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RESEARCH ARTICLE

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The first Gondwanan Euphorbiaceae fossils reset the biogeographic history of the *Macaranga-Mallotus* clade

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Abstract

Premise: The spurge family Euphorbiaceae is prominent in tropical rainforests worldwide, particularly in Asia. There is little consensus on the biogeographic origins of the family or its principal lineages. No confirmed spurge macrofossils have come from Gondwana.

Methods: We describe the first Gondwanan macrofossils of Euphorbiaceae, represented by two infructescences and associated peltate leaves from the early Eocene (52 Myr ago [Ma]) Laguna del Hunco site in Chubut, Argentina.

Results: The infructescences are panicles bearing tiny, pedicellate, spineless capsular fruits with two locules, two axile lenticular seeds, and two unbranched, plumose stigmas. The fossils' character combination only occurs today in some species of the *Macaranga-Mallotus* clade (MMC; Euphorbiaceae), a widespread Old-World understory group often thought to have tropical Asian origins. The associated leaves are consistent with extant *Macaranga*.

Conclusions: The new fossils are the oldest known for the MMC, demonstrating its Gondwanan history and marking its divergence by at least 52 Ma. This discovery makes an Asian origin of the MMC unlikely because immense oceanic distances separated Asia and South America 52 Ma. The only other MMC reproductive fossils so far known are also from the southern hemisphere (early Miocene, southern New Zealand), far from the Asian tropics. The MMC, along with many other Gondwanan survivors, most likely entered Asia during the Neogene Sahul-Sunda collision. Our discovery adds to a substantial series of well-dated, well-preserved fossils from one undersampled region, Patagonia, that have changed our understanding of plant biogeographic history.

KEYWORDS

biogeography, Euphorbiaceae, Gondwana, Laguna del Hunco, *Macaranga*, *Mallotus*, Malesia, Patagonia, Sahul-Sunda exchange

The angiosperm family Euphorbiaceae Juss. s.s. (Malpighiales) has at least four subfamilies, more than 220 genera, and over 6000 species of primarily tropical trees, shrubs, and climbers (Radcliffe-Smith, 2001; Wurdack et al., 2005; Webster, 2014). The family has remarkable variation in morphology and habitat, from its significant arid-biome radiation to its status as one of the few abundant and diverse families in all three of Earth's wet tropical regions in Africa, South America, and Asia. The Euphorbiaceae often dominate understories in Southeast Asian lowland rainforests and are second only to Dipterocarpaceae in stem frequency (e.g., Newbery et al., 1996; Slik et al., 2003b).

The origins of Euphorbiaceae s.l. were classically ascribed to the Old World (Bentham, 1878; Webster, 1994) and West Gondwana (Raven and Axelrod, 1974; Gentry, 1982), but there is little modern consensus on the biogeographic history of Euphorbiaceae s.s. or its major lineages. The discussion is limited by the family's scarce

macrofossil record, which is historically dominated by problematic occurrences of isolated leaves (Nucete et al., 2012; Reback et al., 2022). However, findings of nonfoliar material have increased, including fruits and woods of Euphorbiaceae from the Deccan Intertrappean Beds, near the Cretaceous-Paleogene boundary in central India (Lakhanpal and Dayal, 1962; Wheeler et al., 2017; Reback et al., 2022) and several Eocene fruits from the eastern United States and western Europe (Reid and Chandler, 1933; Mazer and Tiffney, 1982; Vaudois-Miéja, 1986; Collinson et al., 2012). Fossils with affinities below the family level include middle Eocene fruits and inflorescences of Hippomaneae (subfamily Euphorbioideae) from Tennessee (Crepet and Daghlian, 1982; Dilcher and Manchester, 1988); middle Eocene wood assigned to *Hura* (Euphorbioideae) from Peru (Woodcock et al., 2017); late Eocene fruits from Oregon similar to *Aleurites* (subfamily Crotonoideae; Manchester and McIntosh, 2007); early Oligocene fruits similar to Crotonoideae from Peru (Hamersma et al., 2022) and Australia (Rozefelds et al., 2017b); a potentially Miocene *Aleurites* seed from Australia (Rozefelds et al., 2017a); and early Miocene fruits, inflorescences with in situ pollen, and leaves related to *Macaranga* and *Mallotus* (subfamily Acalyphoideae) from New Zealand (Lee et al., 2010; Conran et al., 2016).

The reproductive record of Euphorbiaceae fossils, coupled with silicified fruits of the closely related family Phyllanthaceae from the Deccan Traps (Kapgate et al., 2017), shows that the Euphorbiaceae must have diverged by the Late Cretaceous, broadly consistent with molecular divergence-age estimates (van Ee et al., 2008; Xi et al., 2012; Ramírez-Barahona et al., 2020). Furthermore, the extant subfamilies apparently diverged and became widely distributed by the Paleogene. Still, no reliable macrofossils of Euphorbiaceae are known from Gondwana, although there are many palynological reports (summarized by Kooyman et al., 2014; Rozefelds et al., 2017a). All the mentioned macrofossil occurrences from India, New Zealand, Africa, Australia, and South America are post-Gondwanan, in each case significantly postdating the separation of the respective landmass from the Gondwanan supercontinent (e.g., Scotese, 2021).

Macaranga Thouars and *Mallotus* Lour. (Acalyphoideae) are well-studied, closely related Old World genera that mainly consist of small trees and some shrubs, lianas, and large trees. *Macaranga* and *Mallotus* have broadly similar, extensive ranges, including Africa, Madagascar, India, Sri Lanka, East and Southeast Asia, Australia, New Guinea, and some West Pacific islands (Airy Shaw, 1975; Wurdack et al., 2005; Whitmore, 2008; van Welzen et al., 2009, 2014; Sierra et al., 2010; Cervantes et al., 2016; Utteridge, 2021a). Malesia has the highest diversity for both genera, including ca. 182 of 280 *Macaranga* and ca. 54 of 110 *Mallotus* species (e.g., Sierra et al., 2010; van Welzen, 2020). Many of the ca. 390 total species, especially in *Macaranga*, are disturbance specialists, and representatives are easily found along roads, trails, and burned areas (Slik et al., 2003a). Many disturbance-adapted species have notably large or peltate leaves, making them conspicuous at a distance. The leaves of both genera can bear an array of foliar nectaries and domatia, and many species, especially in *Macaranga*, have ant associations (Elias and An-Ci, 1985; Fiala and Maschwitz, 1991; Davies et al., 2001). Observed pollination vectors include thrips and heteropterans in *Macaranga* and both wind and insects (especially Hymenoptera) in some *Mallotus* species (Fiala et al., 2011; Guicking et al., 2013; Yamasaki and Sakai, 2013). Seeds often have fleshy exotestas and are animal-dispersed, particularly by small birds and squirrels (Davies, 2001; Esser, 2003; Guicking et al., 2013).

Macaranga and *Mallotus* are morphologically similar (Davies, 2001; van Welzen et al., 2009, 2014; Webster, 2014; Utteridge, 2021a; see Discussion). Many characters appear more often in one genus than in the other but are not exclusive to either, while features restricted to one genus usually do not appear in all its species. The only character that consistently separates the genera is the number of anther locules, which is 3–4 in *Macaranga* but always two in *Mallotus*, like most Euphorbiaceae. *Macaranga* and *Mallotus* form a monophyletic group, which we will refer to as the MMC (*Macaranga-Mallotus* clade), and the genera usually separate as sister groups in molecular analyses (van Welzen et al., 2014).

The origins and biogeography of the MMC have long been discussed (e.g., Whitmore, 1969), but there are few reliable macrofossils (Nucete et al., 2012; Wang et al., 2017). In a review of the fossil record for the MMC, Nucete et al. (2012) only accepted leaves from the middle Eocene of Japan (Tanai, 1989, 1990) and the late Oligocene of Ethiopia (García-Massini et al., 2010), along with a suite of leaves, a male inflorescence bearing in situ *Nyssapollenites endobalteus* pollen, and fruits from the early Miocene of New Zealand (Lee et al., 2010; see also Pole, 1996; Conran et al., 2016; Kaulfuss et al., 2022). The New Zealand fossils from ca. 23 Myr ago (Ma) are significant because they include the only prior reproductive macrofossil occurrence of the MMC. Notably, *N. endobalteus* pollen has a rich Cenozoic record in Australia and New Zealand (Conran et al., 2016; Rozefelds et al., 2017a) and occurs in Patagonia during the late Oligocene–Miocene (Barreda, 1997). More recently, Wang et al. (2017) reported a middle Miocene *Macaranga* leaf from Fujian, southeast China. Early Eocene fruits from northwest India, reported as closely related to *Mallotus*, were not distinguished from other likely families (e.g., Sapindaceae; Shukla and Mehrotra, 2019).

Most biogeographic analyses of the MMC favor tropical Asian (Sundan) areas of origin (Slik and van Welzen, 2001; Kulju et al., 2007; Ashton, 2014; Cervantes et al., 2016; Brambach et al., 2019). Using the accepted macrofossils in Nucete et al. (2012) and other calibration data, van Welzen

et al. (2014) found Sunda (especially the region that is now Borneo) to be the most likely ancestral area for MMC genera. Age estimates were equivalent to the Paleocene or early Eocene for the crown MMC, Paleocene to late Eocene for crown *Mallotus*, and late Eocene to Miocene for crown *Macaranga* (van Welzen et al., 2014). Cervantes et al. (2016) inferred a younger, Miocene-equivalent origin for the MMC in tropical Asia. A Sunda origin of the MMC has remained challenging to reconcile with the most reliable prior record of the group worldwide, from multiple reproductive structures and leaves, occurring at ca. 23 Ma in the southern temperate latitudes of New Zealand (paleolatitude ca. 40°S; Lee et al., 2010). At that time, the Sahul-Sunda collision was only in its earliest stages in the tropics; Zealandia was isolated and much more distant from Sunda than Sahul (Hall, 2017). Trethowan et al. (2022) recently coded *Macaranga* for Sahul origins in their biogeographic analysis of Mount Jaya (Indonesian New Guinea) based on modern biodiversity distributions.

Here, we report the first Gondwanan macrofossils of Euphorbiaceae and the oldest occurrence of the MMC, based on two infructescence fossils and 11 associated leaves. The fossils were collected at the floristically diverse, early Eocene (ca. 52 Ma) Laguna del Hunco fossil caldera-lake site in Chubut, Patagonian Argentina, where we have participated in collecting more than 8000 plant-fossil specimens representing ca. 187 currently estimated species (based on distinct foliage morphotypes). Intensive sampling and outstanding fossil preservation, rock exposure, and age control at Laguna del Hunco have generated an extraordinary, high-resolution window on South American terrestrial life during the last stage of Gondwana, coinciding with the extended global warmth of the Early Eocene Climatic Optimum (Wilf et al., 2003, 2013; Barreda et al., 2020). Plant fossils from Laguna del Hunco and other well-dated Patagonian fossil sites have contradicted many prior divergence-age and biogeographic reconstructions, most of which were based on dated molecular phylogenies (Wilf and Escapa, 2015, 2016; Wilf et al., 2017b, 2019). Significantly, numerous plant genera previously described from Laguna del Hunco (see Discussion) have extant relatives in Old World rainforests containing the MMC, where they are often threatened by deforestation and climate change (e.g., Kooyman et al., 2022). New Guinea, a major center of diversity for the Euphorbiaceae and the MMC (Airy Shaw, 1980; van Welzen, 2020; Utteridge, 2021a), is also the area with the highest richness of Laguna del Hunco "survivor" lineages (Wilf et al., 2019), especially in montane rainforests where the MMC is notably diverse (Ashton, 2014). Our discovery of well-preserved, early Eocene fossils of the *Macaranga-Mallotus* clade from Laguna del Hunco adds a well-known component of living Old World rainforests to the expanding legacy of West Gondwanan paleovegetation and makes unlikely an origin of the MMC in Sunda, or anywhere in Asia.

