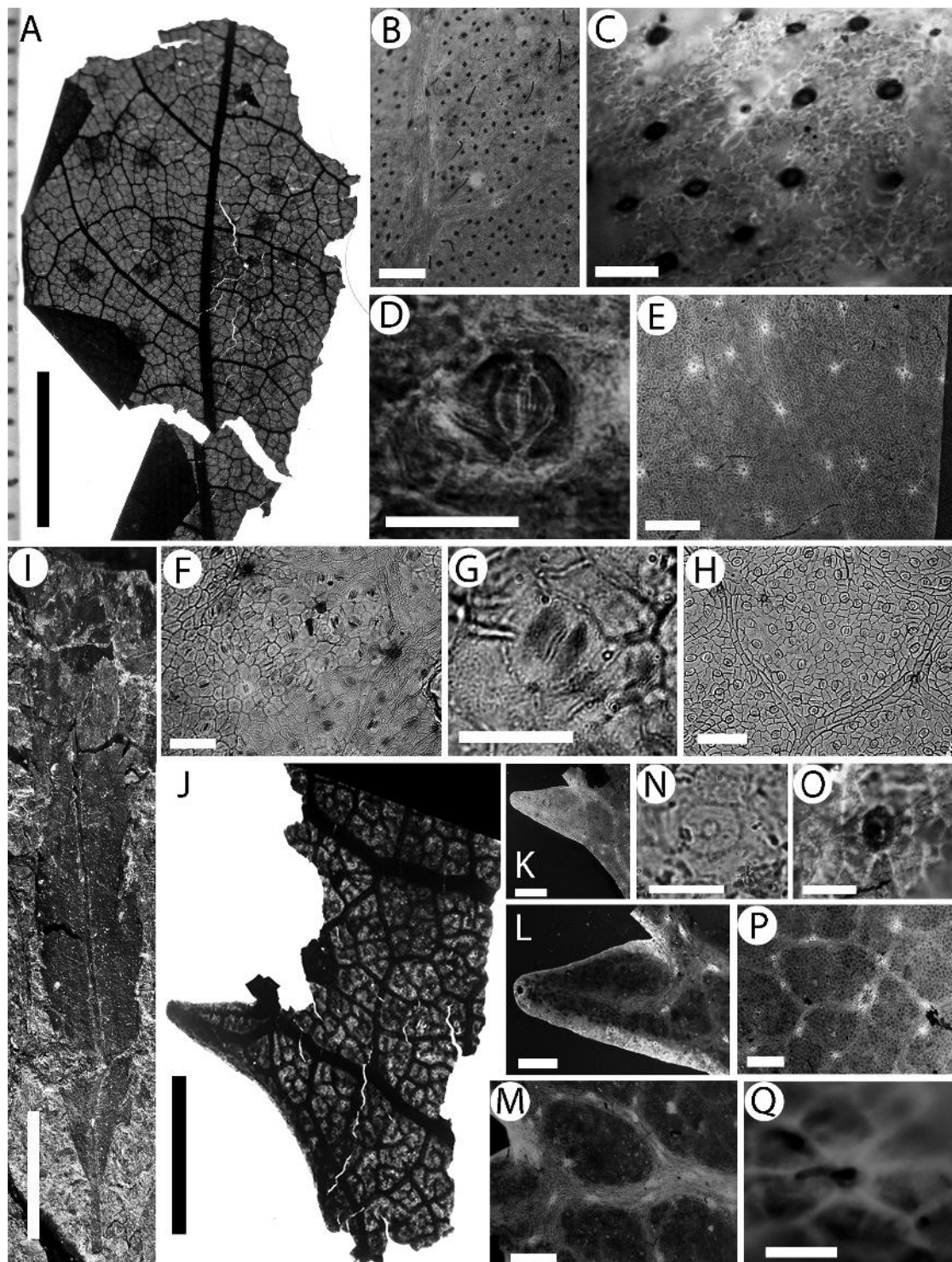


Fig. 6 Lauraceae sp. 3 (A–E), dispersed Lauraceae cuticle (MPM-Pb-18760a; F, G) and angiosperm sp. 4 (?Cunoniaceae; MPM-Pb-18756; I–Q) from the Ligorio Márquez Formation (LMF) and extant Lauraceae cuticle (H). A, Incomplete leaf specimen MPM-Pb-18754; scale bar = 5 mm. B, Epifluorescence microscopy (EfM) image of higher-order venation, showing stomata (black dots) within small areoles, a few thickened, poral trichome bases (some with attached thin, black trichomes), and sinuous cell walls; MPM-Pb-18754; scale bar = 200 μm . C, EfM image showing stomata (black) within an areole, a poral trichome base (near center, left) and tightly sinuous cell walls; MPM-Pb-18755; scale bar = 50 μm . D, EfM image of a single paracytic stomatal complex. The guard cells are very small; MPM-Pb-18754; scale bar = 20 μm . E, EfM image showing tightly sinuous cell walls and some poral trichome bases on the adaxial side; MPM-Pb-18754; scale bar = 200 μm . F, Light microscopy (Lm) image showing stomata (black) within a vein areole and poral trichome bases on veins; scale bar = 50 μm . G, Lm image of a single paracytic stomatal complex. The guard cells are very small and have associated broad, butterfly-like cuticular scales; scale bar = 20 μm . H, Lm cuticle image of the Australian species *Cryptocarya glaucescens* R.Br. showing stomata within a vein areole and poral trichome bases on veins. Note the striking similarity to LMF Lauraceae cuticles (especially F, G); scale bar = 100 μm . I, Leaf specimen; scale bar = 1 cm. J, Part of the specimen in

Cuticular remains of Lauraceae are also common in the sieved residues and potentially include at least one more species, which shows prominent, butterfly-like, guard cell cuticular scales (MPM-Pb-18760a; fig. 6F, 6G).

Inconsistencies in leaf and cuticular preservation make it difficult to assign our fossil specimens to discrete taxa of Lauraceae. Nevertheless, these specimens can be confidently assigned to the family, based principally on well-understood cuticular characters that are evident in extant species (Christophel and Rowett 1996) and that have been recognized in fossils from around the globe (e.g., Bandulska 1926, 1929; Dilcher 1963; Hill 1986; Upchurch and Dilcher 1990; Carpenter et al. 2007, 2010; Bannister et al. 2012; Shi et al. 2014). These characters include the apparent synapomorphies of the stomata being paracytic with small guard cells and cuticular scales between guard and subsidiary cells and stomata confined to small areoles. Many LMF fossils also have trichomes or trichome bases with poral bases and resin bodies adherent to the inner cuticle surface, traits that are highly characteristic for the family.

However, we follow many recent authors (e.g., Bannister et al. 2012) in not placing any of our fossils into living species or genera. This is because venation type is of little use in discriminating extant taxa; as just one example, triplinerved (acrodromous) species occur in at least 11 Lauraceae genera (Bannister et al. 2012). Similarly, although cuticular evidence is critical in determining whether a fossil leaf belongs to the family, this evidence is less useful for identifying generic affinities. Nevertheless, we argue that our fossils have features consistent with those of the largely Southern Hemisphere clade known as the *Cryptocarya* group (Rohwer et al. 2014). For instance, the type of narrow cuticular scales seen in some of the LMF stomata (fig. 5K, 5L) are a feature of *Endiandra* R. Br. (Christophel and Rowett 1996), and the butterfly-like scales (fig. 6F, 6G) are characteristic of *Cryptocarya* R. Br. (fig. 6H; Christophel and Rowett 1996). However, affinities with other lineages cannot be ruled out. For instance, butterfly-like cuticular scales also occur in several genera of the *Ocotea* complex of the Neotropical Laureae clade (Nishida and van der Werff 2011).

Unidentified Angiosperms

?Cunoniaceae

Angiosperm Leaf sp. 4 (Fig. 6I–6Q)

Specimen examined. MPM-Pb-18756 (fig. 6I–6Q).

The leaf is narrow and serrate, ~52 mm long and 8 mm wide (fig. 6I), with an acute base angle and prominent petiole ~7 mm

long and 0.8 mm wide. The primary vein is strong with a straight course, and the secondary venation is semicraspedodromous, with ~12 pairs of veins and no evidence of intersecondaries. Third- and fourth-order venation is regular polygonal reticulate (fig. 6M). Each tooth is tipped with a prominent pore, which is the terminus of a vein that branches into the tooth just before the angular tooth sinus, where the secondary vein loops up to join with the superadjacent secondary vein (fig. 6J–6L). The teeth are apically more or less straight to concave and basally straight to convex. Round-appearing stomata occur within vein areoles on the abaxial side and are anomocytic (fig. 6M–6O). Trichome bases surrounded by typically five to eight cells are abundant along the veins on both surfaces, and some small, simple, unicellular trichomes remain attached (fig. 6M, 6P, 6Q).

?Cunoniaceae

Angiosperm Leaf sp. 5 (Fig. 7A–7G)

Specimens examined. MPM-Pb-18757 (fig. 7A, 7D–7F), MPM-Pb-18758 (fig. 7B, 7C, 7G), MPM-Pb-18759.

This species is similar to leaf sp. 4, but it is most readily distinguished by the presence of teeth that are convex apically and basally and prominently gland tipped (fig. 7A–7C). Rounded stomata occur within the areoles (fig. 7D, 7E) and appear to be distinct from those of angiosperm leaf sp. 4 in being variably sized, including with large hydathodes along the veins (fig. 7F). Another apparent distinction is that trichome bases are much rarer, including on the adaxial surface, which shows epidermal cells with angular junctions (fig. 7G).

Angiosperm spp. 4 and 5 are consistent with Cunoniaceae, including *Weinmannia*, in their characters of semicraspedodromous venation, trichome bases with radially modified epidermal cells, and anomocytic stomata (e.g., Carpenter and Buchanan 1993; Barnes 2001; Carpenter et al. 2004). Formal placement in the family is not possible in the absence of more extensive work on well-preserved fossils and extant cuticle morphology, including within Elaeocarpaceae and other closely related Oxalidales. Nevertheless, diverse fossils of Cunoniaceae, including wood, flowers, fruits, and leaves, occur at several other early Paleogene sites in Patagonia (Gandolfo and Hermsen 2017; Jud et al. 2018).

Angiosperm Leaf sp. 6 (Fig. 7H–7L)

Specimen examined. MPM-Pb-18761 (fig. 7H–7L).

The only known specimen is a small, entire-margined, curved leaf (or leaflet; the base is asymmetrical), ~35 mm long and 11 mm wide, with brochidodromous secondary venation and

I isolated from the sedimentary matrix. Note the venation details: the lower major (secondary) vein runs toward the tooth sinus before looping upward (the vein and associated leaf margin above the tooth is largely incomplete), with another vein branching off toward the tooth apex; scale bar = 1 mm. *K, L*, EfM images of the tooth in *J* as seen from the adaxial (*K*) and abaxial (*L*) sides. Note the venation and large pore at the tooth apex (*L*); scale bars = 200 μ m. *M*, EfM image showing stomata within areolation and abundant evidence of trichomes along veins (mostly as pores surrounded by cuticular thickening that shows strong fluorescence); scale bar = 200 μ m. *N, O*, Lm (*N*) and EfM (*O*) images showing round-appearing, anomocytic stomata; scale bars = 20 μ m. *P*, EfM image of adaxial surface, showing obvious areolation and abundant evidence of trichomes along veins (mostly as pores surrounded by cuticular thickening that shows strong fluorescence); scale bar = 200 μ m. *Q*, EfM image showing a small trichome in situ with a poral base surrounded by six epidermal cells; scale bar = 20 μ m. A color version of this figure is available online.