MATERIALS AND METHODS

All fossils described here came from the early Eocene fossil caldera-lake site at Laguna del Hunco, northwest Chubut Province, Patagonian Argentina, paleolatitude ca. 47°S. Laguna del Hunco and its surrounding area have been extensively reported elsewhere for extraordinarily diverse and well-preserved fossil assemblages and exposures of varied igneous and sedimentary rocks (e.g., Berry, 1925; Petersen, 1946; Aragón and Mazzoni, 1997; Wilf et al., 2003, 2013; Barreda et al., 2020; Gosses et al., 2021; and others cited in this article). Laguna del Hunco is probably best known for preserving a large number of unique and unexpectedly old South American occurrences of plant clades, of which many have close living relatives in the West Pacific region today (Wilf et al., 2013; Kooyman et al., 2014; Wilf and Escapa, 2015, 2016; see Discussion).

Laguna del Hunco preserves a 170-m-thick local section (Wilf et al., 2003) of the Tufolitas Laguna del Hunco, an informally named, visually distinctive, white-weathering package of tuffaceous caldera-lake sediments embedded in the Huitrera Formation of the Middle Chubut River Volcanic Pyroclastic Complex (Aragón and Mazzoni, 1997; Gosses et al., 2021). Over the past two decades, intensive field investigations by international teams launched from the Museo Paleontológico Egidio Feruglio (MEF) in Trelew, Chubut, Argentina, have yielded collections of ca. 8000 specimens from Laguna del Hunco. Many fossil quarries (LH01–LH30), documented by Wilf et al. (2003) and in subsequent articles (Gandolfo et al., 2011; Deanna et al., 2020), have been excavated throughout the local profile; however, most fossils come from the ca. 60-m, densely sampled interval in the lower-middle section (Wilf et al., 2005a: figure 2). Geochronologic constraints include an ^{40}Ar-^{39}Ar age of 52.54 ± 0.17 Myr analyzed on sanidine from the uppermost strata of the underlying, caldera-forming Ignimbrita Barda Colorada (Gosses et al., 2021), setting a maximum age for all fossils reported here. Several ^{40}Ar-^{39}Ar ages have been reported from within the fossil-lake beds (Wilf et al., 2003), of which one, ash 2211A, was analyzed on sanidine and is thus considered the most reliable. Ash 2211A has a recalibrated age of 52.22 ± 0.22 Myr, as most recently discussed by Gosses et al. (2021). It sits in the middle of the densely sampled interval (slightly above quarry LH04), setting a minimum age for all fossils below its position. Nearly all the new fossils reported here, including the holotypes of both new species described below, came from quarries (see Systematics) stratigraphically bracketed by the two dated tuffs mentioned above, constraining their ages to the interval 52.0–52.7 Ma (including one sigma uncertainty). Unpublished U-Pb analyses from the local section (authors' unpublished data) indicate that all fossils from Laguna del Hunco are between ca. 52.0 Ma and 52.2 Ma.

This contribution reports two infructescences and 11 leaf fossils from Laguna del Hunco. All but one of these

fossils is housed in the Paleobotany Collections of the MEF (repository acronym MPEF-Pb; see Systematics). The remaining specimen, an infructescence, was found at Museo Jorge H. Gerhold (MJHG), Ingeniero Jacobacci, Río Negro, Argentina, in undated (possibly the 1950s) historical collections from Laguna del Hunco made by the late Rodolfo Magín Casamiquela. The quarry site is unknown, but the lithology appears to be the same as an accessible sampling level equivalent to locality LH04 of Wilf et al. (2003), which seems to be the source of nearly all historical collections from Laguna del Hunco (see Wilf, 2020). We treat the infructescences and leaves separately because they come from a highly diverse angiosperm flora (Wilf et al., 2005a) and are not found in organic attachment. However, they plausibly represent a single source species because they occur together in the same strata and are the only fossils in the assemblage referable to Euphorbiaceae.

Specimens were processed at the MEF, the Penn State Paleobotany Lab, and the University of Comahue (MJHG specimen). For the most part, we used the same equipment, software, and methods described previously for mechanical preparation, DSLR macrophotography, reflected light microscopy, epifluorescence microscopy, reversible whole-image adjustments (brightness, contrast, and color temperature), and keywording of images with morphological features (Wilf, 2012; Wilf et al., 2014; Rossetto-Harris et al., 2020, 2022). One infructescence fossil (the holotype) was CT scanned at the Penn State Center for Quantitative Imaging on a General Electric v|tome|x L300 system (General Electric, Boston, Massachusetts, USA) at 0.022 mm voxel resolution. Higher-resolution regional scans were not feasible because of the size and fragility of the specimen. Scans were collected using 120 kV voltage and 165 μA current, with aluminum for filtering on the detector. Post-processing and rendering were done using Dragonfly v. 2022.1 software (Object Research Systems, Montréal, Quebec, Canada); Photoshop v. 23 (Adobe, San Jose, CA, USA) was used to remove noise objects and stray pixels from the image perimeter. Despite the low density-contrast between the fossil and matrix and other constraints, the result is one of the only successful CT images of a fossil from the highly compressed Laguna del Hunco flora (Hermsen and Gandolfo, 2016). An image library containing full-resolution photographs of the fossils, high-resolution versions of the composed plates of fossils published here, and CT-scan stacks is deposited in Figshare and linked to this article (see Data Availability Statement).

A whitish, apparently amorphous mineral partly fills several locules of the infructescence holotype in three dimensions, along with other fossils such as insect remains from the same quarry (LH29). The replacement of organic remains by this mineral, which resembles pyrophyllite, appears to have a role in the increased three-dimensional preservation of compression fossils at LH29 compared with other Laguna del Hunco quarries, allowing the CT reconstruction reported here. We attempted to identify the mineral in situ using several configurations for Raman microscopy at the Penn State Materials Characterization Laboratory. However, the specimen's high fluorescence caused excessive spectral noise. A configuration that avoided fluorescence (deep ultraviolet laser excitation at 229 nm wavelength) truncated the spectrum below 750 cm^{-1} Raman shift, thus missing several possible inorganic materials. Only one strong peak, for carbon, emerged in the detection range, probably representing a very thin surface layer of coal. No peaks were consistent with kaolinite and gypsum, two common whitish minerals whose spectra were within the detection range. Further work will require using a wide range of instruments beyond the scope of this article. A report and technical data for the Raman experiments are deposited in the linked Figshare archive (see Data Availability Statement).

In addition to the systematic literature cited in this article, we examined living trees of *Macaranga* and *Mallotus* on various field trips (primarily in northeastern Australia, Malaysian Borneo, and Brunei) and visits to living collections (e.g., Kebun Raya Bogor, Indonesia) over several years. We also examined specimens from several herbaria, primarily using high-resolution digital resources because of pandemic travel restrictions during the research. Digital herbarium collections that were particularly useful included the Naturalis Biodiversity Center, Leiden (L, https://bioportal.naturalis.nl), the United States National Herbarium of the Smithsonian Institution (US, https://collections.nmnh.si.edu/search/botany), and JSTOR Global Plants (https://plants.jstor.org) for its emphasis on type material. To compare the fossil foliage, we also consulted an open-access image compilation of cleared and x-rayed leaves (Wilf et al., 2021). Figure 1 shows a selection of reference specimens with features observed in the fossils. Leaf architecture terminology follows that of Ellis et al. (2009). For easier readability of the large number of taxa mentioned in the text, we restricted the use of botanical authorities to the minimum necessary to define new taxa. Authorities for all nomenclature used here may be found in standard databases such as Plants of the World Online (https://powo.science.kew.org) and Tropicos (https://www.tropicos.org) or, for fossil taxa, in the respectively cited paleobotanical literature.

RESULTS

Systematics

Family—Euphorbiaceae Juss. sensu stricto

Subfamily—Acalyphoideae Beilschm.

Tribe—Acalypheae Dumort.

Genus—*Tineafructus* Wilf, A. Iglesias & Gandolfo, gen. nov.

Generic diagnosis—As for the type species, due to monotypy.

Type species—*Tineafructus casamiquelae* Wilf, A. Iglesias et Gandolfo, sp. nov. (Figures 2–5).

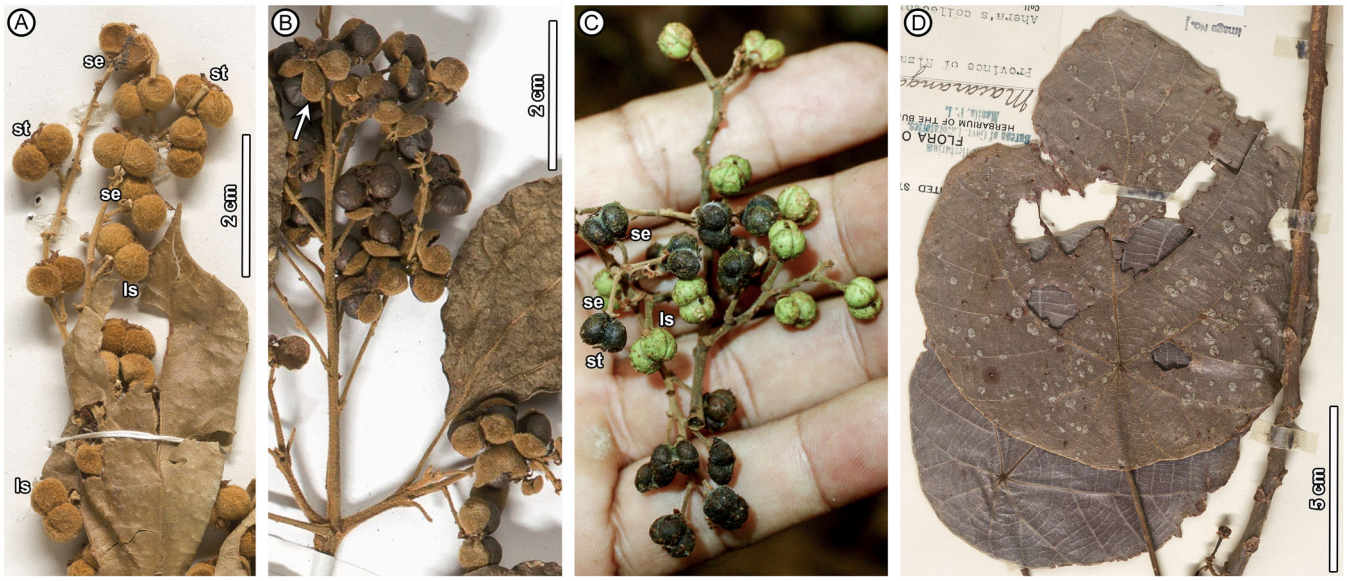

FIGURE 1 Selected extant reference material with features comparable to the new Patagonian fossils (Figures 2–6). (A) *Mallotus repandus*, racemose infructescence with two-loculed fruits before dehiscence. Note pedicels and persistent sepals (se), columella dividing the two convex locules, loculicidal sutures (ls), and persistent, plumose stigmas (st; US 01259288, Haragama, Central Province, Sri Lanka). (B) *Mallotus repandus*, paniculate infructescence in various stages of loculicidal-septicidal dehiscence, leaving persistent seeds. Note globose, dark, axile seeds and four-lobed dehisced capsules with pedicel remnants (arrow; L 3800011, Namtok Samlan National Park, Saraburi Province, Thailand). (C) *Macaranga gigantea*, fresh paniculate infructescence. Note light brown loculicidal capsules with sutures (ls); lenticular, axile, persistent seeds with purple arils, paired persistent sepals (se), and persistent short-plumose stigmas (st; Bukit Tagar, Selangor, Malaysia). (D) *Macaranga bicolor*, peltate leaves with numerous near-circular patches of epiphyllous lichens (US 01280419, Province of Rizal, Philippines). Image information: A and D, available via https://collections.nmnh.si.edu/search/botany under Creative Commons CC0 license. B, downloaded from https://bioportal.naturalis.nl/?language=en under Creative Commons CC0 1.0 license. C, Photograph by Ahmad Fuad Morad, cropped from the original, available under Creative Commons CC BY-ND 2.0 license at https://www.flickr.com/photos/adaduitokla/6682802205/in/photostream.

Holotype here designated—MPEF-Pb 7989a,b (part, counterpart; Figures 2–4, except Figure 3I), from Laguna del Hunco, Tufolitas Laguna del Hunco, Huitrera Formation, early Eocene (Ypresian), quarry LH29 of Deanna et al. (2020), collected 21 March 2019 by P. Wilf, M. Gandolfo, P. Puerta, and others. Repository: Museo Paleontológico Egidio Feruglio, Trelew Argentina.

Paratype—MJHG 26 (Figure 5), collected by R. M. Casamiquela at Laguna del Hunco, precise location and date unknown. Repository: Museo Jorge H. Gerhold, Ingeniero Jacobacci, Río Negro, Argentina.

Additional specimens—Dispersed capsules: MPEF-Pb 7983, 7984 (Figure 3I), Laguna del Hunco quarry LH29, collected 21 March 2019 by P. Wilf, M. Gandolfo, P. Puerta, and others.

Etymology—The generic name, *Tineafructus*, translates as "moth fruit," from the Latin *tinea* (moth), referencing the moth-like appearance of the individual compressed fruits in the type species, including plumose stigmas reminiscent of moth antennae. The species epithet honors Rodolfo Magín Casamiquela (1932–2008), a renowned Argentine vertebrate paleontologist and anthropologist (Haller, 2009). Dr. Casamiquela worked extensively in his native Patagonia and published a fossil frog species from Laguna del Hunco, *Shelania pascuali* (Casamiquela, 1961, 1965). He collected the here-described paratype and other plant material and deposited it in Museo Jorge H. Gerhold, which he founded and named in honor of his uncle.

Diagnosis

Panicle-bearing capsules closely spaced on secondary axes. Capsules short-pedicellate with persistent calyx, obovate, ca. two times wider than long; basal and lateral margins convex and smoothly rounded; without spines or wings; apex bilobed. Capsules two-locular, with two narrow-lenticular, axile seeds that persist after dehiscence and two persistent, projecting stigmas. Dehiscence loculicidal or loculicidal-septicidal; fully opened capsules four-lobed. Stigmas thick, plumose, and unbranched, the projecting portion nearly as long as the apical margin of the subtending valve.

Specific description

Infructescences (Figures 2, 3 and 5) are paniculate and axillary on a branch segment (holotype; Figure 2A) with a preserved length of 66 mm. The preserved primary axes (Figures 2B, 2C, 5A) are at least 44–47 mm long by 2.2–2.6 mm wide. At least eight secondary axes are preserved in the holotype, preserved length to 20 mm (holotype) and

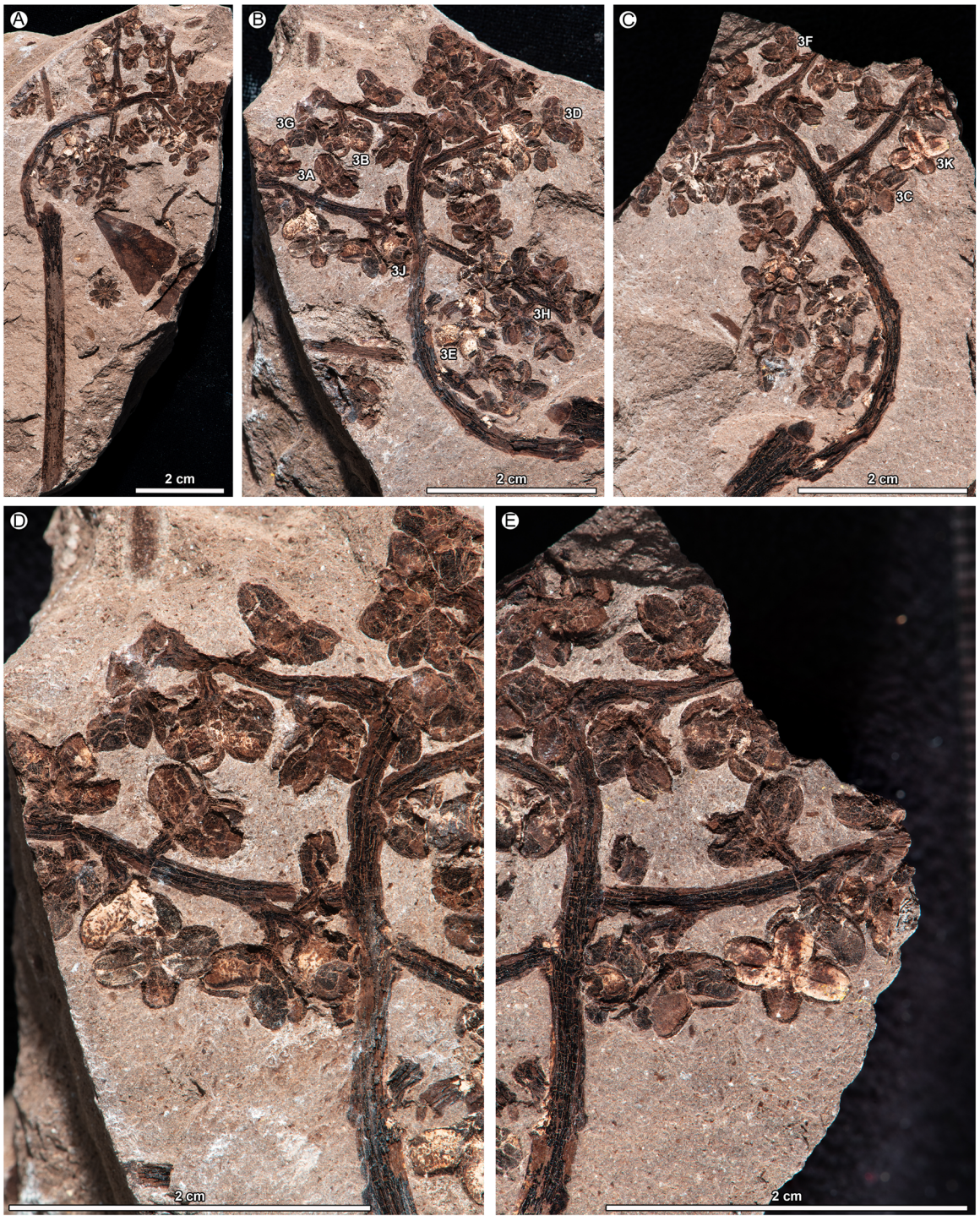

FIGURE 2 *Tineafructus casamiquelae* gen. et sp. nov., holotype (MPEF-Pb 7989a,b; part 7989a: A, B, D; counterpart 7989b: C, E), general aspect. Labels 3A–K in panels B and C indicate locations of detailed illustrations in Figure 3. (A) Full view showing panicle of ca. 50 fruits axillary on a long axis, as well as unrelated reproductive structures, leaves, and insect remains. (B–F) Intermediate focal distances showing infructescence structure; preservation of fruits (several with persistent stigmas preserved), seeds, and capsules (see Figure 3 for detailed morphology); dehiscence stages; and whitish, amorphous mineral replacement of some plant material (see text).

14.7 mm (paratype). Approximately 50 fruits (holotype; 22 on the paratype) are positioned laterally and terminally (Figure 5B), densely spaced on the secondary axes, up to perhaps 10 preserved per axis (holotype), preserved both closed and in various stages of dehiscence. *Fruits* (Figures 2–5) are two-loculed capsules, clearly derived from a superior ovary; they are subtended by two free, narrow-triangular, persistent sepals (e.g., Figure 3A, F) that project ca. 0.7 mm from the top of the pedicel, either laterally or slightly reflexed; pedicels are short and stout, to 1.4 mm