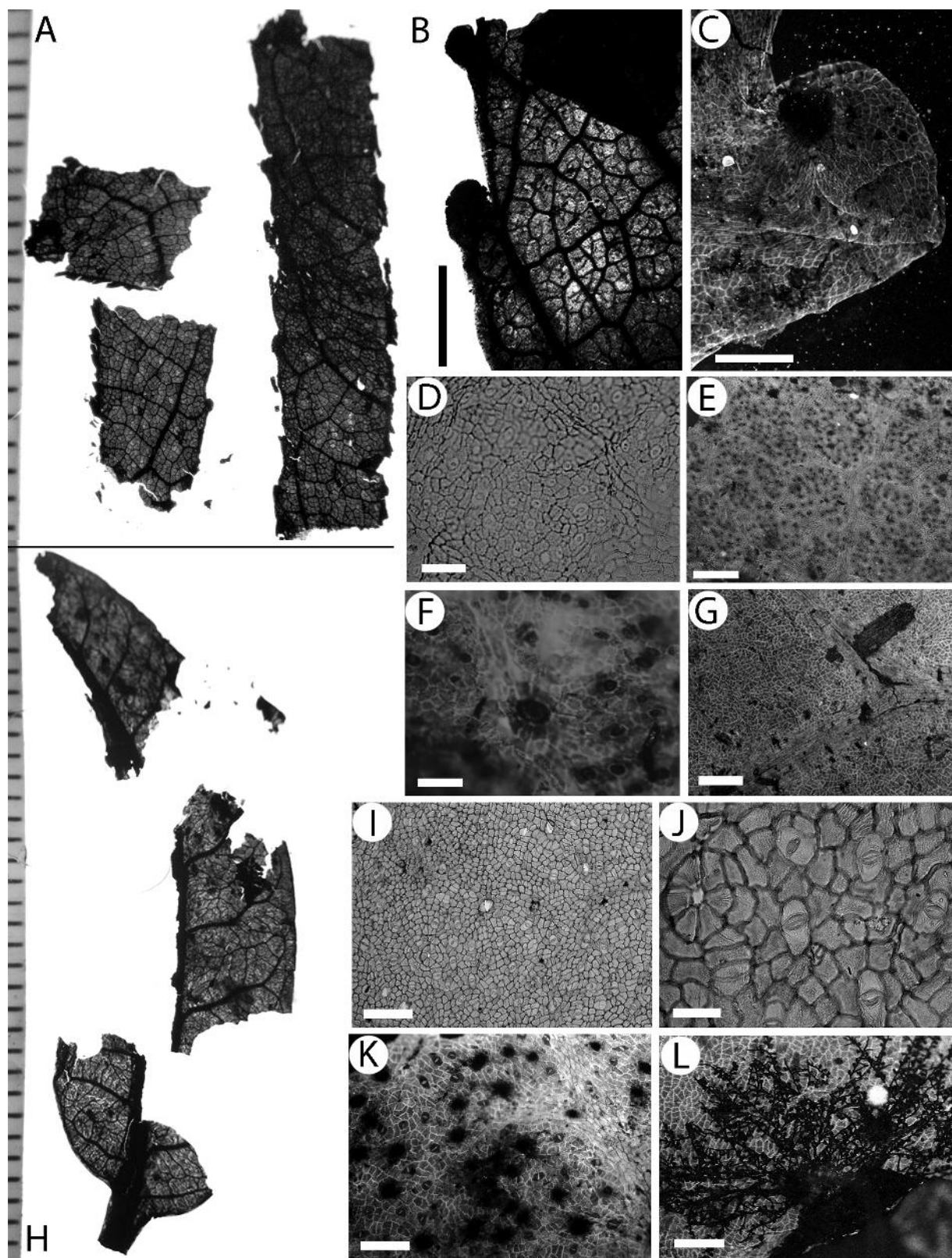


Fig. 7 Angiosperm sp. 5 (?Cunoniaceae; A–G) and angiosperm sp. 6 (MPM-Pb-18761; H–L). A, Fragmentary leaf specimen; MPM-Pb-18757; scale is in millimeters. B, Part of leaf margin showing semicraspedodromous venation and prominently gland-tipped teeth; MPM-Pb-18758; scale bar = 1 mm. C, Epifluorescence microscopy (EfM) image showing a gland-tipped tooth; MPM-Pb-18758; scale bar = 200 μ m. D, E, Light microscopy (Lm; D) and EfM (E) images showing variably sized, anomocytic stomata within areoles and apparent absence or scarcity

admedially ramified tertiary venation (fig. 7H). Its cuticle features randomly aligned, paracytic stomata with distinctively broad, winglike subsidiary cells and poral trichome bases that are each associated with a ring of six radially striated epidermal cells (fig. 7I–7K). The adaxial epidermal-cell cuticle shows slight buttressing (fig. 7L). Affinities are currently unknown. The fossil leaf shows extensive fungal invasion (fig. 7K, 7L), including evidence of hyphae entering the mesophyll via stomata (visible as black dots under low magnification).

Angiosperm Leaf sp. 7 (Fig. 8A–8N)

Specimens examined. MPM-Pb-18762, MPM-Pb-18763, MPM-Pb-18764 (fig. 8A), MPM-Pb-18765 (fig. 8B), MPM-Pb-18766 (fig. 8C), MPM-Pb-18767 (fig. 8F), MPM-Pb-18768, MPM-Pb-18769 (fig. 8E), MPM-Pb-18770, MPM-Pb-18771, MPM-Pb-18772 (fig. 8D), MPM-Pb-18773 (fig. 8L, 8M), MPM-Pb-18774, MPM-Pb-18775 (fig. 8G, 8H, 8K), MPM-Pb-18776, MPM-Pb-18777, MPM-Pb-18778, MPM-Pb-18779 (fig. 8J), MPM-Pb-18780, MPM-Pb-18781, MPM-Pb-18782 (fig. 8I, 8N), MPM-Pb-18783.

This species is the most common leaf type from the LMF sediments. It is highly variable in shape and size, ranging up to 80 mm in length and 35 mm in width and bearing weakly brochidodromous to eucamptodromous venation (figs. 1B, 8A–8G). Leaf apices are acute to rounded and emarginate. Margins are entire, although a minute tooth was observed on one leaf (fig. 8G, 8H). Typically, there are five or six secondary veins on each side of the primary vein (the basalmost pair being prominent), and in many cases the secondary veins are obviously decurrent to some extent along the primary vein (e.g., fig. 8A, 8E). Secondary veins are homogeneously curved in course. Also, distinctively, the leaves have abundant, closely spaced, opposite percurrent tertiary veins that are largely perpendicular to the primary vein. A fimbrial vein is present. Stomata are randomly and irregularly distributed across the abaxial leaf surface (fig. 8I, 8J). They are anomocytic to cyclocytic (fig. 8K, 8L), and the cuticle of the apparent subsidiary cells stains weakly relative to that of the normal epidermal cells. Peristomatal rims are evident on the cuticle surface, which is variably adorned with striations of similar width to the rims (fig. 8M). Large pores (fig. 8J) that are associated with radiating epidermal cells are scattered across both leaf surfaces. These probably represent trichome insertion points, and there is no evidence of oil cells. Adaxial cells have straight walls with angular junctions (fig. 8N).