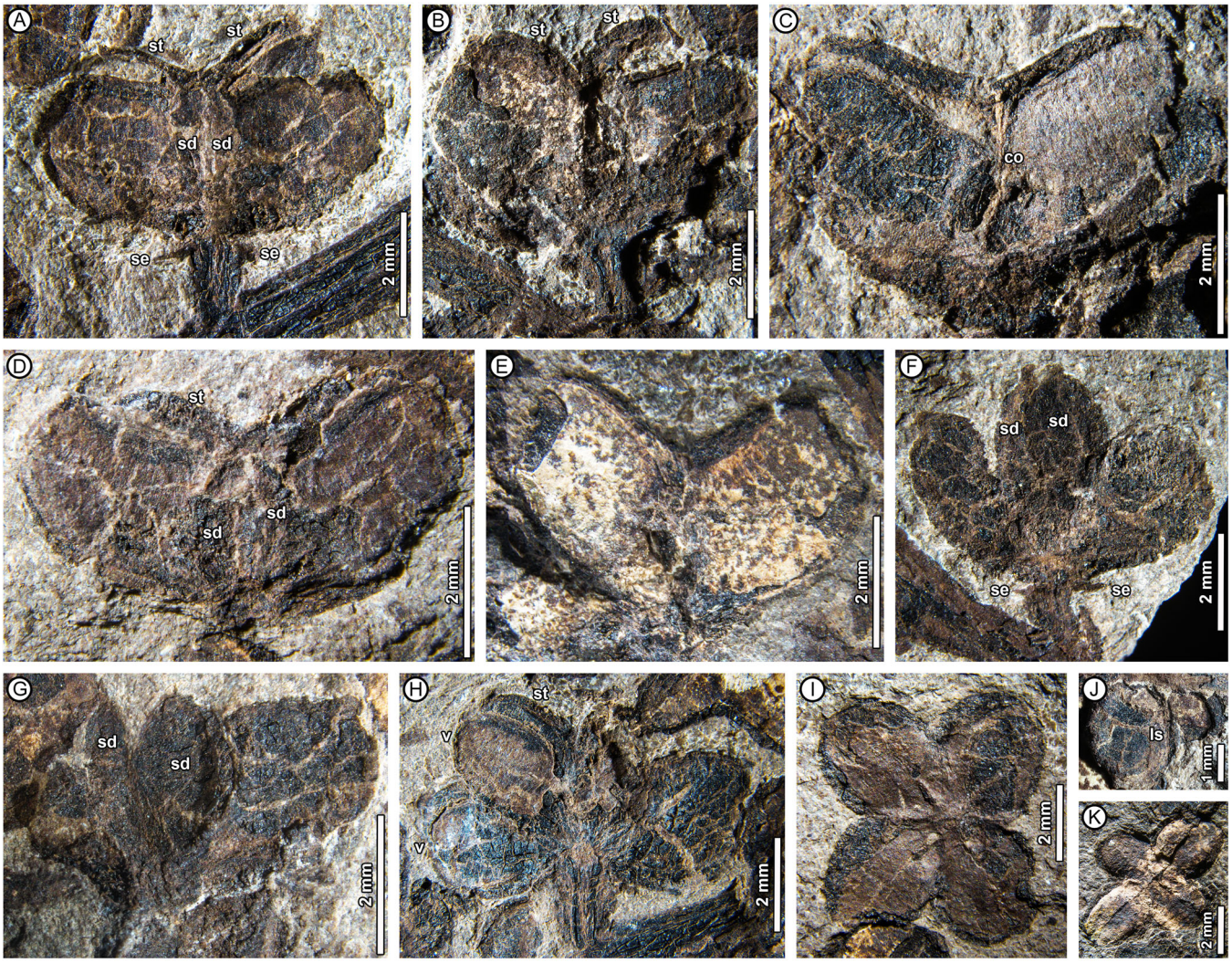

FIGURE 3 *Tineafructus casamiquelae* gen. et sp. nov., holotype (MPEF-Pb 7989a,b; part 7989a: A, B, D, E, G, H, J; counterpart 7989b: C, F, K) and additional specimen (MPEF-Pb 7984, panel I), details of fruits, seeds, and dehiscence. Panel locations are labeled in Figure 2. (A–E) Undehisced fruits showing pedicels; narrow sepals (se; cf. Figure 1C); columellae (co) dividing paired locules; crescent-shaped, coalified compressions and impressions of paired, axile, lenticular seeds (sd); and paired, persistent plumose stigmas (st; cf. Figure 1A). In E, locules are three-dimensionally replaced with an unidentified whitish mineral (see text). (F, G) Partially disintegrated loculicidal or possibly loculicidal-septicidal capsules, revealing paired axile, persistent, lenticular, apiculate seeds (sd), their shape in compression dependent on their rotation (compare with Figures 1C, 4). (H–K) Dehiscent loculicidal capsules (cf. Figure 1B, C). H, Initial dehiscence with loculicidal separation of locule at left into two offset valves (v) subtending one large, plumose, persistent stigma (st). I, Fully dehisced four-lobed capsule with strong longitudinal lineations on each lobe and persistent pedicel remnant at the base (center). J, Lateral view of a locule beginning to dehisce (see Figure 1B; 3D view marked in Figure 4), showing convex locule shape and prominent loculicidal suture (ls; oriented vertically). K, Fully dehisced four-lobed capsule with longitudinal lineations on each lobe, minor apical splitting of lobes, and whitish mineral replacement.

long and 1.3 mm wide, with ca. 90–135° insertion on the axis. The fruit body before dehiscence is bilaterally symmetrical, obovate, and more than twice as wide as long (to 3.1 mm long by 6.5 mm wide), with a smoothly curved, convex basal and lateral margin and a less curved, bilobed apical margin. Each fruit is spineless and has two locules separated by a narrow columella (e.g., Figure 3C), two seeds (one per locule; Figures 3F, 3G, 4, 5C), and two projecting stigmas (one per locule; Figures 3A, 3B, 3H, 4, 5B); there is no evidence of fruit wings. The fruit walls are strongly convex (Figures 3J, 4). Stigmas (stylodia) are persistent, plumose, unlobed, thick (0.3–0.6 mm wide), and elongate, nearly as long (to 2.8 mm) as the apical margin of the subtending locule, with a well-marked longitudinal axis and a rounded apex that allows them to be distinguished from the adjacent fruit wall when the two are resting in contact (e.g., Figure 3H). Pollen is not preserved. Dehiscence is loculicidal to possibly loculicidal-septicidal (Figures 3F, 3G, 5C) and preserved in several orientations and stages (Figures 3H–K, 4, 5A), suggesting tardy (i.e., asynchronous) dehiscence. Fully dehisced capsules (Figures 3I, 3K, 5A; see also Figure 1B) are four-lobed; the opened sutures make two lobe incisions that separate the two obovate valves of the fruit, which are flattened in mirror symmetry and joined at their basal hinge. The two additional lobe incisions originate from the persistent apical lobes of the two bilobed valves.

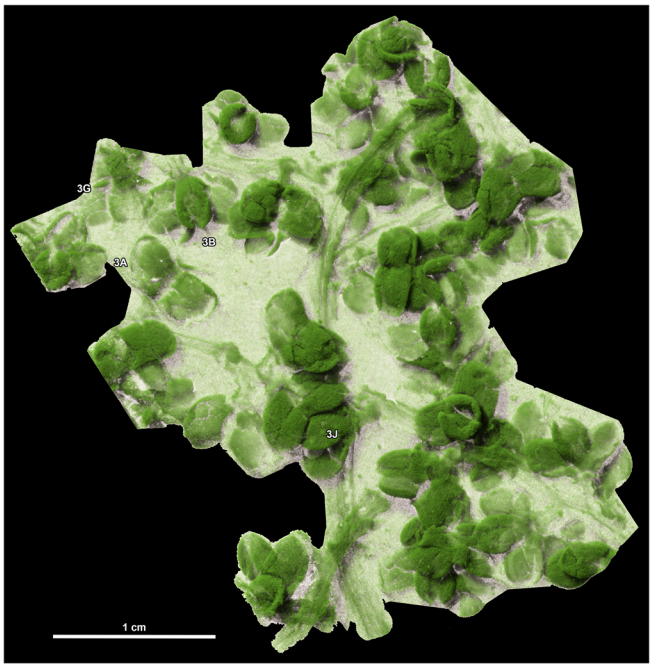

FIGURE 4 *Tineafructus casamiquelae* gen. et sp. nov., holotype (MPEF-Pb 7989a), CT-scan rendering. The view is from the inside of the rock toward the surface, mirrored on the vertical axis to expedite comparisons with external views (Figures 2, 3). Some reference points corresponding to Figure 2B and the panels of Figure 3 are labeled accordingly. The overall capture differs because the CT view is in the opposite direction and samples deeper in the matrix than the surface views (Figures 2, 3). Notable features (not labeled to reduce clutter; refer to labeled features in Figure 3) include the paired locules of each fruit, separated by a columella; numerous paired, thickened, lenticular axile seeds within the fruits or exposed by rupturing fruits; persistent paired sepals; and paired plumose stigmas. Label "3J" indicates the submerged edge of the same capsule dehiscing in lateral view whose other edge-suture is shown at the surface in Figure 3J (also Figure 2B).

Open valves preserve the pedicel remnant (Figure 3I) and show ca. 0.3-mm-thick walls and a marked longitudinal lineation, along which some valves partially split from the apex (Figure 3K). These distinctive features make the capsules recognizable even when found dispersed. *Seeds* (Figures 3F, 3G, 4, 5C) are narrow-lenticular, length 3.1–4.0 mm, width 1.5–1.8 mm (0.5–1.0 mm width seen in lateral view, as most are preserved: Figure 5C), oppositely attached to the columella with presumed axile placentation, thickened, and persistent as the enclosing valves disintegrate or dehisce. Seed sculpturing, arils, and other details are not preserved; no dispersed seeds were found.

Genus—*Macaranga* Thouars

Species—*Macaranga kirkjohnsonii* Wilf, A. Iglesias et Gandolfo, sp. nov. (Figure 6)

Holotype here designated—MPEF-Pb 7993a,b (Figure 6A), from Laguna del Hunco, Tufolitas Laguna del Hunco, Huitrera Formation, early Eocene (Ypresian), quarry LH04 of Wilf et al. (2003), collected 3 December 2002 by P. Wilf, M. Gandolfo, K. Johnson, and others. Repository: Museo Paleontológico Egidio Feruglio, Trelew Argentina.

Paratypes—MPEF-Pb 7990a,b and 7991a,b from Laguna del Hunco quarry LH02; MPEF-Pb 195, 7992, and 7994–7997 from quarry LH04 (Figure 6D, E: MPEF-Pb 7996a,b); MPEF-Pb 7998 (Figure 6B) from quarry LH06; and MPEF-Pb 7999 (Figure 6C), a float specimen; these were collected on various dates in 1998, 1999, and 2002 by P. Wilf, K. Johnson, M. Gandolfo, P. Puerta, and others. Quarries and stratigraphic positions are as reported by Wilf et al. (2003). Repository: Museo Paleontológico Egidio Feruglio, Trelew Argentina.

Etymology—The specific epithet honors Kirk R. Johnson, paleobotanist and Sant Director of the Smithsonian National Museum of Natural History (Washington, D.C., USA). Dr. Johnson discovered the first of these leaves at Laguna del Hunco during the late 1990s and noted their similarity to *Macaranga*.

Specific diagnosis

Petiole insertion eccentrically peltate, well inside the margin. Blade ovate, untoothed, unlobed or incipiently lobed, symmetrical to asymmetrical. Base convex, rounded or slightly cordate; apex acute, not mucronate. Midvein, first pair of secondary veins, and several minor secondary veins of the agrophic complex radiate directly from the petiole insertion with minimal offsets. Primary venation pinnate; secondary venation eucamptodromous to brochidodromous; secondaries usually 5–7, often forking well inside the margin. Basal secondary-pair angle greater than or equal to the second pair; spacing between the first and second pair of secondaries less than or equal to that between the second and third pair. Agrophic veins simple and well-developed. Tertiary veins mostly thick, strongly to weakly percurrent, variably angled, concentric around the petiole insertion, and moderately spaced. Marginal ultimate venation looped.