Abundant dispersed leaf cuticle sourced from this morphology and several specimens of a four-parted calyx or corolla tube (fig. 8O) were also recovered from disaggregated LMF sediment. Derivation of the flower parts from the same

source plants as angiosperm leaf sp. 7 is suggested by the presence on the floral material of straight-walled epidermal cells with angular junctions, scattered pores, striations, and a few stomata (fig. 8P), which are all features that are morphologically consistent with those of the leaves. Given the well-preserved nature of the floral parts and the fact that they are likely associated with the most common leaf species in the assemblage, the source plants may have been locally abundant and perhaps were directly overhanging the depositional site. If the hypothesis of a single source species is correct, then the triaperturate pollen (fig. 8Q) adherent to several of the floral parts indicates affinities of the leaves and flowers within the eudicots. Further studies will be reported in detail elsewhere.

Other Fossils

Although cuticular remains referable to Lauraceae and angiosperm leaf sp. 7 dominate in the sieved residues, several novel dispersed cuticle types are recognizable, and these are illustrated here to show their diversity (fig. 9A–9O). Similarly, useful cuticle has yet to be prepared from some of the fossil leaves, implying that so far unrecognized taxa may also exist among these leaves. One possible example is a toothed leaf, MPM-Pb-18784 (fig. 9P), which is much broader than the other Cunoniaceae-like toothed specimens (angiosperm leaf spp. 4 and 5). A degraded fern sporangium (fig. 9Q) and several propagule organs (fig. 9R) have also been found, and the assemblage overall is characterized by the presence of abundant and diverse fungal forms, including high-grade “germlings” (e.g., Lange 1976, 1978; García-Massini et al. 2004; Bannister et al. 2016; Conran et al. 2016), microthyriaceous shields, and prolific hyphal growth (e.g., figs. 7L, 9S, 9T).

Dispersed cuticle sp. 1 (fig. 9A, 9B) is very thick and suggestive of Araucariaceae in having stomata with four to six surrounding cells mostly aligned transverse to the long axis of normal epidermal cells. However, no close affinity with Araucariaceae is indicated because the stomata are relatively sparse and typically have an elongated subsidiary cell on each side of the guard cells, producing an unusual, broadly paracytic appearance. All other cuticle types are more certainly derived from angiosperms. Dispersed cuticle sp. 2 (fig. 9C, 9D) shows randomly aligned stomata that have elongated, more or less rectangular-appearing guard cell pairs. Dispersed cuticle sp. 3 (fig. 9E–9G) is thin but shows very thick, presumed trichome-base platforms. Dispersed cuticle sp. 4 (fig. 9H) has extremely stout, large bristles or basal parts of trichomes over its surface. Dispersed cuticle sp. 5 (fig. 9I) has extensive surface ridging, narrow stomata, and distinctive shield-like structures (which may be peltate scales) along the veins. Dispersed cuticle sp. 6 (fig. 9J) has relatively large, paracytic stomata and sinuous cell

of trichome bases; MPM-Pb-18757; scale bars: D = 50 μ m; E = 200 μ m. F, EfM image showing rounded anomocytic stomata, including a large hydathode along a vein; MPM-Pb-18757; scale bar = 50 μ m. G, EfM image of adaxial surface. Note the epidermal cells with angular junctions and apparent absence of trichome bases; MPM-Pb-18758; scale bar = 200 μ m. H, Leaf specimen. Note the asymmetrical base; scale bar is in millimeters. I, J, Lm images showing randomly aligned, paracytic stomata with broad, winglike subsidiary cells and poral trichome bases (J, left) that are associated with a ring of six radially striated epidermal cells; scale bars: I = 200 μ m; J = 50 μ m. K, EfM image showing randomly aligned, paracytic stomata. A poral trichome is located at the lower right of the label; scale bar = 200 μ m. L, EfM image showing slight buttressing of adaxial epidermal cells. Note the pronounced fungal development; scale bar = 200 μ m. A color version of this figure is available online.

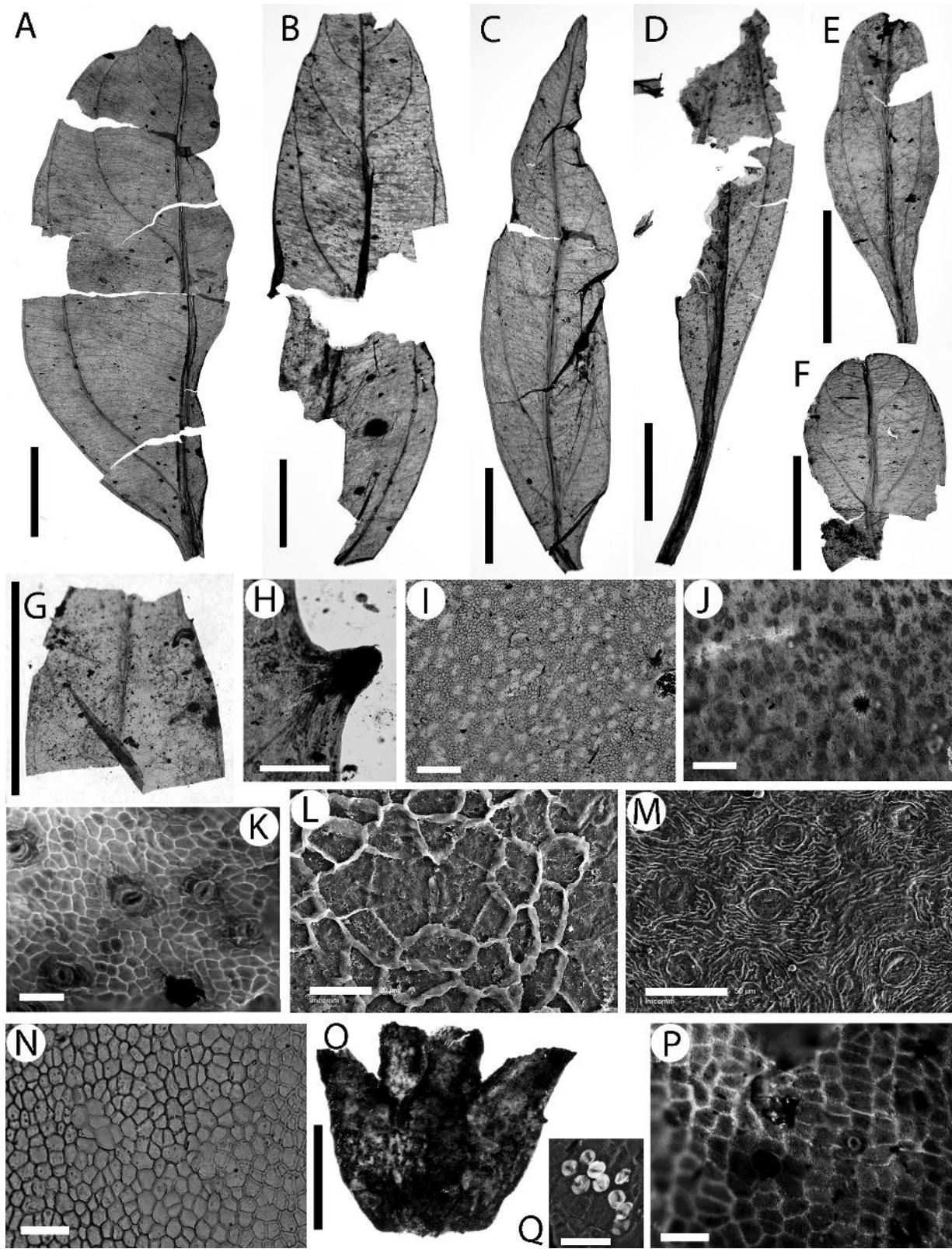


Fig. 8 Angiosperm sp. 7. Leaves and leaf fragments (A–H), images of cuticular details (I–N), and floral remains recovered from sieved Ligerio Márquez Formation residue (O–Q) that are attributable to sp. 7. A, MPM-Pb-18764. B, MPM-Pb-18765. C, MPM-Pb-18766. D, MPM-Pb-18772. E, MPM-Pb-18769. F, MPM-Pb-18767. G, H, MPM-Pb-18775. Note the high variation in leaf shape and size, the weakly brochidodromous to eucamptodromous venation with closely spaced, perpendicular, opposite percurrent tertiary veins, and the single, minute

walls. Dispersed cuticle sp. 7 (fig. 9K) features anomocytic stomata that appear to have an oval-shaped surface rim surrounding their apertures and unusual, thinly cuticularized glandular structures. Dispersed cuticle sp. 8 (fig. 9L) is delicate and has fine striations, especially radiating from certain unusual stomata, that also differ from most others in having thickened peristomatal rims. Dispersed cuticle sp. 9 (fig. 9M, 9N) has thin, poorly preserved subsidiary cells but highly distinctive peg-like protuberances at cell junctions. Dispersed cuticle sp. 10 (fig. 9O) has typical features of a monocot leaf (e.g., Pole 2007a), including the fact that the stomata, although sparse, are paratetracytic.

Discussion

Floral Composition

This study adds a new dimension to ongoing studies of Patagonian Paleogene floras, which mostly lack cuticular preservation (especially among angiosperms), and contributes the first detailed macrofloral information from a significant, recently discovered site. Our relatively well-preserved specimens confirm the conclusions of Troncoso et al. (2002) that Lauraceae and *Dacrycarpus* occur in the LMF flora, and our identifications of these taxa and *Coronelia* support their suggestion that the LMF flora has much in common with the Chilean Concepción-Arauco flora (Engelhardt 1891; Berry 1922; Florin 1940; Collao et al. 1987). However, our results introduce a cautionary note for interpreting floras that lack cuticular evidence. For instance, impression-only specimens of the most common leaf type (angiosperm leaf sp. 7) in our material might (erroneously) be referred to Lauraceae because of their brochidodromous secondary veins with horizontally percurrent tertiaries and acute basal secondaries (e.g., compare leaf images in fig. 8 with those of Lauraceae in Hyland [1989] and Christophel and Rowett [1996]).

Troncoso et al. (2002) placed many of the Chilean LMF leaves that they identified as Lauraceae in fossil species erected by Engelhardt (1891) and Berry (1925, 1938), while also proposing undescribed species of *Cinnamomum* Schaeff., *Nectandra* Rol. ex Rottb., and *Persea* Mill. Overall, the extant species that were considered to most closely resemble the fossils are centered in the Neotropics, and these taxa belong to what is known as the terminal Perseeae-Laureae clade, which is probably of Laurasian origin (Chanderbali et al. 2001; Li et al. 2011). However, Troncoso et al. (2002) warned that their fossils were mostly poorly preserved and with few specimens (see also the comments of Florin 1940, p. 24, with regard to the angiosperm specimens of the Concepción-Arauco flora). Moreover, as we have discussed, assigning even well-preserved leaf fossils with

cuticle to extant genera of Lauraceae is fraught. Therefore, fossils from the LMF and elsewhere that have previously been assigned to Neotropical genera of Lauraceae could just as logically belong to one or a range of other genera. Indeed, we argue for the first time here that at least some Patagonian Paleogene Lauraceae fossils could belong to *Cryptocarya* group genera. This group occurs in the Neotropics, but it is strongly represented in Australasia and is probably of Gondwanan origin (Chanderbali et al. 2001; Rohwer et al. 2014; van der Merwe et al. 2016).

Although Troncoso et al. (2002) compared most of their fossils from the LMF with leaves of extant Neotropical taxa, they considered that one toothed specimen was comparable with the Australian *Daphnandra* Benth.; that genus belongs to Atherospermataceae (Laurales), a family with a distinctly Gondwanan distribution. We cannot discount the presence of *Daphnandra* or related leaves in the LMF, especially considering that *Daphnandra*-like fossil leaves of Atherospermataceae have been reported at the Eocene Laguna del Hunco and Río Pichileufú sites (Berry 1935b, 1938; Knight and Wilf 2013). However, we found no leaves or cuticle (see Pole 2008 for images of extant species) at our site that could be referred to the family. Similarly, we did not recognize in our material the other LMF leaf taxa proposed by Troncoso et al. (2002). These taxa include *Myrcia* cf. *Myrcia reticulato-venosa* Engelm. of Myrtaceae, a family that typically has leaves with distinctive intramarginal veins and evidence of characteristic oil glands on the cuticle surface (e.g., Christophel and Lys 1986).