Specific description

Petiole width is ca. 2.6 mm, and the attachment is peltate eccentric with insertion 9–26 mm from the margin; the insertion area on the blade is large and elliptical (long axis 2.2–3.6 mm). *Laminar size* is notophyll to macrophyll; length of nearly complete leaves is to 11.6 cm, width to 8.2 cm, l:w ratio 1.0–2.8:1. Blade areas for these leaves (listed as "cf. *Macaranga*/*Mallotus*") were reconstructed using vein scaling and other methods as 3605–19,500 mm^2 (Merkhofer et al., 2015). One specimen (Figure 6C) preserves at least a 10.4-cm length in a basal fragment of an even larger blade. *Shape* is ovate and symmetrical to strongly asymmetrical (Figure 6D), the base convex to smoothly rounded (Figure 6C) or slightly cordate (Figure 6B); the apex is acute to slightly acuminate (Figure 6A), not mucronate. The blade is unlobed or incipient-lobed (Figure 6A, arrow), and the margin is untoothed and thickened (Figure 6E). *Primary venation* is pinnate, deflected (Figure 6A) or not at

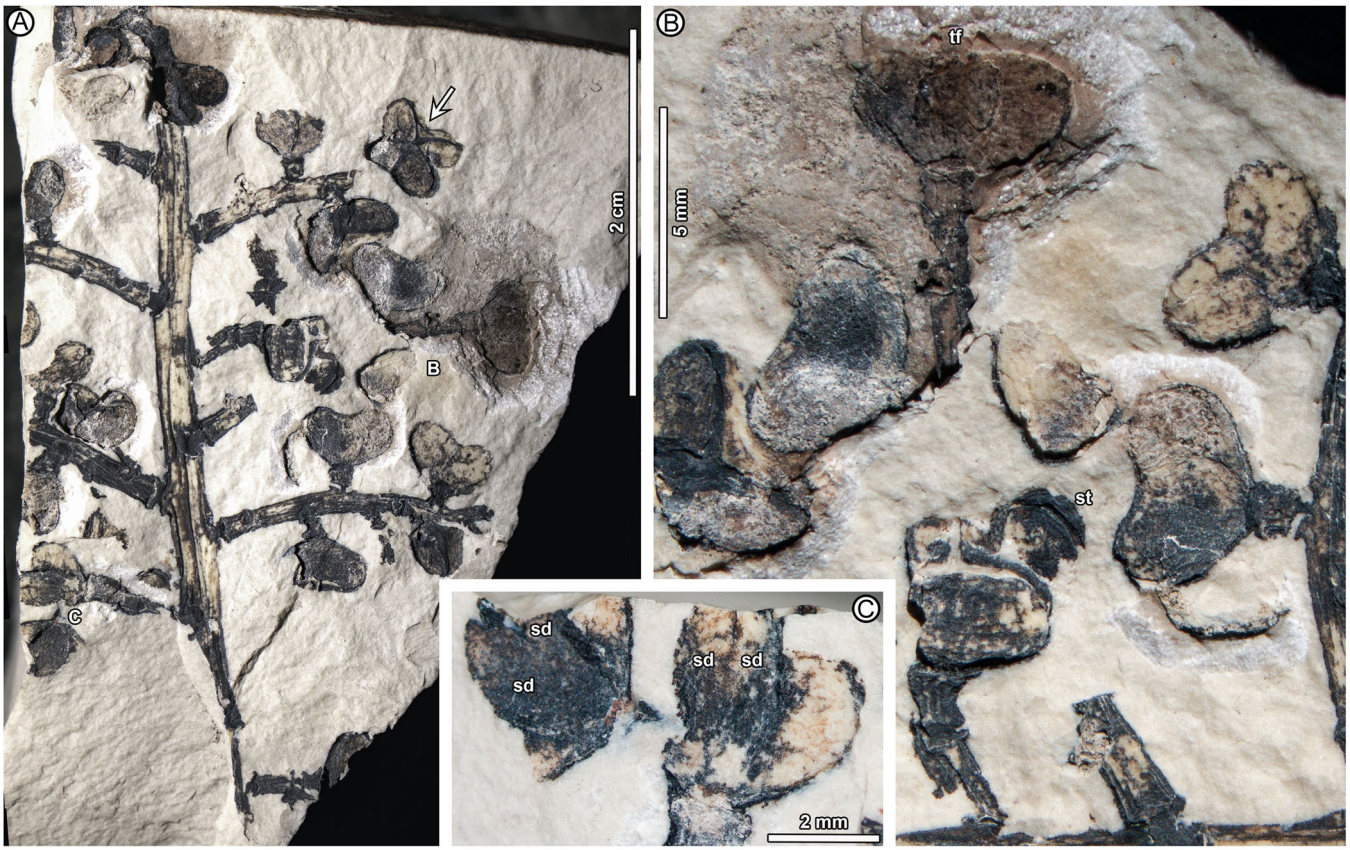

FIGURE 5 *Tineafructus casamiquelae* gen. et sp. nov., paratype (MJHG 26), preserved in white-weathered matrix. Locations of insets B and C as marked on panel A. (A–C) Panicle with ca. 22 fruits exposed, preserving a terminal fruit (tf); two disintegrating or loculicidal-septicidal capsules revealing paired, axile, lenticular seeds (sd; cf. Figure 1C); a fully dehisced capsule (arrow; cf. arrow in Figure 1B), and a single remaining plumose stigma (st).

secondary junctions. The midvein, the first pair of major secondaries, and several minor secondaries diverge from the petiole insertion without offsets. *Major secondaries* are eucamptodromous, in ca. 5–7 subopposite to offset pairs, usually dichotomizing near the margin, some becoming weakly brochidodromous near the apex; the secondary course is often deflected at tertiary junctions. Major secondaries are nearly regular in angle and spacing; the divergence angle of the first pair is at the same angle or slightly more obtuse than the second, and there is no large gap along the midvein between the first two pairs, which may be closer together than the second and third pairs. Intersecondaries are absent. *Agrophic veins* are prominent and simple. Minor secondaries of the agrophic veins are prominent, usually restricted to the basal half of the blade, dichotomizing to form several ranks of weak loops, including a final rank of looped marginal ultimate venation. Minor secondaries below the first pair of major secondaries radiate from the petiole insertion; the basalmost minor secondaries may fork very close to the insertion point (Figure 6E). *Tertiary veins*, both intercostal and epimedial, are thick, moderately spaced, and mostly opposite percurrent (sometimes alternate or reticulate) and basally concentric around the petiole insertion, with course variably straight to convex and deflected at quaternary junctions. The tertiary angle to midvein is obtuse and variable, increasing basally. *Fourth- and fifth-order venation* is random reticulate; *sixth-order venation* is regular reticulate; freely ending veinlets are indistinctly preserved. Leaf damage types (DTs) previously noted (Wilf et al., 2005b) include fungal lesions (DT83; Figure 6B; see Discussion), circular and polylobate hole feeding (DTs 1, 4, and 5, on several specimens; Figure 6E), and a small serpentine mine (DT41, on MPEF-Pb 7994).

Informal prior references

The *Macaranga kirkjohnsonii* leaves were previously referenced, without descriptions or illustrations, in survey and paleoecological papers as "probably Euphorbiaceae" (Wilf et al., 2003: 125) and as morphotype TY046, "cf. *Macaranga* or *Mallotus*" (Wilf et al., 2005a: table A2; Merkhofer et al., 2015: data supplement S1). Images of these fossils, provided by P. Wilf, were analyzed by Nucete et al. (2012), and the material was additionally discussed by Lee et al. (2010) and Conran et al. (2016).

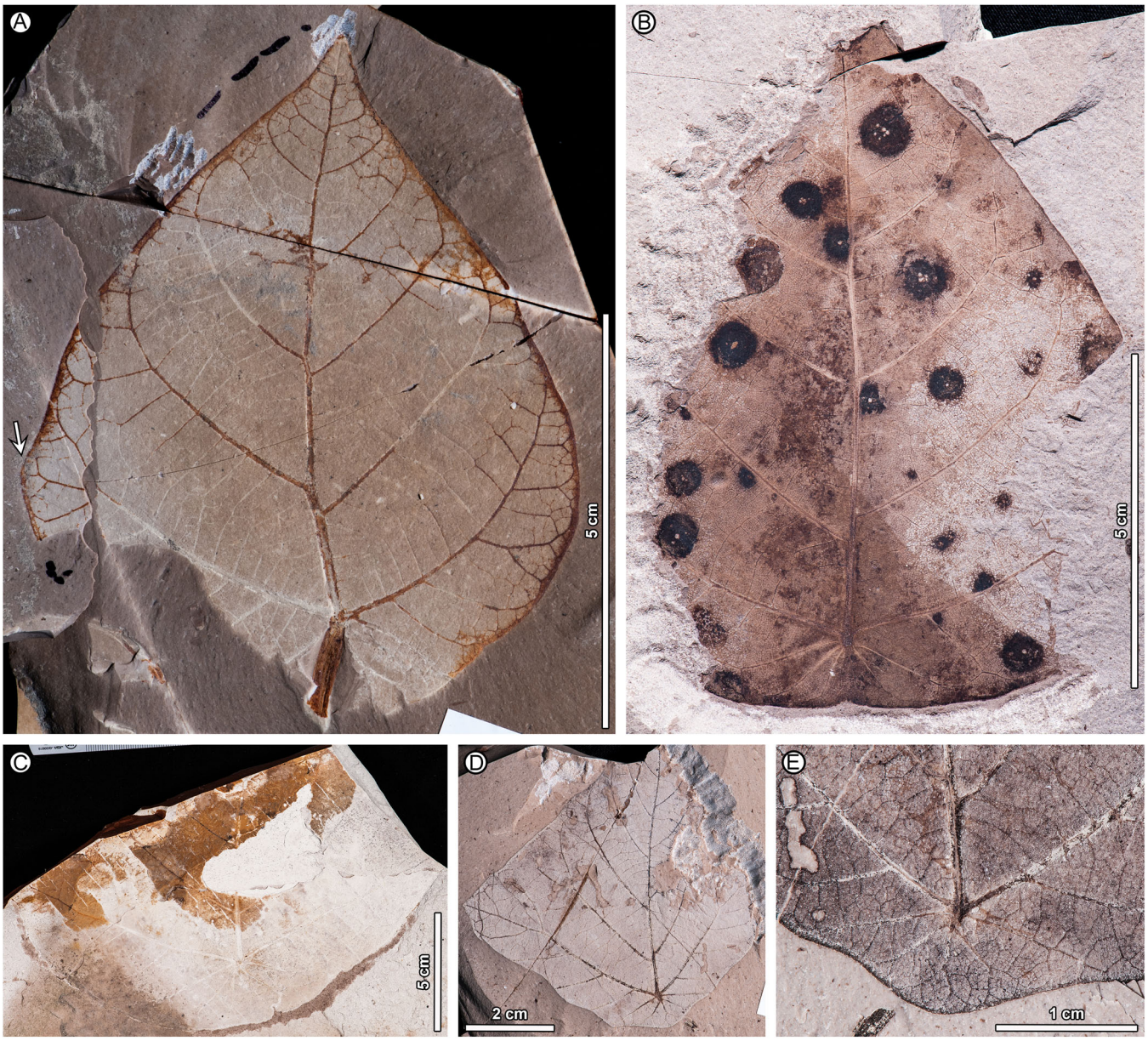

FIGURE 6 *Macaranga kirkjohnsonii* sp. nov. (A) Holotype, showing eccentric petiole insertion, an incipient lobe (arrow), simple agrophic veins, and other described leaf-architectural features (MPEF-Pb 7993b). (B) Specimen with cordate base and numerous near-circular fungal lesions (DT83, see Discussion; MPEF-Pb 7998). This specimen was referenced as the informal exemplar for morphotype TY046, "cf. *Macaranga* or *Mallotus*" by Wilf et al. (2005a: table A2) and as the exemplar and only specimen of DT83 (Labandeira et al., 2007). (C) Large specimen with a smoothly rounded base (MPEF-Pb 7999). (D, E) Specimen part and counterpart with strongly asymmetrical, possibly lobed blade, well-preserved venation, and hole-feeding insect damage (D, MPEF-Pb 7996a; E, MPEF-Pb 7996b).

DISCUSSION

Remarks on *Tineafructus casamiquelae* gen. et sp. nov.