As in a previous study of Argentinean LMF microfossils (Macphail et al. 2013), we found no evidence of *Nothofagus*. The occurrence of this genus throughout the LMF is evidently variable: although Troncoso et al. (2002) also reported its absence, Hinojosa et al. (2016) recently described and illustrated *Nothofagus subferruginea* (Dusén) Tanai and *Nothofagus serrulata* Dusén leaves from the basal section of the LMF at its type locality in Chile (Mina Ligorio Márquez).

Proteaceae are perhaps the most notable group among those absent from the LMF macroflora. Some types of Proteaceae pollen are represented in the LMF (Troncoso et al. 2002; Quezada-Arriagada et al. 2003; Okuda et al. 2006; Macphail et al. 2013) as elsewhere in the Paleogene of Patagonia and the Antarctic Peninsula (e.g., Askin and Baldoni 1998; Melendi et al. 2003; Palazzesi and Barreda 2007), but we found no evidence of Proteaceae leaves. This family is represented by abundant, highly diverse, and generally well-preserved leaf fossils in Australian Paleogene sediments. The apparent uncommonness of such fossils in Patagonia, including from the well-studied Laguna del Hunco flora (Wilf et al. 2005; see also González et al. 2007) probably reflects a less important role in the vegetation than in Australia,

tooth (G, H); scale bars: A–G = 1 cm; H = 200 μ m. I–M, Light microscopy (Lm; I), epifluorescence microscopy (EfM; J, K), and SEM (L, M) images of the abaxial cuticle. I, J, Randomly and irregularly distributed stomata among relatively small epidermal cells. I, MPM-Pb-18779; scale bars = 200 μ m. K, Stomata of differing sizes associated with weak-walled subsidiary cells and striations. Note evidence of a peristomatal rim in the middle complex; MPM-Pb-18775; scale bar = 50 μ m. L, Inner view showing an anomocytic to cyclocytic stomatal complex with the apparent subsidiary cells being weakly walled relative to the normal epidermal cells; MPM-Pb-18773; scale bar = 20 μ m. M, Outer view showing peristomatal rims and striations; MPM-Pb-18773; scale bar = 50 μ m. N, Lm image of adaxial cuticle showing angular cell junctions; MPM-Pb-18782; scale bar = 50 μ m. O, Four-parted flower fossil; scale bar = 2 mm. P, EfM image of floral cells, showing stomata and striations. Note that the stomata are similar to those of angiosperm leaf sp. 7 (I–L); scale bar = 50 μ m. Q, EfM image of triaperturate pollen grains adherent to floral material; scale bar = 50 μ m. A color version of this figure is available online.

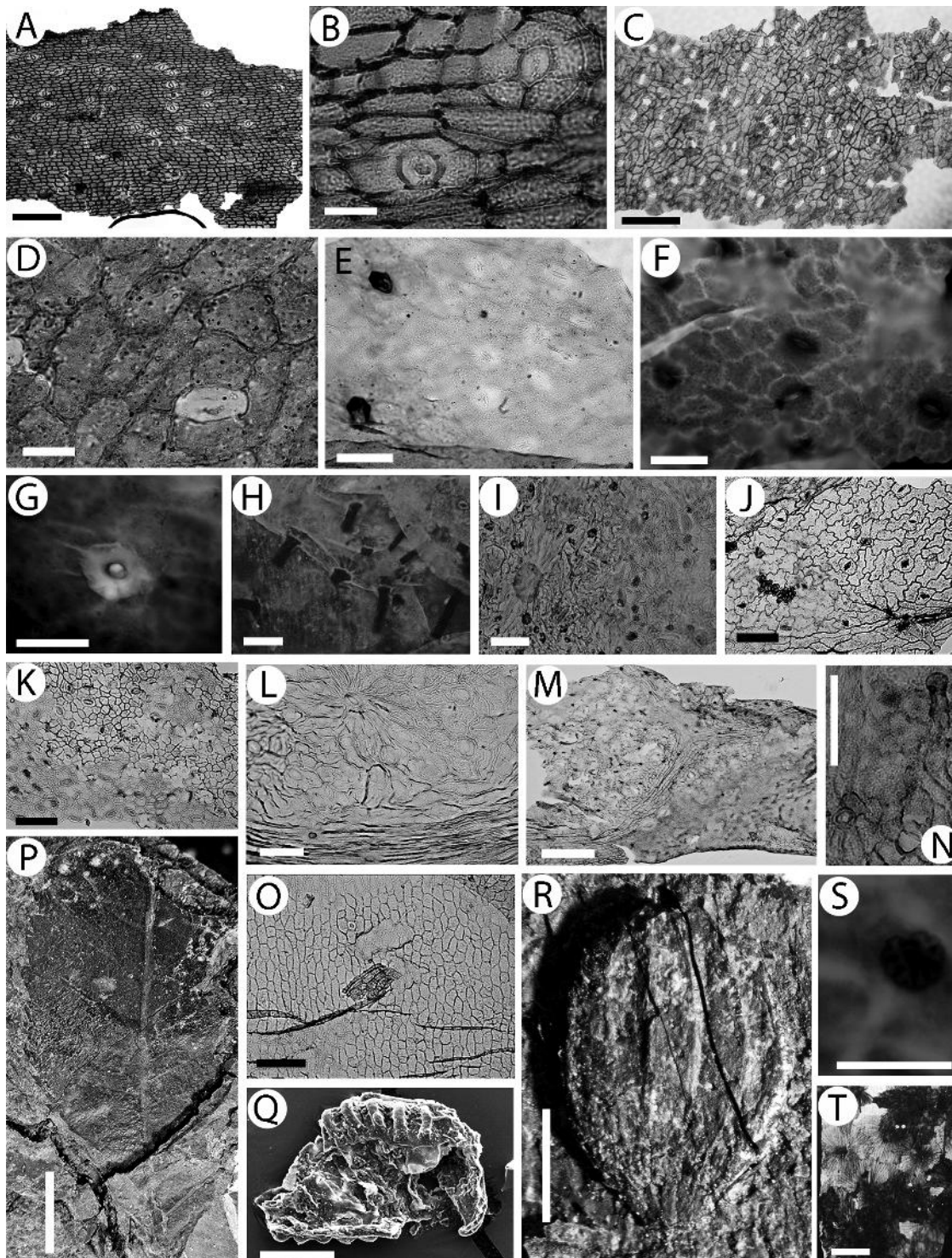


Fig. 9 Miscellaneous fossil material from the Ligorio Márquez Formation. A–O, Cuticular remains recovered from sieved residue. A, B, Light microscope (Lm) images of dispersed cuticle sp. 1; MPM-Pb-18760b. Note that the stomata are mostly aligned transverse to the long axis of normal cells and that the stomata appear broadly paracytic; scale bars: A = 200 μm ; B = 50 μm . C, D, Lm images of dispersed cuticle sp. 2; MPM-Pb-18785; scale bars: C = 200 μm ; D = 50 μm . E–G, Dispersed cuticle sp. 3; MPM-Pb-18788. E, Lm image showing thin cuticle but with very thick, presumed trichome-base platforms at left; scale bar = 50 μm . F, Epifluorescence microscopy (EfM) image showing stomata; scale bar = 50 μm . G, EfM image showing a very thick, presumed trichome-base platform; scale bar = 20 μm . H, EfM image of dispersed cuticle sp. 4. Note the stout bristles; uncataloged cuticle; scale bar = 200 μm . I, Lm image of dispersed cuticle sp. 5; MPM-Pb-18760c. Note the distinctive shield-like structure along the vein at left; scale bar = 50 μm . J, Lm image of dispersed cuticle sp. 6; MPM-Pb-18748b; scale bar = 100 μm . K, Lm image of dispersed cuticle sp. 7; MPM-Pb-18748c. Note the thinly cuticularized glandular structures distributed among the stomata; scale bar = 100 μm . L, Lm image of dispersed cuticle sp. 8.

perhaps associated with generally more fertile soils in South America (Carpenter 2012).

In over 100 h of searching ~70 kg of LMF mudstones for leaf and cuticular remains, we found evidence of fewer than 20 angiosperm spp., a diversity estimate much lower than the 55 morphotaxa in the LMF in Chile (Hinojosa et al. 2006*b*, 2010, 2016). However, we acknowledge that there could be floristic variation across the extent of the LMF that is related to ecological or taphonomic processes and preservation biases. Similarly, we cannot confirm that our fossil assemblage is precisely stratigraphically correlative with that of the LMF from where the Chilean material was collected, and it is also possible that our extraction methods destroyed delicate leaf types.

Paleoclimatic Implications

More validation of the 55 leaf taxa used in recent paleoclimate estimates for the LMF (Hinojosa et al. 2006*b*, 2010, 2016) is required, but our fossils provide new evidence in support of the conclusions of these studies calling for mesotherm mean annual temperatures (MAT) and ever-wet climates. Mesotherm elements (*sensu* Nix 1982) are now dominant where MAT is >14°–20°C and have optimal growth temperatures of 19°–22°C. First, the co-occurrence of *Dacrycarpus* and multiple species of Lauraceae is found today in Australasian rainforest habitats with mild to warm and wet climates, and *Dacrycarpus* in particular is physiologically restricted to ever-wet environments (Brodrribb and Hill 2004; Brodrribb et al. 2014). Second, although our extraction processes favored the recovery of small leaves that are less vulnerable to breakup than large ones, most leaves recovered were microphylls (<76 mm long), and only some (Lauraceae) leaves were larger (notophyll sized). This relative abundance of smaller leaf sizes is not typical of modern tropical rainforests (e.g., Webb 1959; Wright et al. 2017). Third, an extremely wet climate is supported by the presence of fern sporangia (fig. 9Q) and spores (Macphail et al. 2013), leaf drip-tips (fig. 5H), and perhaps especially by the abundant and diverse epiphyllous fungal material (e.g., figs. 7L, 9S, 9T).

There has been a widespread view that tropical-like climates prevailed in Patagonia during the early Eocene (e.g., Troncoso and Romero 1998; Gayó et al. 2005; Hinojosa et al. 2006*a*; Palazzesi and Barreda 2007; Iglesias et al. 2011; Le Roux 2012; Quattrocchio et al. 2013; Woodburne et al. 2014). For instance, Palazzesi and Barreda (2007) concluded that although early Eocene palynodata are scarce in Patagonia, there are several records of pollen taxa from this time that are indicative of very warm (upper mesotherm–megatherm) climates in the region, including *Anacolosa* Blume (Olacaceae), Cupanieae (Sapindaceae), and diverse palm types, notably the mangrove palm *Nyba* Steck (see also Quattrocchio et al. 2013). However, we consider that the macrofossil record of definite megatherm

taxa in Patagonia is quite limited, and much more work is required to determine whether the early Paleogene macrofloral records of extensive Neotropical lineages established by early researchers including Edward Berry (1938) are valid. Also, although our Argentinean LMF sediments contain pollen of the mesotherm to possible megatherm lineages *Proxapertites* Hammen (Araceae/Arecaceae) and *Bombacacidites* Germeraad (bombacoid Malvaceae), evidence of a dominant regional microtherm to mesotherm rainforest vegetation in these sediments may be apparent as diverse Podocarpaceae pollen (Macphail et al. 2013).

Although it is uncertain whether the Argentine and Chilean LMF fossils are of precisely the same age, the most recent paleoclimate estimates for the LMF in Chile, based on coexistence and leaf physiognomic analyses (Hinojosa et al. 2016), also do not support earlier conclusions of tropical-like climates. Overall, Hinojosa et al. (2016) concluded that the *Nothofagus* fossils have both mesotherm (subgenus *Brassospora* Philipson & M.N. Philipson) and microtherm (at least subgenus *Fuscaspora* R.S. Hill & J. Read) nearest living relatives.

The LMF may be more or less contemporaneous with the best-known Patagonian Paleogene macroflora, from Laguna del Hunco, Chubut, Argentina, dated to the early Eocene (~52 Ma; Wilf et al. 2005). The foliar physiognomic and floristic features of this flora are also overall mesotherm and very humid (e.g., Wilf et al. 2009; Merkhofer et al. 2015), with an estimated MAT of only 16.6° ± 2.0°C, too cool to support a tropical-like rainforest (Wilf et al. 2005).