Tineafructus casamiquelae presents a highly distinctive combination of paniculate infructescences bearing short-pedicellate, two-loculed, two-seeded, spineless, tiny, bilobed, and loculicidal capsular fruits with paired persistent, elongate, plumose, and unlobed stigmas (Figures 2–5). To our knowledge, this suite of characteristics is uniquely found, among all angiosperms, in a subset of species of the MMC (Figure 1A–C), which more often have three-locular, spiny fruits (Radcliffe-Smith, 2001; Webster, 2014). Few angiosperm families have species that plausibly resemble the new fossils, including the Sapindaceae, Phyllanthaceae (part of Euphorbiaceae s.l.), and Euphorbiaceae s.s. In Sapindaceae, some genera, such as *Harpullia* and *Arytera*, may have two-loculed, loculicidal fruits that resemble the fossils (Leenhouts and Vente, 1982). However, the fruits of these

sapindaceous genera differ from the fossils in many characteristics. For example, they often carry visible remnants of their thin, often twisted styles, which have stigmatic lines, unlike the obscured styles and the exserted, broad, plumose stigmas seen in the fossils.

Fruits of Phyllanthaceae (Radcliffe-Smith, 2001; Wurdack et al., 2004; Hoffmann et al., 2006; Webster, 2014; Utteridge, 2021b) have two seeds per locule, compared with one seed per locule in Euphorbiaceae s.s. and in the fossils; one of the two seeds sometimes aborts, a condition that would not be visible in the fossils. Moreover, Phyllanthaceae usually have nonpaniculate infructescences and three-or-more-loculed fruits with typically smooth and bifid stigmas. In contrast, the fossils' paniculate infructescences, two-loculed bilobed fruits, and plumose, undivided stigmas are rare features in Phyllanthaceae and do not appear in combination in that family. *Didymocistus* (a monotypic neotropical genus) produces panicles of two-loculed, short-pedicelled, loculicidal capsular fruits with thickened, persistent stigmas. However, unlike the new fossils, the fruits are strongly obcordate, and the stigmas are markedly fimbriate.

Within the Euphorbiaceae s.s., the feature set of the fossils is unique to the MMC (Radcliffe-Smith, 2001; Webster, 2014). The few euphorbiaceous genera with plumose, undivided stigmas outside the MMC are also in the Acalypheae (e.g., *Mareya*, *Lobanilia*, *Micrococca*, and *Homonoia*) and have at least three locules. Even within the MMC, most species have spiny fruits with three (or more) locules. Nonetheless, many species in both *Macaranga* and *Mallotus* have two-loculed, spineless fruits similar to the fossils (Whitmore, 2008; Sierra et al., 2010; Figure 1A–C), as discussed below. Thus, we found the closest generic affinities to the fossils in *Macaranga* and *Mallotus*.

Despite a long history of study of the highly diverse and variable Euphorbiaceae s.l. and several molecular investigations (as cited earlier), no comprehensive morphological character matrix exists to test the phylogenetic position of the new infructescence fossils within the family. To date, there is also no suitable morphological matrix for the MMC with complete species-level coverage of both constituent genera and the inclusion of most characters preserved in the fossils. Many keys of the MMC species exist (e.g., Slik et al., 2000; Whitmore, 2008; van Welzen et al., 2010, 2020), but most nodes in the keys depend on characters not preserved in the fossils. However, Sierra et al. (2010) developed a 90-character morphological matrix for their phylogenetic analysis of *Mallotus* that incorporated most *Mallotus* species along with several species of *Macaranga* and other close relatives as outgroups, such as *Hancea* and *Blumeodendron*. We scored the fossils for 17 applicable fruiting characters in the Sierra et al. (2010) matrix, along with the most similar-scoring extant species, after filtering out a few taxa that do not have two locules (Table 1). We decided not to attempt a phylogenetic analysis of the fossils using the Sierra et al. (2010) matrix because of the need for significantly more coverage of the diverse *Macaranga* species and scoring adjustments to better account for fossil preservation.

Unsurprisingly, no living species in the data set of Sierra et al. (2010) has the same character-state combination as the Eocene fossils from Patagonia (Table 1). Similarities to the fossils in the filtered *Macaranga* species (Table 1) include small fruits (character 85) and lenticular seeds (character 39; Figure 4). However, the fossils have long stigmas (Figure 3), whereas most *Macaranga* species (Davies, 2001; Radcliffe-Smith, 2001; Whitmore, 2008; Figure 1C), like those in Table 1, have short stigmas (character 84). Only a few species of *Mallotus* have lenticular seeds or loculicidal-first (loculicidal or loculicidal-septicidal) dehiscence like the fossils (Sierra et al., 2010). *Mallotus* species with lenticular seeds are not similar to the fossils (e.g., all have three locules, such as *M. blumeana* and *M. sphaerocarpa*), but

TABLE 1 *Tineafructus casamiquelae* gen. et sp. nov. and the most similar living species, based on matrix of Sierra et al. (2010).

	Character																
Species	**25**	**26**	**28**	**29**	**30**	**31**	**33**	**34**	**35**	**36**	**39**	**80**	**82**	**84**	**85**	**87**	**88**
Tineafructus casamiquelae	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**0**	**0**	**0**	**1**	**1.4**	**2**	**2.8**	**3.1**	**0.3**	**3.1**
Macaranga denticulata	**0**	**0**	**0**	**0**	0	0	0	2	**0**	**0**	0	**1.5–1.8**	**2**	1.3–1.5	**3–4.5**	0.1–0.2	1.5
Macaranga gigantea	**0**	**0**	**0**	1	?	0	0	**0**	**0**	**0**	**1**	?	**2**	?	?	?	?
Mallotus didymochryseus	**0**	**0**	**0**	**0**	0	**1**	**1**	**0**	**0**	**0**	0	?	**2**	**2.3–2.7**	10–12.5	0.5	?
Mallotus leucocarpus	**0**	**0**	**0**	**0**	**1**	**1**	0	3	**0**	1	0	**1–1.5**	**2**	?	13.5–13.5	**0.3**	5.5
Mallotus philippensis	**0**	**0**	**0**	**0**	**1**	**1**	0	3	**0**	**0**	0	**0.5–2**	**2–3**	?	4–12	**0.3–0.5**	?
Mallotus repandus	**0**	**0**	**0**	**0**	**1**	**1**	0	3	**0**	**0**	0	?	**2–3**	1.5–2.5	5–11	0.5–1	**3–7.5**

Notes: Character numbering, definitions, and scores of extant species are found in appendices 1 and 3 of Sierra et al. (2010). Bold indicates fossil matches or overlaps, allowing 0.1 mm measurement discrepancies for some characters. Scores for the new fossils, discrete characters: 25, Pistillate inflorescence (0), racemes or panicles. 26, Pistillate bracts enclosing the flowers (0), absent. 28, Pistillate flower calyx persistence (0), persistent in fruit. 29, Pistillate flower sepal fusion (0), free to basally connate. 30, Pistillate sepal shape (1), narrowly triangular. 31, Stigmatic surface (1), plumose. 33, Fruit dehiscence (1), tardily dehiscent. 34, Fruit opening sequence (0), loculicidal only, although loculicidal-septicidal dehiscence (3) is also a possibility. 35, Fruit wings (0), absent. 36, Fruit spines (0), absent. 39, Seed shape (1), lenticular. Continuous characters, as shown: 80, Pistillate pedicel length, mm. 82, Number of locules in ovary. 84, Stigma length, mm. 85, fruit length, mm. 87, Fruit wall thickness, mm. 88, Fruit column length, mm. *Macaranga gigantea* was coded as unknown for locule number by Sierra et al. (2010), but it is a two-loculed species (e.g., Figure 1C; Davies, 2001).

several species with loculicidal-first dehiscence, such as *M. repandus*, appear in Table 1. In summary, the species scores in Table 1 collectively overlap with the fossils; they strongly support the inclusion of the fossils in the MMC and slightly favor *Macaranga*, but there is also support for *Mallotus* affinities.

A second comparison of the fossils with living species is made possible by Slik and van Welzen (2004), who presented non-dichotomous spot characters for 53 *Macaranga* and 25 *Mallotus* species found in Borneo. From these spot-character lists, 28 *Macaranga* and one *Mallotus* (*M. repandus*; Figure 1A, B) species have two-locular fruits. Of those, 12 *Macaranga* species match the fossils with the spot characters of panicles, no accrescent bracteoles, and lateral and spineless fruits (*Macaranga conifera*, *M. costulata*, *M. didymocarpa*, *M. endertii*, *M. gigantea*, *M. hosei*, *M. pearsonii*, *M. pruinosa*, *M. puberula*, *M. rufescens*, *M. winkleri*, and *M. winkleriella*). *Macaranga gigantea* was also treated in the study by Sierra et al. (2010; Table 1, Figure 1C). *Mallotus repandus* joins the 12 *Macaranga* species just listed if we allow that it sometimes has a panicle infructescence (Figure 1B). *Macaranga* is considered to more often have panicles (Figure 1C) than racemes and *Mallotus* the reverse (Figure 1A); however, this difference is not consistent (Sierra and van Welzen, 2005; van Welzen et al., 2009; Sierra et al., 2010). Thus, the Borneo species comparison also supports the affinities of the fossils with the MMC but not to *Macaranga* or *Mallotus* exclusively.

Our observations establish that the affinities of the early Eocene *Tineafructus* fossils from Patagonia are in the acalyphoid Euphorbiaceae, particularly with the closely related extant genera *Macaranga* and *Mallotus*. The new generic name *Tineafructus* accommodates this uncertainty in the precise relationships of the fossils with living genera. The most suitable alternative generic name is *Euphorbiotheca* (Reid and Chandler, 1933); however, that name was defined, without any diagnostic characters given, for fruits assignable only at the family level and not to lower taxonomic levels in Euphorbiaceae like the new fossils. The diagnosis of *Mallotocarpon* (Shukla and Mehrotra, 2019) required capsular fruits with three locules and thick trichomes, neither of which applies to the new fossils. Other names used for fossil fruits of Euphorbiaceae (see introduction) apply to non-acalyphoid subfamilies.

More features of *Tineafructus casamiquelae* suggest affinities with *Macaranga* than to *Mallotus*, including panicle infructescences with thick axes (F. Slik, University of Brunei, Darussalam, personal communication, 2022), paired sepals (more common in *Macaranga* than in *Mallotus*, per Figure 1; Whitmore, 2008; van Welzen, 2020), and the combination of tiny, two-loculed spineless fruits with lenticular seeds. On the other hand, the elongated, plumose stigmas of the fossils are more suggestive of *Mallotus*. Of all extant species considered, we found perhaps the closest morphological similarity to the *Tineafructus* fossils in *Macaranga gigantea* (Figure 1C) and *Mallotus repandus* (Figure 1A, B). Considering the early Eocene age of the material and the limitations of inference from one plant organ type (infructescences), a conservative placement of the fossils would be the stem lineage of the MMC, thus providing a minimum divergence of 52 Ma of the MMC from other acalyphoid Euphorbiaceae.

Remarks on *Macaranga kirkjohnsonii* sp. nov.

Most *Macaranga kirkjohnsonii* leaves (Figure 6) come from quarry LH04, which appears to be the same provenance as the *Tineafructus casamiquelae* paratype (Figure 5; see Materials and Methods). Images of the leaf fossils were provided to Monica Nucete for a revision of the MMC fossil record. Nucete et al. (2012) determined that the fossils' affinity to the MMC or Euphorbiaceae could not be confirmed because of the lack of nectaries or domatia and the nonpreservation of cuticles, glands, and hairs. We recently re-prepared and re-examined all the relevant leaf material from Laguna del Hunco and confirmed that nectaries, domatia, glands, and other documented but hard-to-preserve surficial features of MMC foliage (Hussin et al., 1996; Fišer Pečnikar et al., 2012) are not preserved in the fossils. The preservation quality is sufficient (Figure 6) to determine that nectaries and domatia are probably genuinely absent unless they are located on the petiole and obscured by the blade. Nevertheless, nectaries and domatia are absent in numerous living MMC species (Fiala and Maschwitz, 1991; Radcliffe-Smith, 2001; Whitmore, 2008). Therefore, the absence of those features is not diagnostic.

We agree with Nucete et al. (2012: table 2) that many architectural features often used to assign leaf fossils to *Macaranga* or *Mallotus* are convergent among genera in several non-euphorbiaceous families and that cuticular and other surficial characters are usually needed for confident identification of a fossil leaf to the MMC. However, most of the examples of convergence discussed by Nucete et al. (2012) involved nonpeltate foliage. The fossils discussed here are strongly peltate (Figure 6), a conspicuous feature in many MMC species. Peltate insertion of the petiole is a biomechanically specialized trait and is not widespread among angiosperms (Wunnenberg et al., 2021); thus, its presence in the fossils rules out many potential affinities. Accordingly, based on our specific diagnosis, we re-examined the possible relationships of the *M. kirkjohnsonii* leaf fossils (Figure 6) by comparing them with extant peltate genera.

A recent survey (Wunnenberg et al., 2021) found peltate leaf occurrences in 357 species from 99 genera and 40 families (not exhaustive of several clades rich in peltate species, such as Piperaceae). Most of these species are from herbaceous clades, which are unlikely sources of the fossils because they do not abscise their leaves and have low biomass. A simple overlap of the Wunnenberg et al. (2021) list of peltate species and the woody genera noted as similar to the MMC in table 2 of Nucete et al. (2012) yielded species in only seven genera: Euphorbiaceae (*Macaranga*, *Mallotus*, *Endospermum*), Hernandiaceae (*Hernandia*), Malvaceae

(*Pterospermum*, *Brownlowia*), and Menispermaceae (*Coscinium*). We also checked all other woody species, including lianas, with peltate leaves listed by Wunnenberg et al. (2021), most of which had no similarity to the fossils. Species having some comparability with the fossils occur in additional genera of Euphorbiaceae (*Manihot*, *Homalanthus*) and Menispermaceae (*Cissampelos*), Phyllanthaceae (*Astrocasia*), Urticaceae (*Dendrocnide*, notorious for stinging hairs), and Convolvulaceae (*Decalobanthus*). Finally, we considered additional peltate species of *Macaranga* and *Mallotus* listed by Sierra et al. (2010).

From our comparison of the fossils with peltate-leaved angiosperms, it is clear that *Macaranga kirkjohnsonii* leaves (Figure 6) differ from the peltate foliage of non-euphorbiaceous families and genera of Euphorbiaceae other than *Macaranga*. Outside of Euphorbiaceae, *Hernandia nymphaeifolia* and *H. sonora* leaves have very few secondaries, the basal pair is markedly acute, and the first and second secondaries are widely spaced. In Malvaceae, the leaves of all taxa examined that resemble the fossils are either actinodromous or have acute basal secondaries widely spaced from the second pair. Furthermore, the malvaceous agrophic veins are often compound, with dense minor secondaries that take up a large portion of the blade base; tertiary veins are thin, numerous, and regular, and many species are toothed. Some species are variable far outside the range of the fossils, such as *Pterospermum acerifolium*, which is often strongly lobed and toothed. In Urticaceae, *Dendrocnide peltatus* is semicraspedodromous and markedly toothed, with a noticeably higher density of secondary and tertiary veins than the fossils; basal secondaries are acute and well spaced from the second pair. Menispermaceae species examined have very few secondary veins and can be actinodromous with compound agrophic veins (i.e., *Coscinium blumeanum*); areolation fields are small and squarish, and a mucro is present. Subpeltate fossil leaves of Menispermaceae previously reported from Laguna del Hunco and associated with cissampelid endocarps (Jud et al., 2018) are also quite different from the present fossils. *Astrocasia peltata* (Phyllanthaceae) and *Decalobanthus peltatus* (Convolvulaceae) are inconsistent with the fossils in basal venation and leaf shape.

Within Euphorbiaceae, we found that several *Macaranga* species have leaves (Figure 1D) very similar to the fossils (Figure 6) and less convincing similarities in *Mallotus* and *Endospermum* (Crotonoideae). However, all three genera were more similar to the fossils than the non-euphorbiaceous taxa reviewed above. In *Mallotus*, the peltate-leaved living species do not closely resemble the fossils, despite several shared features; the peltate species mostly have toothed leaves with craspedodromous secondary venation, or the petiole insertion is much closer to the margin than in the fossils; in addition, most have acute basal secondary veins. *Mallotus roxburghianus* is perhaps the most similar to the fossils, although its leaf margin is toothed. *Endospermum moluccanum* differs from the fossils in having actinodromous primaries, compound agrophic veins, and sometimes toothed leaves; *E. peltatum* is less similar to the fossils.

Several *Macaranga* species have leaves with nearly all the architectural features listed in our diagnosis of *M. kirkjohnsonii* and also lack nectaries (e.g., *M. bicolor*, Figure 1D; *M. brachytricha*), while several others only differ substantially in having toothed or crenate margins (e.g., *M. cuspidata*, *M. tanarius*, *M. thompsonii*). Based on these comparisons and the here-confirmed presence of acalyphoid Euphorbiaceae infructescences at the same fossil site (Figures 2–5), we are confident that the leaf fossils represent Euphorbiaceae as initially considered (Wilf et al., 2003, 2005a). Moreover, *Macaranga* is the only genus with living species, such as *M. bicolor* (Figure 1D), whose leaves show no diagnosable differences from the fossils. This result adds circumstantial evidence for the associated *Tineafructus* fruits having a closer relationship with *Macaranga* than with *Mallotus*.

We use the generic name *Macaranga* for the leaf fossils with caution, but we do so for practical reasons to maximize ease of use. Most importantly, no characters preserved in the fossils are sufficient to diagnose a new genus distinct from *Macaranga*. Thus, the alternatives are either to continue using informal names, to propose a new genus without a reliable diagnosis and cause name proliferation, or to attempt to find a solution from the problematic legacy of nomenclature for euphorbiaceous leaf fossils. To our knowledge, there is no appropriate prior name in the paleobotanical literature for these Patagonian fossil leaves. For example, the diagnosis of *Malloranga* (Lee et al., 2010; Conran et al., 2016) includes several characters that conflict with the present fossils (i.e., subpeltate insertion, consistently brochidodromous secondary venation, percurrent fourth-order venation, nectaries). *Macarangaephyllum*, from the early Oligocene of eastern Europe, has been synonymized with *Sloanea* (Elaeocarpaceae; Kvaček et al., 2001). There are a variety of names for generalized euphorbiaceous foliage from older literature (e.g., *Euphorbiophyllum*) based on type specimens whose affinities would require reassessment with modern methods before using them here. Several names used for leaf fossils, such as *Malloranga* and *Macarangaephyllum*, are phonetically similar to *Macaranga*; thus, any new name would need to be more distinct to stand out and harder to associate with its natural group. For all these reasons, we decided to use the name of the extant genus (*Macaranga*) most similar to the fossils, based on our leaf architectural analysis filtered on peltate taxa. If new information later emerges supporting an extinct genus, there would be no orphaned synonym from the present article in the literature.

One specimen of *Macaranga kirkjohnsonii* (MPEF-Pb 7998; Figure 6B) has at least 12 roughly circular, coalified lesions, several of which have multiple holes of variable size and location. These lesions were previously illustrated as the exemplar for DT83 in Labandeira et al. (2007, pp. 13, 23), who described them as "circular galls, 4.5 to 8.0 mm in diameter, with a finely particulate, raised fusainized core

encompassing 1 to 6 centrally positioned exit holes (or possibly larval chambers) less than 0.5 mm in diameter; positioned on blade and typically avoiding veins." Further examination shows that the lesions are flattened and not woody, leaving little relief in the matrix, and the borders are irregular and diffuse; these factors make an epiphyllous fungal origin much more likely than galling. Herbarium inventories and field studies beyond the scope of this paper are needed to resolve living analogs, and relevant reports are scarce in the literature. Micropeltidaceae (e.g., Zeng et al., 2019), a group of flyspeck fungi, is one possibility based on lesion position, large and variable size, and size variation in the central openings (possibly ostioles; L. Le Renard, Eversio Labs, personal communication, 2023). We note an herbarium specimen of *Macaranga bicolor* with near-circular lichen growths that superficially resemble the fossil lesions (Figure 1D).

Paleoecology

The *Tineafructus* plant had fruits with small, thickened, presumably fleshy, lenticular seeds (e.g., Figure 4), similar to those of living MMC species such as *Macaranga gigantea* (Figure 1C) that small birds and other animals consume heavily (Davies, 2001). The new species joins several other taxa from Laguna del Hunco with reproductive structures strongly associated with animal dispersal, including *Physalis* berries, *Castanopsis* nuts, and *Dacrycarpus* podocarpia (Wilf, 2012; Wilf et al., 2017b, 2019). Based on modern analogs (Slik et al., 2003a; Ashton, 2014), the *Tineafructus* plant probably inhabited volcanically disturbed areas, unstable steep slopes, forest margins, and understories around the dynamic Eocene caldera lake. Similarly, Gandolfo et al. (2011) postulated disturbance specialization for *Eucalyptus* at Laguna del Hunco related to volcanic activity. Likely associates in understory habitats included herbaceous *Physalis* species, diverse ferns, cycads, *Ripogonum* shrubs or vines, menisperm climbers, and members of Laurales, Chloranthaceae, Asteraceae, and Rubiaceae (as recently summarized by Barreda et al., 2020; Deanna et al., 2020).

Biogeography

The new *Tineafructus casamiquelae* infructescence fossils and associated *Macaranga kirkjohnsonii* leaves comprise the first reliable macrofossil occurrences from Gondwana of the Euphorbiaceae. The fossils demonstrate that the *Macaranga-Mallotus* clade (MMC) was present in West Gondwana during the final phase of the supercontinent (e.g., Scotese, 2021) and diverged by 52 Ma from related Euphorbiaceae, such as the ancestors of *Blumeodendron* and *Hancea* (van Welzen et al., 2014). The fossils are consistent with the molecular timetree hypothesis of early Paleogene divergence of the MMC (van Welzen et al., 2014). However, the new fossils and prior evidence from the southern hemisphere middle latitudes (Lee et al., 2010; Conran et al., 2016) make the consensus view of MMC origins in tropical Asia doubtful, despite the group's high diversity in that region today.