Increasing evidence of climates in the early Eocene of Patagonia being at least warmer than at present is consistent with evidence from high latitudes elsewhere in the Southern Hemisphere. However, even greater terrestrial warmth may have been centered in Tasmania (Carpenter et al. 2012), despite that region being at much higher latitude (~65°S) than Patagonia. Interestingly, macrofossil admixtures of *Nothofagus* subgenera also occurred in Tasmania but apparently not until the Oligocene (Hill 2001*a*, 2001*b*), when local conditions were much cooler following the opening of the Tasman Gateway (Kennett 1977; Exxon et al. 2004).

Biogeographic Significance

The most confidently identified fossils in our material of the LMF are of biogeographic interest. *Dacrycarpus* is one of many formerly Patagonian conifer genera that are currently restricted to Australasia (Florin 1940; Wilf et al. 2009, 2014; Wilf 2012). The new record of *Coronelina* shows that this extinct genus must have been relatively common in the early Paleogene of at least the western part of southern South America and perhaps across Antarctica to Tasmania. However, *Coronelina* does not seem to have extended to greatly lower latitudes and is unknown from both older and younger sites.

Note the fine striations, especially radiating from the stomatal complex at upper left; uncataloged cuticle; scale bar = 50 μm. M, N, Lm images of dispersed cuticle sp. 9; MPM-Pb-18760d. Note the peg-like protuberances at cell junctions; scale bars: M = 200 μm; N = 50 μm. O, Lm image of dispersed cuticle sp. 10; MPM-Pb-18748d, a probable monocot, with two paratetracytic stomata (*upper center*, *upper right*); scale bar = 100 μm. P, Unidentified toothed leaf specimen MPM-Pb-18784; scale bar = 1 cm. Q, Degraded fern sporangium; uncataloged specimen recovered from sieved residue; scale bar = 50 μm. R, Unidentified propagule; MPM-Pb-18786; scale bar = 2 mm. S, Complex fungal germling on Lauraceae sp. 3 cuticle; MPM-Pb-18754; scale bar = 20 μm. T, Prolific fungal growth on uncataloged cuticular remains recovered from sieved residue; scale bar = 200 μm. A color version of this figure is available online.

There is increasing evidence of Patagonian Paleogene fossil taxa that were probably components of trans-Antarctic mesic vegetation that prevailed during the early Eocene acme of global warming. This list includes the conifers already discussed, as well as certain ferns (Carvalho et al. 2013), Monimiaceae and Atherospermataceae (Knight and Wilf 2013), *Eucalyptus* L'Her. (Myrtaceae; Gandolfo et al. 2011; Hermsen et al. 2012), *Gymnostoma* L.A.S. Johnson (Casuarinaceae; Zamalao et al. 2006), *Ripogonum* J.R. Forst. & G. Forst. (Ripogonaceae; Carpenter et al. 2014), and Cunoniaceae (Gandolfo and Hermsen 2017). Assuming that our hypothesis of *Cryptocarya* group affinities is correct, the LMF Lauraceae fossils could be added to this list. In this respect, we note that well-preserved fossil leaves that probably belong to the *Cryptocarya* group are known widely in Upper Cretaceous and Paleogene sediments of Australia (e.g., Hill 1986; Conran and Christophel 1998; Carpenter et al. 2004), New Zealand (e.g., Pole 2007b; Bannister et al. 2012), and the Ninetyeast Ridge of the Indian Ocean (Carpenter et al. 2010). Lauraceae wood (Poole et al. 2000b), cuticle (Upchurch and Askin 1989), and leaves that probably belong to the family (Iglesias 2016) are also known from the Late Cretaceous of the Antarctic Peninsula, as are Cunoniaceae-like wood (Poole et al. 2000a) and leaves (Iglesias 2016).

Our finding of no conclusive evidence of Neotropical taxa in the LMF flora is consistent with the results of a meta-analysis of South American fossil floras through the Cenozoic by Jaramillo and Cárdenas (2013). These authors found that there are few shared elements in the Paleocene between Neotropical and Argentinean sites and even fewer in the Eocene, the opposite of expectations if tropical biomes expanded southward during the early to middle Eocene global warming. There are numerous potential reasons for the lack of tropical-temperate interchange, such as incompatible insolation regimes (see Jaramillo and Cárdenas 2013). Moreover, the subtropical arid zone has been persistent through geologic time (e.g., Ziegler et al. 2003), and the moisture deficits imposed there during hot Eocene climate regimes would have presented significant challenges to water-demanding plants.

Nevertheless, links to some lineages with extant ranges including the Americas north of Patagonia have in fact been recently

confirmed from the Eocene of Patagonia, although neither of the best-resolved taxa, Juglandaceae (Hermsen and Gandolfo 2016) and *Physalis* L. (Solanaceae; Wilf et al. 2017a), suggest tropical-climate origins. Juglandaceae is interpreted as having reached southern South America from Laurasia (Hermsen and Gandolfo 2016), whereas fossil *Physalis* from Patagonia suggests evolution within pre-breakup Gondwana followed by extinction in southernmost South America and survival and diversification to the north (Wilf et al. 2017a). This is also the likely biogeographic scenario for *Retrophyllum* C.N. Page, a disjunct genus of Neotropical and West Pacific Podocarpaceae represented at Late Cretaceous and Paleogene sites in southern Chile and Argentina (Florin 1940; Wilf et al. 2017b).

Conclusions

Our contribution shows for the first time that the rich Paleogene fossil assemblages of Patagonia include diverse leaves with cuticular preservation. These leaves confirm that Lauraceae were an important component of Paleogene vegetation in the region and probably grew under warm and wet climates. Conifers now extinct in the Americas were present and show clear links to both past and present Australasian floras. This and other evidence challenges the hypothesis that southern South American floras were dominated by Neotropical elements during the globally warm Paleogene.

Acknowledgments

We are grateful to F. J. Goin and J. N. Gelfo (La Plata University); R. Cúneo, P. Puerta, I. Davie, and E. Ruigomez (Museo Paleontológico Egidio Feruglio); and C. Knight and M. Carvalho (then at Penn State) for their interest in this work and for field and laboratory assistance. We thank I. Méndez and B. Pérez for site access and Secretaría de Estado de Cultura, Santa Cruz Province, for collection permits. This project was supported by funding from National Science Foundation grants DEB-1556666 and DEB-0919071.

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