The early Eocene Laguna del Hunco fossil site is an outstanding snapshot of vegetation from the ultimate stage of Gondwana. At that time, South America and Australia remained adjacent to Antarctica with no deep-water separation, and intense global warmth facilitated biotic exchange through the southern and northern polar regions (Wilf et al., 2013). All three southern landmasses held rainforests with a broadly similar suite of plant families and genera (Hill, 1994; Hill and Brodribb, 1999), as listed by Kooyman et al. (2014: table 4), who later termed the taxa with extant survivors "paleo-Antarctic rainforest lineages" (PARLs; Kooyman et al., 2019). The subsequent separation of the three landmasses, aligned with cooling global temperatures, led to drastic vegetation changes through the Cenozoic that caused the old Gondwanan water-demanding genera to largely disappear from South America (Dunn et al., 2015; Barreda et al., 2021). However, many PARLs survived in Australia (Sahul), which maintained wet conditions over large areas throughout the Paleogene as it moved north from Antarctica (Hill, 1994; Sniderman et al., 2004; Carpenter et al., 2011). The onset of the Sahul-Sunda collision from the late Oligocene led to the uplift of New Guinea and much of maritime Southeast Asia, triggering the well-known Sahul-Sunda biotic exchange (Sniderman and Jordan, 2011; Morley, 2018; Kooyman et al., 2019; Joyce et al., 2021). Combinations of interchange, survival in Sahul, and overwater dispersals to islands such as New Caledonia and New Zealand allowed the surviving PARLs to occupy suitable, usually everwet habitats over large areas of Australasia and southeast Asia (Kooyman et al., 2014, 2019).

Laguna del Hunco preserves an exceptional richness of living West Pacific rainforest taxa, and the occurrence of the MMC in the same strata aligns well with prior discoveries and the southern-route-to-Asia scenario just discussed. Examples from Laguna del Hunco include the fern *Todea* (Osmundaceae); the cypress *Papuacedrus*; the araucarian conifers *Agathis* and *Araucaria* Section *Eutacta*; podocarpaceous conifers such as *Dacrycarpus*, *Retrophyllum*, *Acmopyle*, and an extinct relative of *Phyllocladus*; and diverse angiosperms such as *Castanopsis* (Fagaceae), *Eucalyptus* (Myrtaceae), *Gymnostoma* (Casuarinaceae), *Ceratopetalum* and other Cunoniaceae, *Akania* (Akaniaceae), *Ripogonum* (Ripogonacae), engelhardioid Juglandaceae, and extinct relatives of *Bubbia* (Winteraceae), *Wilkiea* (Monimiaceae), and *Daphnandra* (Atherospermataceae) (Romero and Hickey, 1976; Zamaloa et al., 2006; Wilf et al., 2009, 2014, 2017a, 2019; Gandolfo et al., 2011; Wilf, 2012, 2020; Carvalho et al., 2013; Knight and Wilf, 2013; Carpenter et al., 2014; Hermsen and Gandolfo, 2016; Gandolfo and Hermsen, 2017; Andruchow-Colombo et al., 2019; Rossetto-Harris et al., 2020; Brea et al., 2021; Matel et al., 2022). The ranges of a majority of these lineages include the montane rainforests of New

Guinea, where the MMC is highly diverse (Airy Shaw, 1980; Ashton, 2014). Interestingly, a few of the taxa have no fossil record in Australia, even some that inhabit Australia today (*Todea*, *Akania*, *Wilkiea*, *Daphnandra*, and here, the MMC). However, even the listed taxa that lack macrofossil and extant records in Australia occur today in New Guinea, which is also part of Sahul (i.e., *Castanopsis*, engelhardioid Juglandaceae). Although there are Cenozoic records of dispersed *Nyssapollenites endobalteus* pollen from New Zealand (where it also occurs in situ in a male acalyphoid inflorescence), Australia, and Patagonia (Lee et al., 2010; Conran et al., 2016; Rozefelds et al., 2017a), the Patagonian records are post-Gondwanan (Oligocene-Miocene; Palazzesi and Barreda, 2007). Consistently, *N. endobalteus* does not occur at Laguna del Hunco, but neither does other euphorbiaceous pollen (Barreda et al., 2020). This absence probably reflects the low ancient biomass of the family at the site, represented here by only 11 leaves and two infructescences out of ca. 8000 collected plant specimens (<0.2%).

The new reproductive and foliage fossils, at 52 Ma in West Gondwana, are the oldest yet found of the MMC and only the second worldwide occurrence of the clade's reproductive material, significantly increasing the likelihood that the MMC had Gondwanan origins. The immense distances and lack of direct land connection between West Gondwana and Sunda during the early Eocene (and long before) make tropical Asia an improbable point of origin for the MMC. There are no validated fossils of the MMC from tropical Asia, and the only other reproductive fossils of the MMC worldwide are also from the southern hemisphere in (post-Gondwanan) New Zealand (Lee et al., 2010). The early Miocene New Zealand fossils plausibly represent dispersal from similar, temperate Sahul latitudes, with no need to invoke much longer movements from Sunda during the earliest phases of Sahul-Sunda contact. There are many more well-sampled Cenozoic sites with outstanding fruit and seed preservation in the northern than in the southern hemisphere; several northern hemisphere sites have produced reproductive fossils of other Euphorbiaceae lineages but not the MMC (see Introduction). Thus, the lack of MMC reproductive fossils in the northern hemisphere or paleotropics is striking and suggests (but does not prove) a genuine absence.

Fossil leaves still support the Paleogene presence of the MMC outside Gondwana, including the middle Eocene of Japan and the late Oligocene of Ethiopia, as reviewed by Nucete et al. (2012). Those occurrences present a typical conundrum in paleobotany regarding which types of evidence to accept for the presence of a clade (Sauquet et al., 2012). Reproductive fossils are usually considered far more reliable than leaves because of their lower homoplasy, and the Euphorbiaceae are one of many plant families with distinctive fruits and a long history of misidentified leaves (e.g., Hamersma et al., 2022). Nevertheless, if we combine the leaf fossils with the reproductive records of the MMC, a very different scenario emerges wherein the MMC already had an essentially global distribution by the Paleogene, including Gondwanan South America, post-Gondwanan Africa, and temperate East Asia. This pattern would point to an earlier, probably Late Cretaceous divergence of the MMC in an unknown region, allowing the group to reach widely separated areas over time through Holarctic, paleo-Antarctic, and overwater opportunities, such as the ephemeral Cretaceous island-arc connections between the Americas (Iturralde-Vinent, 2006). The recent discovery of well-preserved reproductive fossils of the Australasian genus *Ceratopetalum* (Cunoniaceae) from the Late Cretaceous of Washington, United States (Tang et al., 2022) indicates that an early, widespread history is entirely possible even for classical Gondwanan taxa.

We consider both out-of-Gondwana and early global distribution valid hypotheses for the MMC, but we have greater confidence in the out-of-Gondwana scenario. The exceptionally preserved fossil infructescences and leaves reported here are the oldest records of the group and represent plants that grew in West Gondwana. The fossils co-occur with many well-preserved paleo-Antarctic taxa that document Patagonia-to-Asia floristic connections and associate with the MMC in living forests. The only other fossil reproductive material of the MMC is also from the southern latitudes, from the early Miocene of New Zealand. Finally, no reproductive fossils of the MMC are yet known from the tropics or the better-sampled northern hemisphere, even at sites that preserve the reproductive fossils of other euphorbiaceous lineages.

CONCLUSIONS

From the prolific 52 Ma Laguna del Hunco caldera-lake site in early Eocene Patagonia, we report rare, well-preserved infructescences and associated leaves of the acalyphoid Euphorbiaceae. The new material comprises the first Gondwanan fossils of the family and the oldest known of the *Macaranga-Mallotus* clade (MMC), a diverse and widespread Old World understory group with its highest extant diversity in Malesia. The infructescences are ca. 30 Myr older than the only other reproductive fossils known of the MMC. The infructescences and leaves are both more similar to *Macaranga* than *Mallotus*. They comprise the only Euphorbiaceae recognized in the diverse floral assemblage; thus, both organs are likely to represent a single source plant. The fossil fruits have tiny, fleshy seeds whose living counterparts are heavily consumed by small birds and mammals, joining several other reproductive organs from the same fossil beds with likely animal dispersal. As in the living analog species, the large, peltate leaves strongly suggest small-statured, disturbance-specialized plants adapted to the crater-lake environment's frequent volcanic activity, earthquakes, steep slopes, and landslides.

The new fossils demonstrate that by the early Eocene (52.2 Ma), the MMC had diverged at least as a stem

lineage and was present in West Gondwana. This finding is consistent with some of the older (cf. Paleogene) molecular divergence-age estimates for the MMC. However, our discovery makes the consensus of a tropical Asian (Sundan) origin of the MMC unlikely, requiring an early history in Sunda for which there is no fossil evidence, as well as enormous overwater and latitude-shifting dispersal from Sunda to Gondwana by the early Paleogene. Another possibility is that the MMC had a much larger, global distribution deeper in time, probably by the Late Cretaceous, allowing the group to reach widespread areas as dispersal opportunities arose. The relevant fossils suggesting broader past distributions are leaves, younger than those presented here, from East Asia and Northeast Africa.

The new fossils better support an out-of-Gondwana scenario for the MMC, with entry into Sunda during the Neogene Sahul-Sunda collision and subsequent dispersal to the rest of the extensive modern range, including Africa and mainland East Asia. In addition to their age, factors supporting this scenario include the only other reproductive material of the group occurring in the early Miocene of New Zealand, improbably early to have arrived from Sunda; the lack so far of MMC reproductive fossils from the tropics or the far-better-sampled northern hemisphere; and the site-level co-occurrence of the new fossils with a notably high diversity of other living Southeast Asian plant genera that have established paleo-Antarctic history. Many of these taxa, along with the MMC, occur widely in Australia and New Guinea today, and several have fossil records in Australia, providing abundant evidence for the long history in Sahul of many Gondwanan survivor lineages (e.g., Kooyman et al., 2014; Wilf et al., 2019). The basal phylogenetic placement of several living Sunda species of the MMC (van Welzen et al., 2014) might align with our results via past movements of those lineages westward from Sahul, followed by extinction in the source area. The overwater distances involved in that scenario are negligible compared with others achieved by the clade, usually thought to have traveled the same route in the opposite direction (Sunda to Sahul).

The past decades of fossil discovery in Patagonia have exposed the vast former ranges of many extant paleo-Antarctic rainforest taxa (Wilf et al., 2013, 2019; Kooyman et al., 2014, 2022). Their collective history of movement and survival over thousands of kilometers and tens of millions of years of climatic and tectonic change ranks among the most dramatic biogeographic patterns in the history of life, with profound impacts on understanding modern species distributions, biodiversity, and conservation.

AUTHOR CONTRIBUTIONS

P.W. and M.A.G. acquired funding and directed the fieldwork at Laguna del Hunco. A.I. discovered the paratype specimen in collections at MJHG and prepared, photographed (Figure 5), and analyzed it in the lab. A.I. and M.A.G. arranged loans. P.W. did all other lab work and fossil photography and wrote the manuscript, with regular discussions and feedback on drafts from A.I. and M.A.G.

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DATA AVAILABILITY STATEMENT

All new fossil material presented in this article is curated at Museo Paleontológico Egidio Feruglio, Trelew, Argentina, and Museo Jorge H. Gerhold, Ingeniero Jacobacci, Río Negro, Argentina, as described (see Systematics). An image archive containing 1200-dpi versions of the composed fossil plates (Figures 2–6), individual images of the new fossils at original resolution, and raw CT-scan stacks is deposited in Figshare along with Raman data: https://doi.org/10.6084/m9.figshare.21357921.

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